

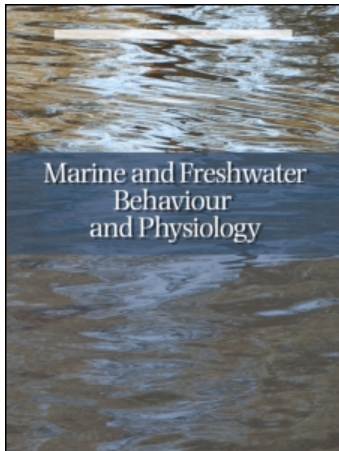
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Marine and Freshwater Behaviour and Physiology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title-content=t713644420>

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Online Publication Date: 01 January 1998

To cite this Article Zworykin, D. D., Budaev, S. V. and Mochev, A. D.(1998)'Alternative tactics of male compensatory behaviour during parental care in *Cichlasoma octofasciatum* (Teleostei: Cichlidae)',*Marine and Freshwater Behaviour and Physiology*,31:3,185 — 191

To link to this Article: DOI: 10.1080/10236249809387072

URL: <http://dx.doi.org/10.1080/10236249809387072>

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Short Communication

ALTERNATIVE TACTICS OF MALE COMPENSATORY BEHAVIOUR DURING PARENTAL CARE IN *CICHLASOMA OCTOFASCIATUM* (TELEOSTEI: CICHLIDAE)

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(Received 6 November 1997; In final form 26 February 1998)

Keywords: Individual differences; paternal behaviour; *Cichlasoma octofasciatum*

Individual differences and alternative strategies have been documented in the behaviour of many species (see Slater, 1981; Dunbar, 1982; Clark and Ehlinger, 1987; Magurran, 1993 for reviews). Currently, they are considered not as a “white noise”, but as an important result of evolution that can be maintained by natural selection for a variety of reasons (Clark and Ehlinger, 1987; Magurran, 1993). In the present article we document alternative tactics in one crucial element of parental care, the compensatory behaviour by males of *Cichlasoma octofasciatum*, for a reduction of parental care on the part of the female during brooding.

This biparental substrate brooding cichlid is a common inhabitant of streams and small rivers in Central America and Southern USA, and exhibits a clear separation of parental roles (Zworykin, 1995). Typically, female

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C. octofasciatum allows males to approach the nest with eggs for only a short time. However, hatching of free embryos (wrigglers) by the female is accompanied by a sharp increase of her locomotion, thereby reducing the time she spends in proximity of the brood. As a result, the male spends much more time near the brood at the wriggler stage and adjusts for the reduced parental care on the part of the female. This has been termed compensatory behaviour (Zworykin, 1995).

Eight pairs of adult *C. octofasciatum* ($N = 16$ individuals), descendants of fish obtained from a private aquarium breeder, were used. Each pair was maintained in a 100-litre aquarium ($70 \times 35 \times 41$ cm) containing natural gravel and half a clay flower-pot as the spawning substrate. Water temperature was maintained at $25 \pm 1^\circ\text{C}$ and the light:dark cycle was 10:14 h. Both adult fish and fry were fed *ad libitum* with bloodworms (*Chironomus* sp. larvae) and commercial fry pellets (TetraMin).

The brood development was classified into five stages: (1) egg (one day after spawning); (2) wriggler stage (one day after hatching); (3) 3 days as fry; (4) 10 days as fry; (5) 17 days as fry. Two independent behavioural variables were scored at each brood stage: (1) the percentage of time spent near the brood (i.e. at a distance not exceeding one body length of the parent) and (2) gross locomotion (i.e. the percentage of time the parent moved to a distance exceeding one body length).

An array of a particular behavioural measure, scored over several time points for a specific individual, may be conceived as a longitudinal profile for that individual. Thus, we obtained two profiles corresponding to the above two behavioural variables for each individual fish. The statistical analysis of the response profiles was organised as follows. First, cluster analysis (Sneath and Sokal, 1973) and nonmetric multidimensional scaling (Kruskal and Wish, 1978) were applied separately for males and females to unravel the patterns of their individual variability. Second, the clusters revealed by clustering subtle aspects of the response profiles were compared to ascertain whether they really represented distinct tactics.

Correlation distance metrics (1 - Pearson's correlation coefficient) were used to measure dissimilarities between individual response profiles. Three aspects of such profiles can be distinguished (e.g. Sneath and Sokal, 1973): level, shape and scatter. Unlike more customary dissimilarity measures like the Euclidean distance, the correlation metric takes account of only the shape, and is used when some subtle patterns of "ups" and "downs", rather than overall similarities of absolute scores are of primary interest.

The test based on the scree plot of the final stress index (see Kruskal and Wish, 1978) was applied to assess the dimensionality in multidimensional

scaling. Ward's minimum variance algorithm was utilised for the cluster analysis (see Batagelj, 1988 for its justification with the correlation metrics). Alternative procedures (e.g. weighted and unweighted pair-group average clustering) and correlation coefficients (e.g. 1 - Spearman's correlation) were also used, with identical results. Because the results of cluster analysis are often severely dependent on the algorithms used (e.g. different computational methods often reveal dissimilar cluster structures within the same data set, see Blashfield, 1976), this confirmation provides important evidence for the robustness and stability of clusters. Furthermore, Monte-Carlo studies have shown that Ward's procedure is most accurate in finding the "true" cluster structure (Blashfield, 1976; Milligan, 1980). Because of the small sample size, randomisation tests were used for group comparisons (Edgington, 1987). All *p*-values reported are two-tailed. The summary statistics are expressed as median (minimum-maximum).

The cluster analysis revealed two distinct clusters (designated as Cluster 1 and Cluster 2, Fig. 1(a)) in the profiles corresponding to the time spent near the brood, but only for males. This pattern was confirmed by the multi-dimensional scaling results (stress=0.003): the first dimension entirely separated the two clusters (Fig. 1(b)). No clear clusters were observed in females and, in addition, the structures were not robust with respect to the clustering procedure used. No stable clusters appeared in the gross locomotion activity profiles of males and females. The averaged profiles for both parents in the Cluster 1 and Cluster 2 are presented in Fig. 2.

Thus, there are two distinct longitudinal patterns of change of the time spent by males near their offspring, and they tend to differ primarily in only one aspect. The interpretation of clusters, and the inference that they are really stable and not caused by random variation and measurement error, is supported by group comparisons. Individuals in the clusters, distinguished on the basis of subtle aspect of longitudinal profile shapes, differed in several behavioural variables reflecting male compensatory behaviour, so that there was no overlap between their distributions.

First, we analysed the absolute value of the difference, in time spent near the brood between male and female within each pair (i.e. near-brood time of female - near-brood time of male) for broods at the wriggler stage. This difference was smaller in Cluster 1 than in Cluster 2 pairs (37.4 (6.4-43.0) versus 63.2 (50.2-69.2), *p* = 0.029, randomisation test). Second, we analysed the absolute value of the difference in near-brood time between male and female within each pair for adjacent brood stages, i.e. (1) [time spent near eggs by female - the time spent near wrigglers by male] and (2) [time spent near wrigglers by male - the time spent near 3-day fry by female]. As may be

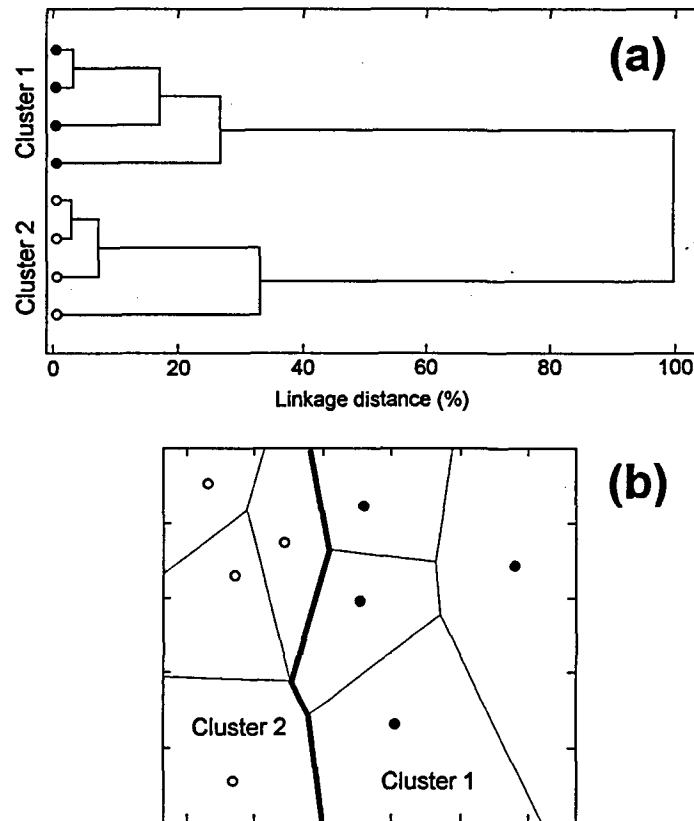


FIGURE 1 The results of cluster analysis (a) and nonmetric multidimensional scaling (b) performed on the male profiles of the time spent near offspring over the five brood stages (eggs, wigglers, 3, 10 and 17 days as fry). Two clusters (1 and 2) are evident in both plots. The Voronoi tessellation (determining areas that are closer to a certain point than to all other neighbouring points) was made on the multidimensional scaling plot and in (b) the bold line divides the two clusters.

seen from Fig. 2, these were large and significant differences between the Cluster 1 and Cluster 2 in both these indices: (1) 17.1 (10.3–20.2) versus 4.2 (1.2–7.3), $p=0.029$, randomisation test; (2) 27.1 (13.4–2.8) versus 6.7 (0.2–13.3), $p=0.029$, randomisation test. Note that the distributions of all these measures show no overlap between the two clusters.

In other words, males representing Cluster 2 maintained a high level of parental care, coincident with its sharp decrease in females at the wriggler stage when a temporal reversal of sex roles occurred (see Fig. 2), and significantly better than males representing Cluster 1. Unlike the Cluster 1

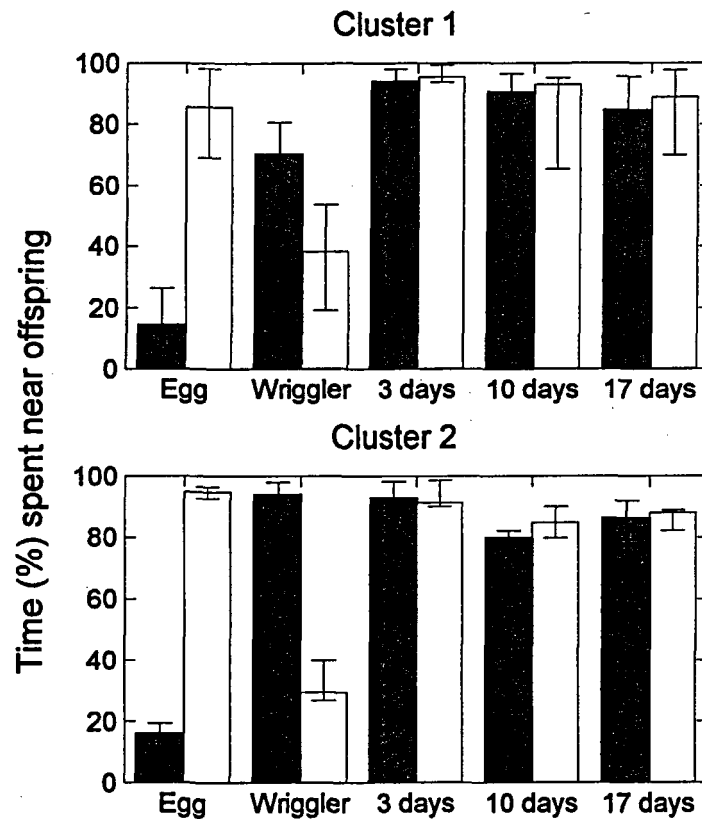


FIGURE 2 The median percentage of time spent near offspring at each of the five brood stages by males (shaded bars) representing Cluster 1 and Cluster 2 and the respective females (open bars). The whiskers show the minimum and maximum values.

males, quite small deviations from the females' scores were characteristic of the Cluster 2 males i.e., they demonstrated a higher level of compensatory behaviour. This interpretation seems to be supported by the analysis of gross locomotion in males. These scores were consistent over the brood stages, Kendall concordance = 0.73, and collapsed into a single composite score. Cluster 1 males exhibited a significantly lower level of locomotion than Cluster 2 males (27.8 (17.8–31.9) versus 35.5 (33.4–44.6), $p = 0.029$, randomisation test). These differences cannot be ascribed solely to the behaviour of female within a given pair, because the two groups of females distinguished according to the cluster to which the male belonged, did not differ significantly in the time spent near offspring at either of the

brood stages (all five $p > 0.23$, but the ranges seem to differ between clusters, see Fig. 2).

These results clearly indicate that there are two alternative styles of male parental behaviour, which are revealed at the wriggler brood stage. Some males (Cluster 2 in our study) exhibit quite precise adjustment for the reduction of care on the part of the female, spending almost the same time in proximity of the brood as she does at the previous as well as subsequent brood stages. The absolute difference between their scores is very small. Other males (Cluster 1) however, show a significantly lower level of this compensatory behaviour. Furthermore, these two categories of males differ in their locomotor activity (which is chiefly associated with patrolling of the local area, see Zworykin, 1995), the former males showing significantly higher level. Thus, the two clusters seem to reflect differences in the overall level of parental investment.

The possible costs and benefits of these two alternative tactics are not yet known. However, assuming that both may involve similar overall (seasonal or lifetime) parental investment, one can speculate that they could differ in the parental effort per brood, and the adjusting males exhibit its higher level. In such a case, the low-adjustment males could compensate for their possibly reduced short-term reproductive success by, for example, a reduced pair bond and a higher frequency of mating. Additionally, a reasonable possibility is that the low-adjustment tactic is a weak form of parental desertion, and it has been shown (Wisenden, 1994) that under good conditions and low-predation pressure (as in our aquarium experiments) the cost of parental desertion to males is relatively low.

An important limitation of the present investigation is that fish from an aquarium population were studied, and a long history of living in absence of predators may have relaxed selection for parental care. A study of wild fish is required to substantiate the above evolutionary speculations, but domesticated stock provide a model of a natural low-predation population, for which parental desertion and the low-adjustment tactic, may be adaptive. Furthermore, anti-predator and parental behaviour are typically conservative and retained long time after the predation stress has diminished.

Acknowledgments

We thank two anonymous referees for their helpful comments on an earlier draft of this article. This study was supported by the Russian Foundation for Basic Research (project No. 96-04-49066).

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