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Factors affecting mate desertion by males in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*)

Convict cichlid fish have biparental care for a period of about 6 weeks lasting from egg laying until the young (fry) have grown to about 10 mm. However, the young can sometimes survive with care from only one parent, and desertion of the mate and offspring by males has been observed. I tested a theoretical model modified from Lazarus (1990) which predicted that mate and offspring desertion by male convict cichlids should be promoted by low predation pressure on fry, high remaining opportunities for males, increasing age of fry, and decreasing number of fry. Males deserted 7.8% of 834 broods studied during two breeding seasons in Costa Rican streams. As predicted, males deserted their broods most frequently at sites with the highest brood survivorship (lowest brood predation pressure), where fry were close to independence and when brood size was smaller than average. Sex ratios and interspawning intervals did not indicate any relationship between mate desertion and opportunities for remating for males. The reuse of spawning caves may favor fidelity to the mate and brood, and defending the young from predators at the same time as defending the cave from specifics may favor biparental care in this species. **Keywords:** biparental care, *Cichlasoma nigrofasciatum*, Cichlidae, Costa Rica, mate desertion, mating system, parental care, parental investment. [Behav Ecol 5:439–447 (1994)]

Biparental care in fishes is believed to have arisen from paternal care (Gross and Sargent, 1985; Keenleyside, 1991) in response to intense predation pressure on young broods (Barlow, 1974, 1984; Perrone and Zaret, 1979). If selective pressures maintaining biparental care are relaxed, or if conditions are such that the costs of providing parental care exceed benefits, then one parent may desert before the young reach independence, leaving the remaining brood care to its mate. The deserting parent accrues the same fitness benefits as its mate (the number of surviving offspring) without the cost of investing additional parental care in the brood. Costs associated with biparental care are not divided equally between the sexes. Because of anisogamy, males generally pay higher costs in lost mating opportunities than females (Baylis, 1981; Gross and Sargent, 1985); thus, males are more likely to desert than females (Lazarus, 1990).

Convict cichlids (*Cichlasoma nigrofasciatum*) are substrate brooding, bipartitional fish occurring in lakes and streams from Guatemala to northwestern Panama (Bussing, 1987; Miller, 1986). During the long dry season (December–May) there is a peak in their breeding activity (Meral, 1973; Wisenden, 1994b), although breeding may also occur during other times of the year (McKay, 1977). Convict cichlids form monogamous pairs and jointly defend a territory (Figure 1). The pair cooperate in the construction of a spawning site, if a spawning site does not already exist, by excavating a cave under a solid object (usually a large rock) on the substrate. The eggs are deposited in the cave and hatch in about 3 days into "wrigglers," in which the fins are poorly developed and the yolk sac is still large and heavy, causing the young to form a dense wriggling mass on the substrate. In another 3 days or so the fins develop more fully and the yolk sac reduces in size allowing the young (fry) to become free-swimming. Fry emerge from the spawning cave and form a compact school hovering above the substrate. Both parents defend the brood from potential predators for about 4 weeks until the fry become strong, agile swimmers. Soon after reaching 10 mm standard length (SL) the fry begin to disperse and become independent from their parents. The reproductive behavior of convict cichlids has been extensively studied in laboratory aquaria (FitzGerald and Keenleyside, 1978; Keenleyside et al., 1985; Lavery and Keenleyside, 1990; Myrberg, 1975; Townshend and Wootton, 1984).

Mate desertion by males has been observed in convict cichlids in experimental ponds in Canada (Keenleyside and Mackereth, 1992) and in Costa Rican streams (Keenleyside et al., 1990; Meral, 1973). Mate desertion by males in other biparental cichlid species has been reported from the field (Carlisle, 1985; Nei, 1984; Townshend and Wootton, 1985) and in outdoor ponds in Canada (Keenleyside, 1983). These studies suggest that mate desertion by males (Keenleyside, 1983; Townshend and Wootton, 1985) or attempts at bigamy (Keenleyside, 1985) result when remating opportunities for males are increased by a female-biased sex ratio (Grafen and Sibly, 1978; Keenleyside, 1983). Intense brood predation pressure may inhibit mate desertion by males by increasing the importance of two parents to provide adequate brood defense (Townshend and Wootton, 1985).

This article has three objectives: (1) to describe the incidence of mate desertion, (2) to test four predictions from a model predicting conditions that
should favor mate desertion, and (3) to consider factors that may constrain mate desertion in free-ranging male convict cichlids.

**Model of mate desertion**

Lazarus (1990) developed a general model of mate desertion that can be applied to the convict cichlid mating system. I adapted his model to demonstrate conditions under which mate desertion by male convict cichlids should occur (Figure 2A). The model considers the benefits of providing parental care (number of surviving offspring) from the beginning ($t_0$) to the end ($t_e$) of the period of care when two parents provide care ($V_2$), and when only one parent provides care and the other deserts ($V_1$). Because field observations have shown that fry without parental protection are consumed almost immediately (Barlow, 1974; Nell, 1984; Perrone, 1978; personal observation), I do not consider the third condition described by Lazarus (1990) where both parents desert ($V_0$), or the evolutionary game that results when the decision to desert by one sex depends on whether its mate will then also do so (Maynard Smith, 1977).

The model considers the costs of providing parental care: the sacrifice of additional breeding opportunities while caring for the present brood; reduced ability to invest in future reproduction; reduced ability to forage; and increased energetic demands and mortality risk associated with providing parental care. A deserting parent no longer pays these costs. The increment in future reproductive success ($RS$), above that which would be obtained if investment was continued in the current brood from the time of potential desertion until $t_e$ for deserting males ($M$) and deserting females ($F$), declines from a maximum at $t_e$ to 0 at $t_e$ (Figure 2A). The mating cost is assumed to be higher for males than for females (Gross and Sargent, 1985); thus, $M$ is larger than $F$ and males are the most likely sex to desert (Lazarus, 1990). It is also assumed that the response of the female to mate desertion is always to stay with the young, because $(F + V_0) = F < V_1$.

When both parents stay with the brood until $t_e$, each sex receives the same net RS ($V_2$). A parent should desert when its RS with uniparental care by its mate ($V_1$) plus its increment in RS by deserting ($M$ or $F$) yield a net RS greater than $V_2$. When the net RS for deserting for males ($V_1 + M$) and females ($V_1 + F$) does not exceed $V_2$ neither parent should desert (Figure 2A). The model demonstrates four conditions that should increase the likelihood of mate desertion by male convict cichlids: predation pressure, the probability of remating, brood age, and brood size. These factors can interact with each other. I have drawn them one at a time holding all factors affecting mate desertion constant except for the variable under consideration to demonstrate the effect of each factor individually.

**Prediction 1.** If biparental care in convict cichlids is maintained by the necessity of two parents to defend a brood, then male desertion should be less common when brood predation is high (Figure 2B). Under high predation pressure, both $V_1$ and $V_2$ are affected. When brood predation pressure is low, one parent may be as good as two parents in providing brood defense, i.e., $V_{1L}$ approaches the value of $V_2$ at an early stage of fry development. When brood predation pressure is high, fry survival under uniparental care ($V_{1H}$) would be expected to be low compared to fry survival under biparental care, i.e., $V_{1H}$ approaches the value of $V_2$ only at the end of the period of care. The male should desert when $(V_{1L} + M) > V_2$ to maximize his net RS (Figure 2B).

**Prediction 2.** Mate desertion should be more likely to occur when the probability of remating for males is high. A high probability of remating in-
creases the mating cost to a male providing care to his current brood and thus increases the increment to his net RS by deserting. Under these conditions the M curve is elevated from M_{1} to M_{8} such that (V_{1} + M_{8}) < V_{0} but (V_{1} + M_{8}) > V_{0} (Figure 2C). High mate availability for males is most likely to occur when the operational sex ratio is female biased. 

**Prediction 3.** The probability of mate desertion should increase with stage of brood development. V_{1} increases in later stages of brood development because fry become increasingly self-sufficient and the female's ability to guard the brood by herself increases. Furthermore, as time remaining until fry independence decreases, the potential effect of the male's absence also decreases. An increase in V_{1} causes V_{1} + M to increase and surpass V_{0} curve near the end of the period of parental care, i.e., at late stages of brood development (Figure 2B, C).

**Prediction 4.** The probability of desertion should increase as brood size decreases. When the number of fry in the current brood is reduced, V_{0} is lowered relative to M from V_{0}H to V_{0}L (Figure 2D). Concomitantly, the expected net RS under uniparental care decreases from V_{0}H to V_{0}L. Males should not desert when brood size is large because net RS of deserting males (V_{0}H + M) does not exceed V_{0}H (dashed line in Figure 2D), but males should desert when fry number is low because V_{1}L + M exceeds V_{0}L (dotted line in Figure 2D).

**METHODS**

I studied convict cichlid reproductive ecology within the species' natural range (Bussing, 1987) in Guanacaste province, northwest Costa Rica, during two breeding seasons, January to June 1990 and December 1990 to June 1991. In Guanacaste, the dry season lasts from early December to mid-May (Frankie et al., 1974). In this region convict cichlids breed during the dry season (Keenleyside et al., 1990; Meral, 1978). The study sites were located in small streams at Lomas Barbudal Biological Reserve, 10º30' N, 85º23' W. Four study sites were used, representing two habitat types. Two sites were in Rio Cabuyo, and two were in Quebrada Amores, a tributary of Rio Cabuyo. In each stream, one site was a relatively deep, wide pool ("pool site") and the other was a series of small, shallow, interconnected pools ("stream site"). Physical and chemical characteristics of the study sites are provided in Wisenden (1993b).

Each site formed a discrete breeding area although only the pool site in Quebrada Amores was closed to immigration and emigration, due to low water levels, during the study periods. I monitored all convict cichlid breeding activity at each site. Spawning locations were marked with flagging tape (1990) or painted stones (1991). I marked parental fish when their brood became free-swimming, about a week after spawning. After surrounding the parents and young with a black fine-mesh seine, I captured the male first because he was the most likely to flee. Next, I captured all the fry using hand nets. The female always remained close to the fry while the fry were being captured, and any fry that strayed quickly returned to her. I then captured the female. I anesthetized each parent with MS222 (tricaine methanesulfonate), then weighed, measured, and gave each fish a unique identifying mark by excising two dorsal spines (Rinne, 1976). I made detailed sketches of the body markings of each parent for later identification of freely swimming fish. I anesthetized (with MS222) 15 fry from the brood and measured their standard length (SL) to the nearest 0.5 mm. I recorded the total number of fry in the brood. When all fish had recovered from the anesthetic, I gently returned the parents to the site of capture, which was still surrounded by the seine to exclude potential fry predators. Upon release, the male often fled and hid. However, the female soon began to search for her fry. I placed a clear plastic tube vertically onto the substrate and put the fry into the tube. When the female approached the fry, I lifted the tube and the female resumed normal brood defense. The male usually joined the female in brood defense soon after the fry and the female were reunited. Controls testing for handling mortality (9 broods resampled 1 h after handling) showed a mean (±SE) loss of 0.78 ± 0.28 fry per sample.

At regular intervals (usually 7 days) until fry dispersal, I checked each brood, and recorded frequency of parental attacks at nearby fish and cave visiting behavior for 10 min per parent. I considered males to have deserted their mate if they did not associate with the female or brood for 25 min. The mean (±SE), median, and 95 percentile of time away from the brood per trip (total time away/number of trips) for males during brood defense was 85.5 ± 5.0, 11.8, and 181 s, respectively (n = 252 10-min observations; unpublished data). I identified individual families by their location in the stream, stage of fry development, and body markings of the parents. I then captured fry as before. I left the parents in the water with <10 fry and made a visual count of the remaining fry. I counted the captured fry and anesthetized and measured 15 of them. I then returned the fry to

**Figure 2**

(A) Mate desertion model based on Lazarus (1990). The model describes the number of offspring surviving under biparental care (V_{0}H), and uniparental care (V_{0}L). t_{1} and t_{2} are, respectively, the beginning and the end of the period of parental care. M and F represent the increment in future RS gained by males and females respectively deserting at time t. (B) When brood predation pressure is relatively low, fry survival under uniparental care (V_{0}L) will be higher than when brood predation is high (V_{0}H). Under these conditions the cost of mate desertion to males is low, thus males should desert. (C) Males should desert when they have relatively greater opportunities for remating because providing care to the current brood represents a higher cost (M_{0}) than when mating opportunities are low (M_{1}). (D) Male desertion should be favored when offspring number is reduced to a low number because the expected RS (benefit) from the current brood is lowered from V_{0}H and V_{0}L to V_{0}L and V_{0}L, which represents a relatively low benefit compared to the cost of delaying the benefit of expected RS from future reproduction (M).
their parents as described above. Each brood was sampled a mean (±SE) of 2.58 ± 0.16 times (range = 1–6, n = 252 broods). To test the fourth prediction, I observed fry number in deserted broods in the sample before male desertion. I calculated fry growth rates for each brood as the rate of change in mean fry SL over time. For convenience, each 2-mm interval of fry size is called a stage of development.

I estimated population sex ratios of adult convict cichlids from samples taken using a 10-nm bag-seine from the Quebrada Amores pool site and the Río Cabuyo stream site. Sex of adults was determined by body coloration (see Bussing, 1987). In the Río Cabuyo pool site and Quebrada Amores stream site, it was not possible to catch samples large enough to estimate sex ratio.

I analyzed the data using PC SAS and PC SPSS. Variation about mean values is expressed as the standard error of the mean.

RESULTS
Desertion frequency
Males deserted their mate and brood in 26 (7.8%) of 354 broods monitored at the four study sites during two years (Table 1). This estimate is conservative because it does not include broods that were deserted by the male parent and subsequently failed (i.e., female and brood separated) before the next sampling date. There is no evidence to suggest that these estimates are inflated or confounded by selective predation on males. During the 22 weeks of the dry season, the number of active broods and the proportion of broods deserted by males increased to a peak, then declined with the approach of the wet season (Figure 3). There was a time lag of about 5–6 weeks between the peak frequency of male desertions, on 24 April in 1990 and 19 April in 1991, and the seasonal peaks in breeding activity on 11 March in 1990 and 7 March in 1991. Male desertion by males occurred more often in stream sites (17 of 187 pairs, 9.2%) than in pool sites (9 of 171 pairs, 5.3%) (χ² = 5.025, p = .08). The

![Graph showing the number of active broods and percent of broods deserted over time.](Image)

Table 1
Number of male convict cichlids that deserted their mate and broods at each study site during two field seasons

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of broods</th>
<th>Number deserted</th>
<th>Percent of total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amores pool</td>
<td>47</td>
<td>2</td>
<td>4.3</td>
</tr>
<tr>
<td>Cabuyo pool</td>
<td>37</td>
<td>3</td>
<td>8.1</td>
</tr>
<tr>
<td>Amores stream</td>
<td>15</td>
<td>5</td>
<td>20.0</td>
</tr>
<tr>
<td>Cabuyo stream</td>
<td>14</td>
<td>3</td>
<td>21.4</td>
</tr>
<tr>
<td>1991</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amores pool</td>
<td>41</td>
<td>2</td>
<td>4.9</td>
</tr>
<tr>
<td>Cabuyo pool</td>
<td>46</td>
<td>2</td>
<td>4.3</td>
</tr>
<tr>
<td>Amores stream</td>
<td>39</td>
<td>5</td>
<td>12.8</td>
</tr>
<tr>
<td>Cabuyo stream</td>
<td>69</td>
<td>6</td>
<td>8.7</td>
</tr>
</tbody>
</table>

The Cuchillo deserting males did not differ in size from nondeserting males (two-way ANOVA, SL: F = 0.018, p = .66, df = 1, 209; site: F = 0.791, p = .50, df = 3, 209) nor did deserted females differ in size from nondeserted females (SL: F = 1.224, p = .27, df = 1, 214; site: F = 16.014, p < .001, df = 3, 214). The above analyses indicate that males did not differ in size in the two types of sites, but females were smaller in the Río Cabuyo pool site.

Forty-eight percent of deserting males attempted more than one brood within a season, compared to only 25% of nondeserting males (χ² = 4.80, p = .03; Table 2). Six of these deserting males attempted a brood after deserting while 15 had attempted another brood previously and deserted their final brood of the season. No males deserted more than one brood per season. Although an unknown number of dorsal clips used to mark individuals may have regenerated during the second season, at least 17% of the 104 males breeding in 1990 also bred in 1991. Of these, only two had deserted a mate in 1990. The proportion of 1991 breedings by deserters and nondeserters from 1990 did not differ (Fisher's exact test p = .417). Mean interspawning interval for males that deserted successful broods (reached fry independence) and then later re-sprawed was 39.5 ± 7.8 days (n = 4) compared to 55.0 ± 4.2 days (n = 29, t = 1.17, p = .25, df = 31) for males that did not desert successful broods before respawning.

Predation pressure
In support of the first prediction of the model, there was a significant positive correlation among site-years between rates of desertion by males and percent brood survival (Spearman r = .833, p = .01, n = 8). Percent brood survival was 46.8% (n = 128 broods) in stream habitat and 14.9% (n = 141 broods) in pool habitat (Figure 4). Contingency analysis showed an interaction between year and habitat (χ² = 23.88, p < .001). However, the effect of habitat was significant in both years (1990: χ² = 8.906, p = .003; 1991: χ² = 24.849, p < .001). The mean number of fry per surviving brood at independence did not differ significantly among sites (27.9 ± 2.0 fry, n = 138 broods, ANOVA, F = 1.428, p = .24, df = 3, 777). Habitat differences in brood survival were not linked to fry growth rates.
Table 2
Seasonal mating frequencies of male convict cichlids that did not desert their mate, males that deserted their mates, and females

<table>
<thead>
<tr>
<th>Number of matings</th>
<th>Males</th>
<th></th>
<th></th>
<th></th>
<th>Females</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nondeserting</td>
<td>Deserting</td>
<td>n</td>
<td>%</td>
<td>n</td>
<td>%</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>115</td>
<td>75.2</td>
<td>11</td>
<td>52.4</td>
<td>218</td>
<td>94.8</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>30</td>
<td>19.6</td>
<td>5</td>
<td>23.8</td>
<td>12</td>
<td>5.2</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>7</td>
<td>4.6</td>
<td>3</td>
<td>14.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>0.7</td>
<td>2</td>
<td>9.5</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

among site-years (Spearman $\tau = -0.238$, $p = 0.57$, $n = 8$), nor to site differences in mean size of breeding females $AmP = AmS > CabS > CabP$, and males $AmP = AmS = CabP = CabS$, AmP = AmS (Student Newman-Kuels $p < 0.05$).

Attacks on potential predators were performed more by females than by males at all sites except Cabuyo pool (AmP: $t = 5.16$, $p < 0.001$, $df = 126$; CabP: $t = 1.59$, $p = 0.14$, $df = 105$; AmS: $t = 5.04$, $p < 0.001$, $df = 71$; CabS: $t = 4.00$, $p < 0.001$, $df = 67$) (Table 3). Rates of parental attacks were highest in stream sites (females: $t = 4.24$, $p < 0.001$, $df = 193$; males: $t = 2.19$, $p = 0.030$, $df = 121$). Percent brood survival was positively correlated with parental brood defense by females (Spearman $\tau = 0.762$, $p = 0.028$, $n = 8$) but not by males (Spearman $\tau = 0.214$, $p = 0.610$, $n = 8$). Thus, parental attack rates were not highest at sites with low brood survival and therefore did not reflect predation pressure as expected. The mean number of fry in broods that failed before the next sample and the mean number of fry in broods that did not fail before the next sample did not differ for any of the site × stage combinations except for Río Cabuyo pool site for fry <6 mm SL ($t = 3.38$, $p = 0.002$, $df = 36$). Thus, for most broods, failure did not occur by a gradual decline in fry number but rather by a sudden, catastrophic loss of fry. These catastrophic events did not occur while I recorded parental behavior, which may partially explain why brood failure was not positively correlated with rates of parental attacks.

Remating opportunities

The sexes differed in frequency of remating during the study period. Twenty-eight percent of breeding males bred more than once (mean = 1.38 ± 0.05, $n = 174$) compared to 5.2% of breeding females (mean = 1.05 ± 0.01, $n = 280$) ($t = 5.95$, $p < 0.001$, $df = 437$). There was no significant difference among sites in seasonal mating frequency of males (ANOVA $F = 0.531$, $p = 0.652$, $df = 5$, 217) including Amores pool, which was closed to emigration and immigration during the dry season. Therefore the sex difference in seasonal mating frequency was not confounded by sex differences in dispersal between broods. This supports the assumption in the model that the mating cost of parental care is higher for males than for females.

The overall sex ratio at two of the sites did not correspond with the rates of male desertion as predicted by the model. At Cabuyo stream, where male desertion was relatively common, the sex ratio of adult convict cichlids tended slightly, but not significantly, toward a female bias ($M:F = 104:128$, $\chi^2 = 1.59$, $p = 0.221$, $n = 5$ sample dates). At Amores pool, where male desertion was uncommon, sex ratio differed significantly from 1:1 ($M:F = 66:103$, $\chi^2 = 8.01$, $p = 0.005$, $n = 3$ sample dates).

The inter-spawning interval for males was the same for all sites (43.7 ± 2.6 days, $n = 64$; ANOVA $F = 2.14$, $p = 0.105$, $df = 3, 60$). Mean inter-spawning interval for males decreased throughout the study period as the time remaining in the dry season in which to initiate a new brood decreased. There was no evidence of change in remating opportunities for males. Therefore, the second prediction of the model cannot be tested with these data.

Table 3
Total number of attacks per 10 min by female and male parents during brood defense at each of the study sites

<table>
<thead>
<tr>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{X}$</td>
</tr>
<tr>
<td>Amores pool</td>
<td>7.21</td>
</tr>
<tr>
<td>Cabuyo pool</td>
<td>7.32</td>
</tr>
<tr>
<td>Amores stream</td>
<td>10.64</td>
</tr>
<tr>
<td>Cabuyo stream</td>
<td>13.84</td>
</tr>
</tbody>
</table>

Stage of brood development

Because fry growth was linear, (mean $r^2 = 0.987 ± 0.002$, $n = 117$ for all broods with samples from three or more sampling dates), each 2-mm interval of fry growth represented the same amount of time. However, the majority of male desertions occurred at late stages of brood development as predicted by the model. Seventy-three percent of 19 desertions occurred when fry were >8 mm SL, that is, <10 days from independence ($\chi^2 = 10.00$, $p = 0.020$, Table 4). All broods deserted by males when mean fry SL was 8 mm or larger survived to independence while broods deserted when mean fry SL was <8 mm failed seven of six times (Table 4).

Brood size

Deserted broods tended to contain fewer fry in the sample than the average number of fry in nonde-
Table 4
Number of male-deserted broods surviving to independence in stream and pool sites (data from 2 seasons combined)

<table>
<thead>
<tr>
<th>Fry SL.</th>
<th>Stream sites</th>
<th></th>
<th>Pool sites</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>S</td>
<td>P</td>
<td>Total</td>
</tr>
<tr>
<td>&lt;6 mm</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>6-8 mm</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>8-10 mm</td>
<td>10</td>
<td>10</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>&gt;10 mm</td>
<td>3</td>
<td>3</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

a Fry standard length at time of desertion.
b Some fry survived to independence.
c Brood failed before fry independence.

asserted broods for each stage of fry development (Figure 5). Deserted broods were smaller than non-deserted broods for 8 of 10 stage × site combinations (binomial test, n = 10, p = .055, 1-tailed), consistent with the fourth prediction of the model. The difference in fry number decreased with increasing brood age (r² = .37, p = .061, df = 8). This is consistent with the model because (M + V₂L) does not exceed V₂L at early stages of brood development unless V₂L is greatly reduced from V₂H (Figure 2D). At late stages of brood development a small decline in brood size reduces V₂ below (M + V₂L) when males should desert.

Cave use
Spawning caves may be an important resource for convict cichlids. The size of the cave entrance is usually as small as will permit the male (the larger of the pair) to enter (Figure 1). The volume of the cave varies from approximately one to three body lengths in diameter with or without a passageway leading from the entrance to an inner chamber. Convict cichlids spawned in caves that they either freshly excavated themselves or reused from previous spawnings, or they used caves abandoned by other pairs. Observations of cave use and subsequent reuse showed that males (and females to a lesser extent) reused the same spawning sites in successive breeding attempts (Table 5). Males with high seasonal mating frequencies were more site tenacious than males with low seasonal mating frequencies.

Table 5
Mean number of different spawning sites used by males that attempted two broods, and by males that attempted two, three, and four broods within a 5–6 month breeding season

<table>
<thead>
<tr>
<th></th>
<th>Seasonal mating frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1.43</td>
</tr>
<tr>
<td>SE</td>
<td>0.125</td>
</tr>
<tr>
<td>p</td>
<td>1.00</td>
</tr>
<tr>
<td>F</td>
<td>0.28</td>
</tr>
<tr>
<td>n</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Females</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>1.50</td>
</tr>
<tr>
<td>SE</td>
<td>0.224</td>
</tr>
<tr>
<td>p</td>
<td>0</td>
</tr>
<tr>
<td>F</td>
<td>6</td>
</tr>
<tr>
<td>n</td>
<td>0</td>
</tr>
</tbody>
</table>

Nocturnal observations showed that after the fry become free-swimming, convict cichlid families continued to take refuge in their spawning caves at night. Typically, the male was stationed just outside the entrance and the female was further inside, close to the fry. This presumably made it more difficult for fry or parents to be captured by nocturnal predators.

I observed cave guarding behavior by both sexes. During the day, families of convict cichlids stayed an average of 1.48 ± 0.04 m from the cave in which the brood was spawned (max = 18.7 m, n = 429 samples from all sites at all stages). One parent occasionally left the vicinity of the brood, traveled to its spawning cave, and chased all conspecifics from the area. Cave visits were performed 0.67 ± 0.05 (n = 155) times per 10 min by males and 0.44 ± 0.04 (n = 161) times per 10 min by females. Cave visiting frequency differed by site but not by sex in 1990 (two-way ANOVA, site: F = 3.057, p = .007, df = 3, 164; sex: F = 3.191, p = .076, df = 1, 164) and 1991 (site: F = 7.955, p < .001, df = 3, 136; sex: F = 0.550, p = .566, df = 1, 136). Site differences in cave visiting frequency were not consistent from year to year. In 7 of the 8 year × site combinations, males visited their caves more frequently than their mates (binomial test, n = 8, p = .055, 1-tailed).

DISCUSSION
Many species of New World cichlids have seasonal peaks in breeding activity especially in riverine populations (Lowe-McConnell, 1991; McKay, 1977). Although the period of study did not encompass the entire annual reproductive period of these populations, a sex difference in seasonal remating patterns was apparent. Females rarely mated more than once during the approximately 150-day study period. In contrast, female convict cichlids in aquaria can respawn in 12 days (Wisenden, 1993a). Whether factors that constrain spawning frequency by free-ranging females are nutritional or social is not known. The low rate of seasonal iteroparity by females in the field suggests that they should not desert the current brood even if their mate does so, because the current brood likely represents a female's only chance for reproduction that season (Dawkins and Carlile, 1976).

The peak in the rate of male desertions occurred 5–6 weeks after the seasonal peak in breeding ac-
tivity. Because most mate desertions occurred at late stages of brood development, desertions by males from broods initiated at the peak of breeding activity should occur about 5 weeks later. This suggests that males deserted in proportion to the number of pairs breeding and not in relation to the time of season.

The mate desertion model modified from Lazarus (1990) performed reasonably well. Conditions under which males deserted their mates and broods matched three of the four theoretical predictions. Generally, males deserted when the expected benefit from investing parental care in the current brood was relatively low and the cost of continuing to provide care was relatively high.

The first prediction of the model was that males should desert when brood predation pressure is low. Males deserted most often from sites where the chances of rearing a brood to independence were greatest and therefore, presumably, predation pressure was lowest. In a previous study with a related species, Cichlasoma panamense, Townshend and Wootton (1985) found a positive relationship between the percent of monogamous pairs (non-deserting male parent) and the rate of parental attacks against brood predators at two sites in Panama. Male remating opportunities potentially confounded Townshend and Wootton's interpretation of their data because the sex ratio was female-biased at the site with low attack rates (1:2:1) but did not significantly differ from 1:1 at the site with high attack rates. In the present study, where male desertion was compared to both the rate of parental attacks and brood survival, the probability of male desertion positively corresponded with high brood survival but, unexpectedly, not with high rates of parental attacks. Possible explanations for this may be that higher defense levels by parents in stream habitat resulted in higher brood survival, that fry loss was catastrophic and therefore unrelated to the general attack rates, or that stream habitat generally supported higher densities of fish, and thus attack rates may simply reflect density of fish that were mostly not important brood predators.

Remating opportunities for males could not be determined directly in this study precluding a direct test of the second prediction of the model. Other measures of mate availability (i.e., seasonal remating frequencies, population sex ratio, and interspawning intervals) that might have provided indirect support for the second prediction of the model did not provide evidence of variation in remating opportunities for males. Therefore these data neither support nor reject the model.

Mate desertion occurred more frequently during late stages of fry development than during early stages, matching the third prediction of the model. This was not an artifact of the sampling method because there was a minimal number of intrusions at each site, and breeding adults were physically handled only once, when the fry first became free-swimming. In contrast, Townshend and Wootton (1985) observed no significant relationship between stage of fry development and desertion by males.

Broods deserted by males contained fewer fry than non-deserted broods for 8 of 10 site × stage combinations, which supports the fourth prediction of the model. It should be pointed out that the alternative prediction may hold for other animal groups such as birds where M could be larger for large broods than for small broods because large broods demand much more care, and therefore males may benefit more (M) by deserting large broods than small broods (Lazarus and Wing, 1986). Parental care in birds has two main components (1) brood defense (unshared parental investment) and (2) provisioning the young with food (shared parental investment). In birds, the parental investment required to provide food for large broods is markedly higher than for small broods, and parents deserting large broods benefit from being spared this investment. However, parental care in fishes (including convict cichlids) is primarily in the form of brood defense (unshared parental investment) and large broods are almost as easy to defend as small ones, within the range of fry numbers discussed here. Although parental investment increases with brood size in fish (Carlisle, 1985; Coleman et al., 1985; Lawes and Keys, 1980; Hensley, 1981; Ridgway, 1989), M decreases for large broods because the expected RS from the current brood is relatively high compared to expected future RS.

Two of the conditions considered in the model may act in opposition to each other. Broods in areas with high predation pressure may have higher rates of attrition and thereby become smaller. Thus, under certain circumstances predation pressure may act to increase or decrease desertion rates. However, brood failure was usually a result of a catastrophic rather than a gradual loss of fry. Thus, attack rates of brood predators or instantaneous rates of fry mortality may not be useful cues to males as predictors of brood success or whether to desert the current brood. Because the rate of brood survival was higher in stream sites, males could expect a higher probability of success in future reproductive efforts in stream habitat than in pool habitat. This seems to be the most important underlying factor determining the likelihood of male mate desertion in this study.

M may increase in response to high predation pressure if future reproductive efforts are likely to occur under more benign conditions. This was not the case in this study. There was no effect of season on brood survival. M should decrease if future broods have a poor probability of survival. V₁ should also decrease in response to increasing predation pressure. Thus, M + V₁ (net RS) decreased relative to V₂ for broods reared in pool habitat where future broods had a poor probability of survival and males were accordingly less likely to desert in pool habitat than in stream habitat.

Although patterns of mate desertion by males conformed qualitatively to the predictions of the model, the data collected in this study failed to support the underlying premise of the model: that males accrue a fitness benefit by deserting. Few males that deserted in the same season remated, and desertion was not necessary for males to breed again, although males with high seasonal mating frequencies were the most likely to desert, and deserting males that attempted subsequent reproduction had slightly (though not significantly) shorter interspawning intervals than non-deserting males. Perhaps relief from brood defense during the final week of care provided enough benefit to
males to favor desertion, particularly if the risk of brood failure resulting from desertion was low (Table 4). A male removal experiment showed that the absence of the male parent in broods with fry <8 mm SL results in high rates of brood failure (Wisdend and Keenleyside, 1992).

The relatively low frequency of desertion may be due to a male's attachment to the complete, functional nest site in his territory. Two pieces of evidence lead to this conclusion. First, nest sites (caves) are used for shelter at night by pairs with broods, presumably for protection from nocturnal predators. Second, although females generally spawned only once per season, 28% of males spawned more than once within a season (48% of deserting males) and often reused the same spawning site. Thus, a male may be constrained from deserting because the cave is needed for his next brood. The current brood may be sacrificed if the current female and brood cannot use the cave as shelter at night. Given this constraint, a male's best strategy may be to help the female guard the cave and assist in brood defense.

Cave guarding behavior performed by both parents suggests that ready-made, high quality spawning caves are limited and therefore valuable to parental convict cichlids and need to be defended from acquisition by conspecific pairs. McKay (1977) observed intense competition for nesting sites in nine cichlid species, including convict cichlids, in Lake Jiló, Nicaragua. Only 29 (13.9%) of 209 cichlid pairs and 20% of convict cichlid pairs were able to rear their brood to independence without being evicted from their nest site by conspecific pairs.

One parent cannot defend both a mobile brood and a cave as effectively as two parents can. This implies that the continued need for a ready nest site may constrain mate desertion. The hypothesis that biparental care exists in substrate brooding cichlids because two parents are required to defend the brood may be only partially correct; two parents may be necessary to both guard the mobile brood from predators and the spawning cave from conspecific breeding pairs.

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