

The effect of partial brood loss on male desertion in a cichlid fish: an experimental test

Michael D. Jennions^a and Daniel A. Polakow^b

^aSmithsonian Tropical Research Institute, Unit 0948, APO AA 34002 0948, USA, and ^bDepartment of Statistical Sciences, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

There is little experimental evidence testing whether current brood size and past brood mortality influence mate desertion. In the cichlid *Aequidens coeruleopunctatus* both parents initially defend offspring. In a field study, all experimental broods, irrespective of initial brood size (222.9 ± 60.4 , mean \pm SD), were manipulated to a size of 100 fry. Neither the duration nor investment of females in parental care differed between control and brood reduced pairs, even though care seemed costly. On average, females lost $5.1 \pm 4.8\%$ of initial weight while guarding a brood until independence. In contrast, males with experimentally reduced broods guarded fry for significantly fewer days before deserting their mate than did males from control pairs with natural-sized broods (20.5 ± 7.5 vs. 14.2 ± 6.2 days). In at least 20% of cases ($n = 9/45$), the deserting male immediately mated with another female. Males with experimentally reduced broods also spent less time guarding fry before deserting and attacked fewer brood predators than did males with control broods. For broods manipulated to have 100 fry, there was a significant negative relationship between the days until male desertion and the proportion of the initial brood removed. This indicates that male assessment of the future success of the current brood (hence its reproductive value) is based on past mortality and/or that there is variation among males in the expected size of future broods. Both current brood size and brood size relative to initial brood size are therefore predictors of male, but not female, parental behavior and mate desertion. Female care may be unaffected by brood reduction due to limited breeding opportunities and partial compensation for reduced male care. *Key words*: brood reduction, brood size, cichlids, mate desertion, parental care, life-history trade-off, mating opportunities. [*Behav Ecol* 12:84–92 (2001)]

Optimal life-history strategies are based on the trade-off between investment in current and future reproduction (Roff, 1992). Investment in the current brood in the form of parental care is beneficial because it increases offspring reproductive value (Clutton-Brock, 1991). Even so, in species with biparental care where a single parent is also capable of rearing a brood to independence, albeit with reduced success, mate desertion often occurs (e.g., insects: Eggert and Müller, 1997; Robertson and Roitberg, 1998; birds: Beissinger and Snyder, 1987; Fujioka, 1989; Hemborg, 1999; Mock and Parker, 1986; Valera et al., 1997; mammals: Kleiman, 1977). The timing of desertion reflects the trade-off between the costs and benefits of continuing to care for the current brood versus those derived from deserting (Grafen and Sibly, 1978; Lazarus, 1990; Maynard Smith, 1977). For example, desertion is more likely when the success of single-parent care is higher (Beissinger, 1986); offspring are older (Sargent and Gross, 1986; Wisenden, 1994); a parent's future fecundity is higher if it deserts rather than continues to care (Balshine-Earn, 1995); current brood size is lower than average (Lazarus, 1990); re-mating opportunities increase (Balshine-Earn and Earn, 1997); and future conditions are, on average, more favorable for breeding (Carlisle, 1982; Pöysä et al., 1997). The influence of these factors may, however, vary among breeding pairs due to differences in intrinsic condition, parental ability, fecundity, and attractiveness (e.g., Eriks-

tad et al., 1997; Galvani and Coleman, 1998; Hōrak et al., 1999; Robertson and Roitberg, 1998).

Despite a long history of theoretical work on mate desertion following Maynard Smith's initial use of game theory (Maynard Smith, 1977; see reviews by Kokko, 1999; Webb et al., 1999), few field experiments have manipulated variables that increase the likelihood of mate desertion (Eadie and Lyon, 1998; Székely et al., 1996). Most examples come from work on birds and involve the manipulation of brood size (e.g., Armstrong and Robertson, 1988; Beissinger, 1990; Winkler, 1991), offspring quality (Erikstad et al., 1997), perceived paternity (see review by Westneat and Sherman, 1993) or attractiveness (Johnsen et al., 1997). In insects, there have also been attempts to manipulate the opportunity for remating (Robertson and Roitberg, 1998) and food availability (Scott and Gladstein, 1993; Trumbo, 1991). In a few fish, reducing brood size sometimes leads to total brood cannibalism, which is equivalent to brood desertion (see reviews by Okuda and Yanagisawa, 1996; Sargent, 1997), but otherwise there is simply a decline in the intensity of parental care (e.g., Ridgway, 1989).

Cichlid fish are an ideal group for the experimental study of mate desertion (2000+ species). There have been a minimum of 21 evolutionary transitions from biparental to female-only care, and a maximum of 10 in the reverse direction (Goodwin et al., 1998); male-only care occurs in only two species (Balshine-Earn and McAndrew, 1995). Moreover, sporadic male desertion has been confirmed in eight species of cichlid fish with biparental care (see review by Balshine-Earn and Earn, 1998). Determining which factors promote desertion in biparental species with occasional desertion and female-only care may help explain the evolution of obligate male desertion, which accounts for at least 68% (21/31 transitions) of the interspecific variation in patterns of sex-based care. Although a few laboratory experiments have looked at the effect

Address correspondence to M. D. Jennions, who is now at Division of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia. E-mail: jennionm@naos.si.edu.

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of remating opportunities (Keenleyside, 1983, 1985; Rogers, 1987) and male size (Balshine-Earn and Earn, 1998) on mate desertion, there is no experimental evidence that reduced brood size promotes mate desertion. The best data come from field observations that convict cichlid broods guarded by females are smaller than those guarded by both parents (Wisenden, 1994). Unfortunately, the direction of causation is unknown. Brood size may have been smaller because males deserted and broods with female-only care suffered greater predation, or because males more often deserted smaller broods. More important, these observational data cannot determine whether current brood size and variation in past brood mortality both affect male desertion.

In the present study we experimentally reduced brood size in the Panamanian acara, *Aequidens coeruleopunctatus*. Both biparental and female-only care have been reported, and male desertion seems to be fairly common (Barlow, 1974; Carlisle, 1981; Townshend, 1984). We asked three main questions:

1. Do males desert smaller broods sooner? Marginal-value theory predicts that whenever parents have the potential to breed in the future, they will desert when the instantaneous rate of return from staying is equal to that from deserting (Grafen and Sibly, 1978). The benefit curve is lower, and hence the rate of return from caring smaller, for reduced broods. Limited observational and experimental studies of birds indicate that smaller broods are more often deserted (Beissinger, 1990).

2. Does the past success of the brood influence the timing of mate desertion? Carlisle (1982) argued that past mortality sometimes predicts future mortality for the current brood. If true, then even when current brood size is identical, the reproductive value of a brood is smaller if it has suffered higher previous mortality. This has only been confirmed in a single empirical study (Pöysä et al., 1997). Alternatively, adults may vary in their future reproductive potential (repeatable fecundity). The value of a brood of a given size is lower for a parent with high fecundity relative to that of a parent with low fecundity because of the former's greater future reproductive prospects. Because more fecund parents suffer proportionately greater loss when current brood size is equalized across pairs, the degree of past brood reduction should predict the value of the current brood (Galvani and Coleman, 1998).

3. Does a reduction in brood size affect male and female parental investment equally? Reduced benefits from guarding a smaller brood should decrease parental investment (Clutton-Brock, 1991; Sargent and Gross, 1986, 1993). Indeed, experimentally reducing brood size in fish providing uniparental care usually results in lower parental investment (e.g., Carlisle, 1985; Coleman et al., 1985; Lavery and Keenleyside, 1990; Lindström and Sargent, 1997; Mrowka, 1987; Sargent, 1981, 1988; Ridgway, 1989). Before mate desertion, brood reduction should have a similar effect on the value of the current brood to both parents, but the alternatives available to each sex may differ. For example, if initiating another breeding attempt is easier for males than for females, then males may engage in extrapair courtship while seeking a new mate. Females could then be forced to compensate for the associated reduction in male care to ensure brood survival (Westneat and Sargent, 1996). Depending on the exact costs and benefits of single and biparental care, females may even increase investment in smaller broods in anticipation of future desertion by their mate. Even after desertion, the sex with the lower potential reproductive rate may continue to invest heavily in the current brood (Lazarus, 1990; Székely et al., 1999; Yamamura and Tsuji, 1993). Thus, although both parents probably place less value on a smaller brood, female investment in smaller broods may increase because of their lim-

ited rebreeding opportunities and compensatory parental behavior.

METHODS

Study species and site

We conducted our experiment on *Aequidens coeruleopunctatus* at Rio Parti, Republic of Panama (9° S, 78°30' W) from January to April 1999. Breeding is mainly confined to the dry season (January–April). In the study area the river was 3–10 m wide and most pools had a maximum depth less than 1 m. Rio Parti drains a mainly deforested area used for cattle ranching for over 15 years (Townshend, 1984). Females lay eggs on a dead leaf (Barlow, 1974), and after eggs hatch both parents orally transfer the yolk-sacked embryos (“wrigglers”) to a previously excavated pit. In 3–5 days the yolk is absorbed, and the 5–6 mm long young school as free-swimming fry. The parents then guard the fry for another 3–5 weeks. Larger cichlid fry are less vulnerable to predation and the benefits of parental care decrease with brood age (Jennions MD, unpublished data; Wisenden and Keenleyside, 1992). Both parents guard fry and attack approaching fish. Although both sexes are equally involved in disputes with neighboring pairs, females stay closer to the fry and more often chase intruding fish (Jennions et al., in preparation). At least nine genera of fish are potential brood predators (Kramer and Bryant, 1995), and juvenile cichlids are the most threatening.

Experimental approach

We captured brood-guarding females at night using a submersible torch and hand-held dip net. We recorded their standard length (± 0.1 mm) and mass (± 0.1 g) and marked them with a subcutaneous injection of dilute acrylic paint. We confirmed the sex of marked parents based on body size, coloration, and subsequent behavior. Once the parents had moved the embryos to an excavated pit, they became available for the experiment. A pilot study showed that brood predators are strongly attracted to sediment disturbance during the day. We therefore carried out brood manipulations at night. The yolk-sacked embryos were siphoned into tubing and transferred to a plastic tray. We then counted out 100 fry and returned them to the pit by pouring them back down a 2 cm wide plastic tube. Initial brood size was 222.9 ± 60.4 wrigglers ($n = 36$). In 35 of 36 cases initial brood size was >100 and fry were removed. In one case it was less than 100 and fry were added. If we refer to the manipulated pairs as “reduced,” we have only used the 35 pairs where brood size was reduced in the analysis. In control broods the fry were sucked into the tubing and then released straight back into the pit. We assigned approximately every fourth brood to the manipulation treatment, with the caveat that, with one exception, every pool in the stream contained broods subject to both treatments. There were no significant differences between control and reduction brood treatment females in standard length ($t = 0.396$, $p = .69$; mean \pm SD, reduction: 63.1 ± 5.2 mm, $n = 35$; control: 63.6 ± 6.8 mm, $n = 111$), body condition (ANCOVA: $F_{1,131} = 0.20$, $p = .654$), or breeding date ($t = 0.759$, $p = .45$; reduction: 61 ± 29 ; control: 57 ± 26 ; day 1 = January 1). The power to detect a difference of medium strength ($d = 0.5$) was 72% (Cohen, 1988).

Behavioral observations

We walked along the bank until we located a brood and then waited 5 min to ensure that the parents were undisturbed by our presence. Using binoculars we then recorded parental be-

havior for 15 min. The summary variables we report are (1) the time spent within 4 body lengths (± 25 cm) of the brood, excluding time away if the parent left to chase another fish and then returned without feeding; (2) the number of bites at the substrate (feeding); (3) the number of attacks directed at potential brood predators. We did not distinguish between short, open-mouthed lunges and prolonged chases. Attacks were clearly recognizable because the intruding fish reoriented and moved away from the attacker. We made focal observations on each pair approximately every 6 days.

Timing of male desertion

We alternated 4 days at the study site with 1- or 2-day intervals of absence. Each day we noted which marked females were guarding fry and whether their mate was present. If the male was initially absent, we continued to watch until he arrived or 15 minutes had elapsed. We defined the date of desertion as the last day on which the male was absent for 15 min and subsequently was not seen guarding the brood. We defined the timing of male desertion as the number of days the male guarded free-swimming fry before this date. Female desertion did not occur. Using this definition of desertion we could not obtain data for all pairs. First, we were sometimes unable to conduct censuses due to poor water visibility and could not accurately determine the date of desertion. Second, if the pair disappeared simultaneously, we could not distinguish desertion by both parents from brood failure or fry independence.

Statistical analysis

For variables measured once per pair, we compared brood-reduced and control pairs using two-sample *t* tests or *G* tests with Williams' correction to compare frequencies. The timing of male desertion was first compared using a two-sample *t* test. This analysis does not, however, take into account pairs where both parents disappeared at the same time (our strictest definition of desertion required that the male leave before the female). We therefore also compared the number of days males guarded using survival analysis (Systat, 1998). The number was treated as an "exact failure" if the male deserted before the female. It was "right censored" if the pair disappeared simultaneously or if we were unable to continue monitoring the pair. We excluded from the analysis censored cases where parents guarded for fewer than 5 days. These were almost certainly instances of brood failure because the earliest confirmed case of male desertion was on day 5. We also excluded two cases (one per treatment) where the male was never seen guarding fry because he could have deserted before the manipulation. (Inclusion of these cases did not change the results.)

The behavioral data involved repeated measurements from 129 pairs ($n = 471$ samples). Both fry size and the number of samples varied among pairs. We therefore analyzed the data using linear mixed-effects models for unbalanced group data (Laird and Ware, 1982), formulated and executed in S-PLUS version 4.5 (Mathsoft, 1998) using the lme algorithm (Pinheiro and Bates, 1999). This allowed us to treat pair identity as a random effect nested within experimental treatment type. Treatment type is a fixed effect, while fry size is a continuous variable that can be considered a surrogate measure of time. Fry size should influence parental behavior because larger fry are less vulnerable to predators. We used a restricted maximum-likelihood approach (REML; Patterson and Thompson, 1971) because the response variables were sampled from a bounded window of continuous time (i.e., fry size). REML is preferable to ordinary maximum-likelihood procedures when

estimation of variance components is required from an unbalanced design (see review by McCullagh and Nelder, 1991).

We built separate models for four response variables: the total number of times the male attacked brood predators; the time the male spent guarding fry; the total number of times the female attacked brood predators; and the number of times the female fed. For male variables we only used samples before male desertion. For females we carried out two sets of analyses. First, we only used samples before male desertion. Second, we included samples taken after male desertion because we were interested in the net effect of brood reduction on total female parental investment. To determine whether any difference in male attack rate between treatments was primarily due to males spending less time near the brood, we built models with and without male time with fry as a covariate.

The model with the smallest Akaike Information Criterion, $AIC = -2(\log\text{-likelihood}) + 2(\text{number of fitted parameters})$ (Sakamoto et al., 1986), was considered the most parsimonious. This approach often performs better than restricting the final model to those variables with statistically significant effects in the full model (Burnham et al., 1995). Interaction terms were nonsignificant in the full model, and examination of the AIC showed that interactions did not increase the fit of our models. Thus, the final models presented exclude the interaction terms between treatment and fry size or male time with fry. The significance of each predictor variable in the final models was tested using the REML parameter estimates to calculate *t* statistics. Finally, we used likelihood-ratio tests to determine whether a model including the experimental treatment effect provided a significantly better fit than the nested alternative model that excluded it (Kendall and Stuart, 1979). We used maximum-likelihood procedures to obtain log-likelihood values for each model and then tested for a significant difference in deviance ($= -2 \times \text{Difference in log-likelihoods}$), which is approximately χ^2 distributed. If there was no difference in deviance, the AIC indicates the most parsimonious model.

Repeated-measures analyses assume multivariate normality within each repeated measure of any response variable (Lindsey, 1993). Where necessary we therefore transformed response variables to approximate multivariate normality [$\log(x+1)$ and \sqrt{x}]. We also carried out diagnostic investigations to ensure linear model suitability. Proportions were arcsine transformed. For power analysis we made the a priori assumption of a medium strength effect (i.e., $r = .30$, $d = 0.5$) against a null hypothesis of no difference between treatments or relationship between variables. The reported power is the probability of detecting an effect of this magnitude when α (two-tailed) = 0.05 (Cohen, 1988). When outliers were identified and removed, their residuals are given in standard deviations (Systat, 1998). Effect sizes are calculated following Cooper and Hedges (1994) and expressed as Pearson's r . Unless otherwise stated, summary data are presented as mean \pm SD and tests are two tailed.

RESULTS

Experimental brood reduction

During the manipulation we reduced brood size by $53.3 \pm 12.8\%$ (range 21.3–68.8%, $n = 35$). There was no significant difference in the frequency with which reduced and control broods failed before becoming free-swimming (*G* test with Williams correction, $G = 0.026$, $p = .87$; reduced: 20.0%; control: 21.3%, $n = 35$, 108; power $\approx 94\%$). Thus experimental brood reduction did not disrupt parenting and lead to brood failure during the sedentary stage of caring. Brood size at the

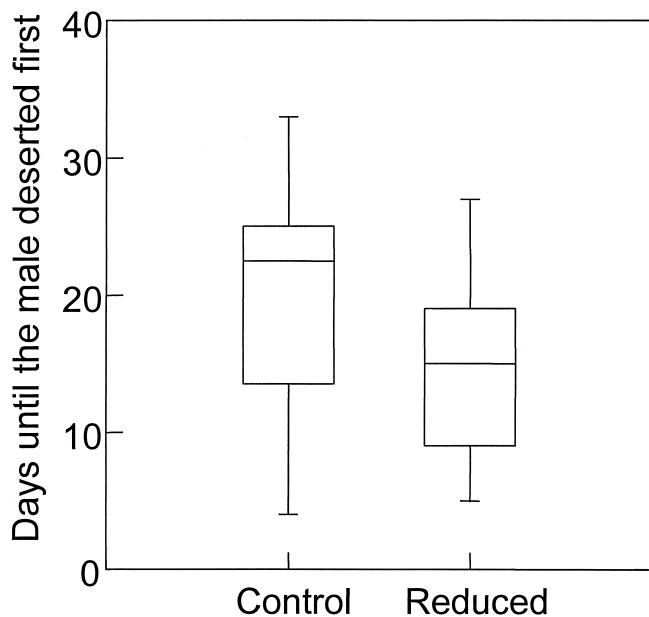


Figure 1
Box-plots of the number of days males guarded in pairs where the male deserted before the female (control $n = 24$; reduced $n = 21$). The line inside the box is the median. The box edges are at the first and third quartiles (Q_1 and Q_3). The whiskers show the range of values that fall between $Q_1 - 1.5 * (\text{median} - Q_1)$ and $Q_3 + 1.5 * (Q_3 - \text{median})$.

egg/wriggler stage was only weakly related to female size (ANCOVA using data from 2 years: size: $F_{1,55} = 2.70$, $p = .053$, one-tailed; year: $F_{1,55} = 0.10$, $p = .76$; interaction: $F_{1,55} = 1.47$, $p = .231$; two outliers removed, residuals 3.9 and 3.3 SD). There was no exponential increase or decrease in fecundity with size (t test of log-log regression coefficient, $t_{57} = 0.89$, $p = .38$; $H_0 = \beta = 1$, power $>90\%$).

Does brood reduction promote earlier brood desertion by males?

When the male deserted before the female, he guarded fry for significantly fewer days in brood-reduced than control pairs ($t = 3.016$, $df = 43$, $p = .004$; Figure 1). The frequency at which the male deserted before the female was also greater for brood-reduced pairs ($G = 19.25$, $df = 1$, $p < .001$; reduced = 21/27, control = 24/81). To include data from pairs where both parents disappeared simultaneously, we performed survival analyses. Males from brood-reduced pairs spent fewer days guarding fry than males from control pairs (stratified Kaplan-Meier estimation of mean survival time: reduced = 16.38 days, control = 27.03 days; Mantel-Haenszel test of treatment effect, $\chi^2 = 25.23$, $df = 1$, $p < .001$; Figure 2). Using only pairs where males deserted before females there was no effect of female size on the number of days males guarded fry (ANCOVA with female size as covariate: female size: $F_{1,42} = 0.096$, $p = .758$; treatment: $F_{1,42} = 8.66$, $p = .005$, power 37%), and there was no interaction between female size and treatment ($F_{1,41} = 0.15$, $p = .70$, power 36%). Survival analysis confirmed that female size is not a significant covariate (stratified Cox Regression: $t = 0.443$, $p = .66$, $n = 104$).

Does the change in brood size affect the timing of male desertion?

We controlled for the effect of current brood size by only examining pairs whose brood size was manipulated to 100 fry.

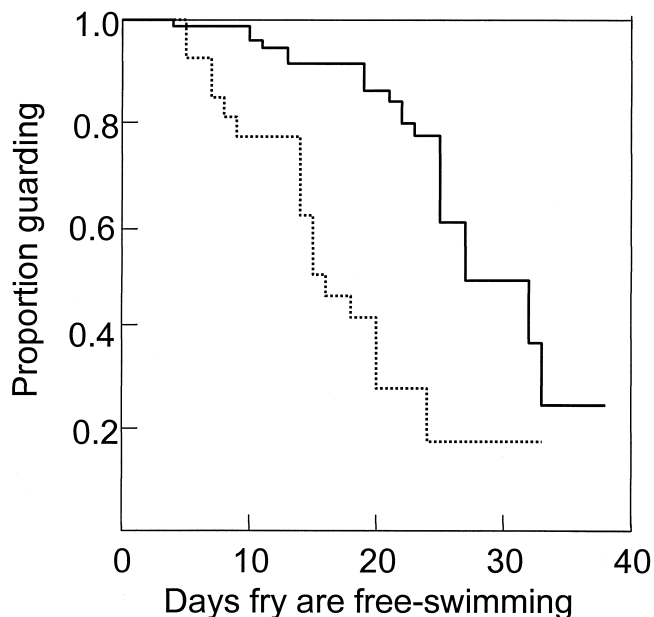


Figure 2
Proportion of males guarding fry according to stratified Kaplan-Meier survival analysis (Systat, 1998). The solid line represents control males ($n = 81$), and the dotted line represents brood-reduced males ($n = 27$).

We then looked at the correlation between the number of days males guarded fry until deserting and the proportion of the brood removed. For 21 pairs, male desertion date was known exactly because the male deserted before the female. In addition, we treated three pairs where the parents disappeared together after 28 or more days of guarding as cases of male desertion. Twenty-eight days is a conservative measure of the time until brood independence (by then mean fry length is >15 mm). Simultaneous disappearance of both parents when fry are this size is almost certainly due to both parents deserting the brood rather than brood failure. There was a significant relationship between the number of days the male guarded fry and the proportion of the brood removed ($r = -.473$, $p = .012$, one-tailed, $n = 23$, outlier removed, residual = 3.0 SD; Figure 3). In one experimental pair brood size was increased because the premanipulation brood size was less than 100. This pair had a strong leverage effect (leverage = 0.87; Systat, 1998), but even when we removed it from the analysis, the relationship remained significant ($r = .367$, $p = .047$, one-tailed, $n = 22$). Finally, we performed a survival analysis in which the number of days males guarded was treated as an exact failure if the male deserted before the female and as right censored if the pair disappeared simultaneously (see Methods). The change in brood size was a marginally significant predictor of the duration of male care (Cox proportional hazards estimation: $t = 1.73$, $p = .045$, one-tailed, $n = 27$; outlier removed).

What happens to deserting males?

Of the 45 males who deserted before their mate, at least nine (20%) formed a pair bond with another female before deserting. It was difficult to detect pair formation by focal males because they were unmarked. In these nine cases, we saw the male repeatedly engage in extrapair courtship and, more important, move between his original mate and the new female while she selected a leaf for egg laying. We infer that mating occurred because shortly after male desertion a new brood

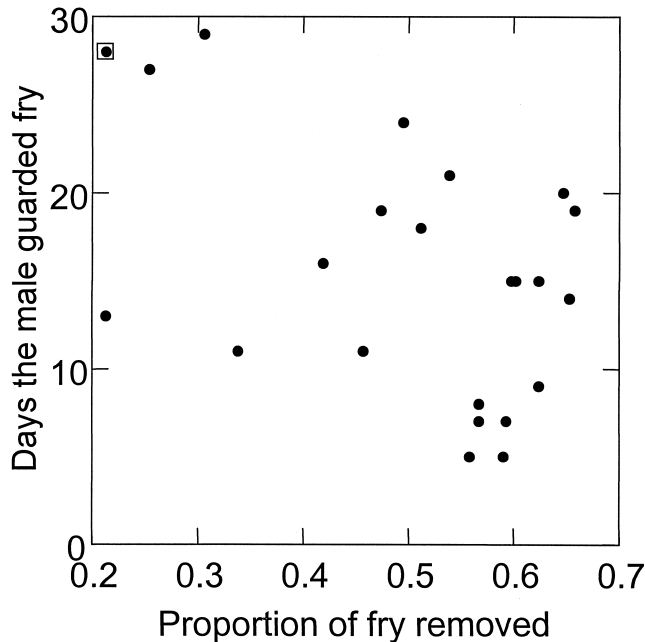


Figure 3
The relationship between the proportion of fry removed and the number of days that males guarded fry before deserting females (or both sexes deserted due to fry independence at 28 or more days). The pair for which proportion removed was set at 21.3% to remove leverage, even though fry were added, is indicated by the square.

appeared near the site where the second female was courted. These nine males deserted after guarding fry for 18.7 ± 6.2 days (range = 11–27 days).

Does the effect of brood reduction on parental care before desertion differ between the sexes?

The time males spent guarding fry decreased with increasing fry size for both control and brood reduced pairs (Table 1). Controlling for fry size, males from brood-reduced pairs spent significantly less time guarding than males from control pairs ($p = .002$, $n = 124$ pairs; Tables 1 and 2). The number of attacks on brood predators by males was also significantly lower for brood-reduced pairs ($p = .014$, $n = 118$ pairs). Once male guarding time was included in the model, however, there was no significant effect of brood reduction on attack rate (Tables 1 and 2). Thus, the decrease in attack rate is mainly due to brood-reduced males spending less time with fry before deserting.

There was no significant difference between treatments in the number of attacks by females on brood predators or in female feeding rate. This was true whether we only looked at samples before male desertion or at all available samples (Tables 1 and 2). Female feeding rate increased with fry size, but attack rate did not (Table 1). Survival analysis showed that the brood reduction treatment did not affect the number of days females spent guarding fry (stratified Kaplan-Meier estimation of mean survival time: reduced = 23.15 days, control = 23.74 days; Mantel-Haenszel test, $\chi^2 = 0.83$, $df = 1$, $p = .36$; Figure 4). There was no significant difference between treatments in the proportion of exact failure and right censored pairs ($G = 0.929$, $p = .34$, reduced = 18/28, control = 60/81). At least 4.8% of females (8 of 168 marked) initiated a second brood.

Table 1
Restricted maximum likelihood (REML) parameter estimates and associated significance for predictor variables in linear-mixed models (see text for details)

Dependent variable/ predictor variables	REML estimate (mean \pm SE)	df	<i>t</i>	<i>p</i>	<i>n</i> (pairs, samples)
Male time					
Fry size	-0.478 ± 0.152	261	3.15	.002	124, 386
Treatment	-4.818 ± 1.443	122	3.34	.001	
Number of male attacks					
Fry size	-0.025 ± 0.014	229	1.76	.079	118, 348
Treatment	-0.308 ± 0.123	116	2.51	.014	
Number of male attacks					
Fry size	-0.007 ± 0.013	227	0.55	.586	118, 347
Treatment	-0.094 ± 0.106	116	0.89	.374	
Male time with fry	0.001 ± 0.0001	227	9.57	<.0001	
Number of female attacks (all samples)					
Fry size	-0.002 ± 0.011	341	0.20	.839	129, 471
Treatment	-0.046 ± 0.090	127	0.52	.607	
Number of female attack (prior to male desertion)					
Fry size	-0.019 ± 0.013	262	1.52	.130	124, 387
Treatment	-0.104 ± 0.099	122	1.06	.293	
Female feeding rate (all samples)					
Fry size	0.048 ± 0.014	341	3.45	.0006	129, 471
Treatment	0.065 ± 0.155	127	0.42	.676	
Female feeding rate (before male desertion)					
Fry size	0.0480 ± 0.016	262	2.96	.0034	124, 387
Treatment	0.086 ± 0.170	122	0.50	.6148	

Table 2
Analysis of deviance (likelihood ratio test) of models with and without the treatment effect

Response variable/ model	df	AIC	Log-likelihood	Deviance	<i>p</i>
Male time with fry					
F + T	5	2747.62	-1368.81	1.97	.0009
F	4	2756.59	-1374.30		
Number of male attacks					
F + T	5	784.97	-387.49	6.27	.012
F	4	789.25	-39.62		
Number of male attacks					
F + T + MT	6	702.87	-345.44	.82	.366
F + MT	5	701.69	-345.85		
Number of female attacks					
F + T	5	818.50	-404.25	1.14	.287
F	4	817.64	-404.82		
Female feeding rate					
F + T	5	1036.73	-513.37	.26	.611
F	4	1034.99	-513.50		

Akaike's information criteria (AIC) is presented for each model. F, fry size, T, treatment, MT, male time with fry.

The cost of female parental care

Females lost weight while defending broods. The interval between weighing sessions was 19.9 ± 4.8 days (range = 15–32 days), and initial mass was 10.5 ± 2.9 g ($n = 23$). We estimated weight loss over 36 days to represent the average time between egg laying and fry independence (8 days as eggs and embryos and 28 as fry). The percentage reduction in mass relative to initial mass was $5.1 \pm 4.8\%$ (range = gain 7.6% to lose 12.3%). Twenty of 23 females lost weight (binomial test, $p < .001$). There was a positive relationship between female size

and percentage weight loss ($r = .496$, $p = .016$, $n = 23$). Larger females lost relatively more weight. Female weight loss is probably costly because it is associated with reduced future fecundity in another cichlid (Balshine-Earn, 1995).

DISCUSSION

We experimentally manipulated broods of *Aequidens coeruleopunctatus* that initially varied in size to a uniform 100 fry. This yielded three main findings. First, males deserted smaller broods sooner. Experimental brood reduction explained 17% of the variation in the number of days males guarded before deserting a female (effect size: $r = .42$). Second, the initial size of the brood influenced the timing of mate desertion. The percentage reduction in brood size was negatively related to the number of days males guarded fry before deserting (effect size: $r = .32-.47$). Third, the reduction in brood size affected male and female parental investment differently. Unlike males, brood reduction did not influence the number of days females guarded fry (effect size: $r = .09$). Brood reduction did not significantly alter female attack or feeding rates (effect size: $r = .037-.096$), while males spent significantly less time guarding fry and attacking brood predators before deserting (effect size: $r = .23-.29$).

Current brood size, past brood mortality, and variation in a male's future prospects

Our finding that smaller brood size is associated with earlier male desertion is in agreement with experimental studies of mate desertion in birds (Beissinger, 1990), as well as studies of brood desertion involving either a single (e.g., Eadie and Lyon, 1998) or both parents (e.g., Winkler, 1991). The simplest and most widely cited explanation for this result is that there is a lower rate of return on investment in a smaller brood (brood size hypothesis; Grafen and Sibly, 1978). There is, however, an additional possibility: a reduced brood may be worth less because past mortality predicts the future mortality of a brood (brood success hypothesis; Carlisle, 1982). The degree of partial brood loss could be a cue as to the proportion of the remaining brood that will survive to independence.

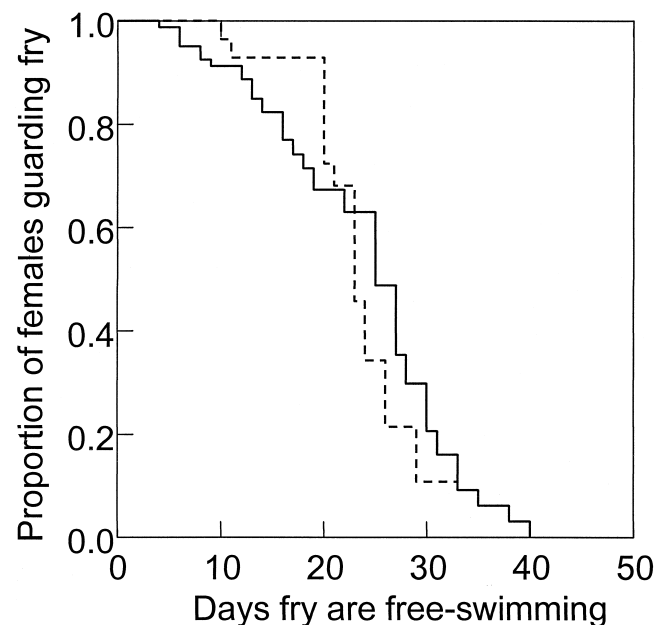


Figure 4
 Proportion of females guarding fry according to stratified Kaplan-Meier survival analysis (Systat, 1998). The solid line represents control females ($n = 81$), and the dotted line represents reduced-brood females ($n = 28$).

Only one study has directly distinguished between these hypotheses (Pöysä et al., 1997). The main problem is that, given similar initial brood sizes, brood size at the time of desertion and past brood mortality are highly correlated, making it difficult to distinguish between the hypotheses (e.g., Bessinger, 1990; Winkler, 1991). In our study, however, initial brood size varied considerably.

We found that the percentage reduction in brood size was negatively related to the number of days male *A. coeruleopunctatus* guarded fry before deserting. Our result is therefore consistent with the brood success hypothesis. Armstrong and Robertson (1988) presented a similar finding for two species of waterfowl, but they reduced brood size to either four or seven eggs and did not present separate analyses for each. In common goldeneyes (*Bucephala clangula*) maternal effort is also modified according to the past mortality of the brood, and past and future brood mortality are positively correlated (Pöysä et al., 1997). In some fish, females use "test egg" survival to assess male parental ability (Kraak and van den Bergh, 1992). Similarly, partial brood loss in *A. coeruleopunctatus* may act as a cue that males can use to assess a female's parental abilities or the suitability of a breeding site. The extent to which past brood mortality predicts future brood success in *A. coeruleopunctatus* is currently unknown but is obviously a crucial prediction of the brood success hypothesis.

To complicate matters, there is yet another explanation for the observed relationship between the duration of male care and the change in brood size. If males vary in a predictable manner in their future reproductive prospects, the value of a current brood of any given size will vary among males (relative value hypothesis; Galvani and Coleman, 1998; Montgomerie and Weatherhead, 1988). The relative value of the current brood depends on the expected size of future broods. For example, in a laboratory study of convict cichlids (*Cichlosoma nigrofasciatum*), female size and fecundity were closely correlated. When brood size was reduced to 100 fry, larger females invested less in parental care (Galvani and Coleman, 1998). A brood of 100 fry is worth less to a large female because her next brood is likely to be considerably larger. At sites where we can measure males, mating in *A. coeruleopunctatus* is strongly size-assortative ($r \approx 0.72$; Jennions et al., in preparation). Male body size will therefore covary with future reproductive prospects if female size is correlated with fecundity. It is surprising that female size was only weakly related to fecundity at Rio Parti. As such, male body size and future brood size are unlikely to be closely correlated. This conclusion is strengthened by the absence of any relationship for experimental pairs between the number of days the male guarded fry and female size. The relative value of a given brood size is therefore unlikely to be closely related to male size. The relative value hypothesis may still apply, however, if other factors, such as among-male variation in access to more fecund females assessed using cues other than body size, results in repeatability of brood size among male *A. coeruleopunctatus*.

In general, researchers need to more carefully distinguish between the three hypotheses that account for a correlation between earlier desertion (or any other decrease in parental investment) and current brood size. The brood size hypothesis may offer an incomplete explanation. Experiments that follow the design we used (see also Pöysä et al., 1997), rather than simply removing a fixed percentage of each brood, provide one test of the brood success' hypothesis of Carlisle (1982). Where possible, the assumption that past and future brood mortality are correlated should be directly tested. Finally, the comparative importance of predictable brood mortality sensu Carlisle (1982) and variation among parents in expected future brood size (the repeatability of brood size) is usually unknown. The lack of attention to these alternatives

may reflect a bias generated by the predominance of work on parental investment in birds. Limited variation in and low repeatability of clutch size may be common in many birds, but this is not true for most invertebrates and ectothermic vertebrates. In these taxa facultative adjustments in parental investment related to brood size occur, and all three hypotheses may apply in a single species. Determining their relative importance is a future challenge.

Does a reduction in brood size affect male and female parental investment equally?

Before desertion, brood reduction decreased male guarding time. This decline was partly attributable to males temporarily leaving the brood to engage in extrapair courtship. A similar decline in male parental care after brood reduction occurs in several other fish (Coleman et al., 1985; Lavery and Keenleyside, 1990; Ridgway, 1989; Sargent, 1981, 1988; but see Lavery, 1995), but in none of these species does brood reduction promote male desertion. A decrease in the reproductive value of a brood will only lead to mate desertion if the deserting sex thereby gains some benefit. In birds the potential benefits of desertion include an earlier onset of moulting (Ezaki, 1988), arriving sooner to breeding grounds the next breeding season (Urano, 1992), reduced energetic costs of providing care (Erikstad et al., 1997; Hōrak et al., 1999), and increased survivorship (but see Székely and Williams, 1995). The most likely benefit of desertion, however, is the opportunity to remate in the same breeding season (Beissinger and Snyder, 1987; Mock and Parker, 1986; Székely et al., 1999; Tait, 1980). We showed that at least 20% of the 45 *A. coeruleopunctatus* males that deserted their mate bred again almost immediately. Unfortunately, we could not determine the exact time until remating because males were unmarked. However, a recent study at another site using marked males showed that a minimum of 50% of males that deserted remated (Jennions MD, unpublished data).

In contrast, there was no significant effect of brood reduction on female care, either before male desertion or over the entire sampling period. Reduced female care after experimental brood reduction occurs in laboratory studies of other cichlids (Galvani and Coleman, 1998; Lavery and Keenleyside, 1990; Mrowka, 1987), so why didn't female *A. coeruleopunctatus* decrease investment in smaller broods? The energetic costs of female parental care may be considerable. On average, females lost 5.1% of their initial weight during one breeding bout. Weight loss has been reported in several species (e.g., Sabat, 1994), and probably arises due to the trade-off between brood defense and foraging (Rangeley and Godin, 1992) as well as the energetic cost of chasing predators. Balshine-Earn (1995) found that female St. Peter's cichlids, *Sarotherodon galilaeus*, lose about 11.8% of body mass during a breeding cycle, which significantly reduces their future fecundity.

Female care may have remained unchanged despite brood reduction for two reasons. First, females appear to have limited breeding opportunities. Only 4.8% of females were seen to initiate a second brood at Parti. This is probably an underestimate, but work at a second site where females were permanently marked and frequently censused revealed that only 11.5% of females ($n = 113$) initiated a second brood (Jennions et al., in preparation). Caring for the current brood may therefore be the only option available to most females. Second, females may have compensated for reduced male care by increasing their own parental investment (Coleman, 1993). Female compensation may start before male desertion because males spend less time guarding the fry before deserting. We found that naturally deserted females attack pred-

ators significantly more often than paired females at Parti (Jennions et al., in preparation). Female compensation may therefore complicate our interpretation of the value of different-sized broods.

Observed female care may reflect a balance between decreased investment due to lower brood value and greater investment to compensate for lower male investment. To remove male effects, Carlisle (1985) manipulated the brood size of already deserted female *A. coeruleopunctatus*. The return time of females who had been chased away from their brood depended on brood size. This suggests that females do adjust their parental investment according to brood size. Our own data show, however, that females rarely leave the brood unattended. The average time with fry was 889 s of a 900-s observation period ($n = 309$ females), and 62 of 62 deserted females spent 100% of each 15-min sample with the fry (Jennions et al., in preparation). The only time we have seen females leave the brood unattended is in response to human intervention. Even large predatory fish capable of killing adults (e.g., *C. turjense* and *Hoplias* sp.) are attacked. Female return time is therefore an unnatural measure of parental investment.

Finally, even though males gain from desertion because they remate, desertion probably comes at a cost. Female cichlids are usually less successful at rearing a full brood to independence on their own (Balshine-Earn, 1997; Keenleyside and Bietz, 1981; Nagoshi, 1987). In this regard, it is interesting that we hastened male desertion at Rio Parti. In an earlier study here, Townshend and Wootton (1985) reported almost no desertion in the cichlid *Cichlasoma panamenses*, but frequent male desertion at a forested site. They attributed this site-based difference in desertion to the higher density of brood predators at Parti (this density difference still exists; Jennions MD, unpublished data). They argued that the greater risk of brood predation at Parti selects for prolonged biparental care. It would therefore be instructive to test whether brood reduction has an even greater effect on desertion by *A. coeruleopunctatus* at the forested site and whether experimental brood reduction will fail to promote desertion by male *C. panamenses* at Parti.

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