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ORIGINAL ARTICLE

A. Manica

Alternative strategies for a father with a small brood: mate, cannibalise or care

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Abstract Brood cycling, the alternation of periods of courtship and mating activity ("mating phase") with days of full brood care ("parental phase"), and total filial cannibalism, the consumption of all current offspring by a parent, have been interpreted as a response to the conflicting demands faced by parental males during the breeding season. Under the assumption that these two behaviours result from trade-offs among mating, caring and feeding, the strategy adopted by the male should depend on egg number and age. This hypothesis was tested in the scissors-tail sergeant (*Abudefduf sexfasciatus*), a common tropical damselfish. Observations of undisturbed males and a brood reduction experiment confirmed all theoretical predictions. The shift from the mating to parental phase occurred when an appropriate number of eggs had been obtained. When the brood was reduced on the first day of the parental phase, males often reverted to the mating phase, but never did so if the manipulation occurred on the second or third day. Only broods that were smaller than average were consumed by the parental male. Artificial reduction of the brood increased the incidence of total filial cannibalism, but the probability of cannibalism decreased with brood age.

Keywords Parental care · Brood cycling · Total filial cannibalism · Abudefduf sexfasciatus

Introduction

Animals are often faced with conflicting needs, such as feeding, finding new mates and caring for their young. An extreme case of conflict is found in polygamous fish with exclusive paternal care, where males continuously have to choose among alternative strategies during the breeding season. Brood cycling, the alternation of periods of courtship and mating activity with days of full brood care, has been interpreted as a response to the conflicting demands faced by males (Perrin 1995; Sargent et al. 1995). Van Iersel (1953) was the first to describe a progressive loss of mating drive in male sticklebacks as egg age or number increases. Eventually, the male fully refuses to court females and spends most of his time caring for the brood until hatching. Van Iersel defined this period as the "parental phase" of the brood cycle, as opposed to the "mating phase", when eggs are obtained. Brood cycling has since been reported in many fish species [e.g. green sunfish *Lepomis cyanellus* (Hunter 1963); painted greenling *Oxylebius pictus* (DeMartini 1987); angel blenny *Coralliozetus angelica* (Hastings 1988); bicolor damselfish *Stegastes partitus* (Knapp and Warner 1991); and fathead minnows *Pimephales promelas* (Sargent et al. 1995)]. However, except for a recent investigation by Kraak et al. (1999) on the correlates of the duration of the mating phase in a field population of sticklebacks, no empirical study has specifically focused on the shift between the mating and parental phase during a brood cycle.

Filial cannibalism, the act of eating one's own offspring, can also be interpreted as a response to conflicting needs during the breeding season. In contrast to previous views, brood consumption has been argued to be adaptive if it balances the loss of foraging opportunities by the guarding male (Rowher 1978; Sargent 1992). Fathers can either eat only some of the eggs (partial filial cannibalism), or cannibalise the whole brood (total filial cannibalism). Whereas the former can be seen as a possible investment in the current brood by enhancing male condition, and thus its ability to provide parental care, the latter is a form of brood termination, and as such it can increase only future reproductive success. Total filial cannibalism is expected to occur when the value of the brood is low relative to the cost of parental care (Sargent 1992). Small broods should therefore be most commonly cannibalised.

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A. Manica (✉)
Large Animal Research Group, Department of Zoology,
University of Cambridge, Downing Street,
Cambridge CB2 3EJ, UK
e-mail: am315@cam.ac.uk
Tel.: +44-1223-336638, Fax: +44-1223-336676

Several field studies have confirmed this prediction (e.g. Petersen and Marchetti 1989; Petersen 1990; Forsgren et al. 1996). In a few cases, artificial brood reduction has also been shown to lead to increased rates of total filial cannibalism (Mrowka 1987; Petersen and Marchetti 1989; Lavery and Keenleyside 1990a). Optimal brood termination should also occur as early as possible to minimise the waste of parental effort on the aborted brood. Early brood termination has been reported in several species (e.g. Petersen and Marchetti 1989; Petersen 1990), but the hypothesis that the incidence of total cannibalism decreases with brood age was rigorously tested only by Lavery and Keenleyside (1990a) with a manipulative experiment on convict cichlids in the laboratory.

Despite the pioneering work of van Iersel (1953), who investigated brood cycling and made several observations on total filial cannibalism, these two behaviours have always been treated independently of each other. The dynamic model developed by Sargent et al. (1995) represents the only exception. This model further emphasises how brood cycling and filial cannibalism are linked, even though these two behaviours might be affected by different ecological factors. In this paper, I describe the natural shift from mating to parential phase during a brood cycle and the occurrence of total filial cannibalism in a coral reef fish, and subsequently test how these two behaviours are directly influenced by brood size and age.

Methods

Study site and species

This study investigated a population of scissors-tail sergeant (*Abudefduf sexfasciatus*) on the reef surrounding Cousin Island, Seychelles. The scissors-tail sergeant is a common damselfish inhabiting shallow coral reefs throughout the Indo-Pacific region (Allen 1991). *A. sexfasciatus* is omnivorous, but its diet is mostly based on plankton. This species is highly social, forming relatively large schools. Males show brood cycling and become territorial during each cycle, defending the nest from conspecifics as well as potential egg predators. During the mating phase, the males' body takes a golden coloration, and males invite females into the nest by performing a series of invitation swims or "jump" signals (Myrberg et al. 1967). Individual males use the same territory during each breeding attempt (Manica, personal observations). A single male can spawn multiple times during a single mating phase. Females lay eggs in a uniform monolayer, and individual clutches cannot be recognised (I define a clutch as all the eggs laid by one female during a single spawn). I use the term "brood" to refer to all the eggs found in a nest. Thus a brood can encompass more than one clutch. The approximate age of eggs can be estimated from their colour, as already described for *Abudefduf saxatilis* (Shaw 1955). Territories are clustered in discrete colonies that can include over 30 nests. Breeding is highly synchronised within a colony, but colonies on the same reef are out of phase (Manica, unpublished results). Females school all the time, visiting the male territories only to spawn and leaving immediately thereafter.

Breeding activity and filial cannibalism in a natural population

All the nests within an area of 50×20 m were individually marked and inspected twice a day, within 2 h from dawn and dusk, from 16 January to 29 March 1999 (except for 3 days in January when the sea was too rough for diving). A total of 33 nests were located during the study. Most males were recognised from natural markings, such as scars, and 12 individuals were marked with acrylic dyes to aid identification. The standard length was measured with a calliper (± 1 mm). During each dive, the identity of nesting males and their activities (cleaning the nest, mating or guarding) were recorded. The area covered by eggs was traced on a transparent plastic sheet with crayons. The tracings were subsequently scanned on a personal computer and the size of the brood was estimated with an accuracy of 1 cm^2 using SigmaScan Pro (SPSS Inc.). The area covered by differently aged eggs (determined by colour) was also estimated. In over 400 h of observations, only parrotfish were recorded to successfully predate on a large proportion of the eggs in the nests (Manica, personal observations). Wrasses and other small fish removed only a few eggs at a time. Conspecific cannibalism by unrelated individuals is very rare (Manica, unpublished data) and was not observed during this study. All instances of conspecific cannibalism I have ever observed involved non-nesting individuals (i.e. non-territorial males and females), which only managed to remove a few eggs before being evicted by the territorial male (Manica, unpublished data). Territorial males probably are unable to predate on others' nests, since they cannot leave their own nest without exposing it to both conspecific and heterospecific predation. Invertebrate predators, such as nudibranchs, were never observed to successfully feed on the eggs. Total filial cannibalism was observed on over 30 occasions, mostly by different males, and premature disappearance of a whole brood was interpreted as cannibalism by the father, unless parrotfish bite marks were present on the nest surface. Although this assumption may potentially result in the overestimation of filial cannibalism, it provides a solution to the impossibility of continuously watching all nests and has been adopted by several authors in the past (e.g. Petersen and Marchetti 1989; Petersen 1990; Hoelzer 1992).

Over the 3 months of this study, several brood cycles were monitored for each male, and males differed in the number of cycles. To account for the non-independence of the data, brood cycles of similar length were averaged for each male. Comparisons between cycles of different length were blocked for each male (either using paired *t*-tests or repeated measure ANOVAs).

Brood reduction experiments

Nests were selected between 2 February and 11 March 1999 for brood-reduction experiments outside the monitored area. Only males with a 2-day-long mating phase, the most common duration at the study site, were manipulated. A male was defined as having switched from the mating to the parental phase when the golden mating coloration was lost and no invitation swims were performed. Control nests of similar size to the treatment nests were chosen in the same colony. Each treatment nest was separated from its control nest by at least one undisturbed nest, to buffer any change in behaviour following manipulation. During manipulations, access to both treatment and control nests by the males was simultaneously blocked with nets (6.25 mm^2 mesh size, weighted on the sides with 50 g lead sinkers). In the treatment nest, approximately 75% of the eggs were removed by hand-brushing and allowed to be carried away by the current. Attempts were made to maintain the original proportion of differently aged eggs in each brood. Tracings taken after manipulations showed that brood reduction was accurate within 5% and that the proportion of differently aged eggs was kept within a 10% boundary. Only a few eggs (less than 5%) were removed from control nests to account for possible responses to substances released by broken eggs. Access to the nests was allowed 10 min after brood reduction, when fish activity around the nest had returned to normal levels. The nests were subsequently inspected twice a day until hatching, following the same procedure used to monitor the undisturbed nests. All manipulations were performed between 9:30 and 10:30 a.m. A total of 20 males had their brood reduced on the first day of the parental

Table 1 Time spent guarding the nest, number of nips, number of attacks and intrusions (mean±SE) during a 5-min focal following brood reduction. Wilcoxon sign-rank test for paired observations using a Bonferroni correction for repeated comparisons

Day of manipulation		*n*	Time guarding (s)	No. of nips	No. of attacks	No. of intrusions
1	Control	20	271.3±9.6 **	4.6±0.7 *	5.1±0.9	12.2+1.3
	Treatment	20	258.6±12.6	2.4±0.6	4.3±0.9	13.6+1.6
2	Control	10	290.9±3.4 **	1.6±0.5	4.6±0.4 *	11.7+1.2
	Treatment	10	272.8±3.9	0.4±0.3	2.9±0.7	10.9+1.7
3	Control	10	270.0±18.2 **	1.7±0.8	5.9±1.5	17.5+3.2
	Treatment	10	204.3±21.7	0.7±0.4	3.4±1.1	14.3+3.0
Pooled	Control	40	275.9±6.6 ***	3.1±0.5 **	5.2±0.6 **	13.4±1.1
	Treatment	40	248.6±9.2	1.5±0.4	3.7±0.5	13.1±1.1

* $P \leq 0.05$; ** $P \leq 0.01$;
*** $P \leq 0.001$

phase, ten on the second day, and ten on the third day. Due to the differences in sample sizes, the power of the tests varied for each manipulation. For this reason, and because of the very large changes in behaviour from day to day, behavioural data were pooled for all manipulations (see Table 1) and no comparisons were made between manipulations.

Focal observations (5 min duration) were conducted later on the day of manipulation (between 3:00 and 5:00 p.m.). The nests were never approached closer than 3 m to avoid disturbing the fish, and a hovering position at least 1 m above the bottom was adopted to avoid favouring the approach of potential predators. Fish were allowed to habituate for 10 min before the focal observations of each treatment-control pair were taken. The order of observation within each pair was random. The following activities were recorded using an underwater data-logger (Psion Workabout in a waterproof bag): guarding time (defined as the time spent within 10 cm from the eggs); number of nips to eggs; number of attacks to other fish; and the number of intrusions by other fish into a circular area of 0.5 m radius around the nest.

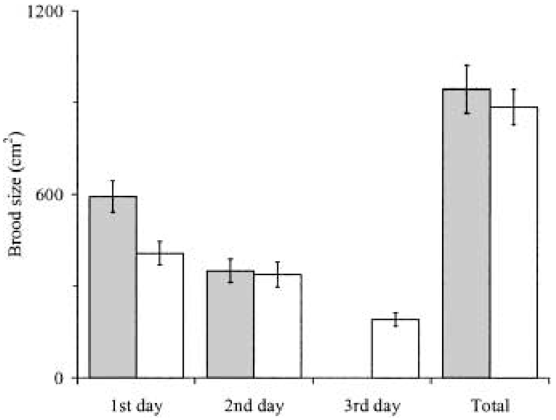

Fig. 1 Size of the broods (mean±SE) obtained during cycles with a 2- (*grey bars*) and 3-day (*white bars*) mating phase, using the averages of all broods of a given category obtained by each male. "*Total brood*" represents the total area covered by eggs at the end of the mating phase.

Results

Breeding activity and filial cannibalism in an unmanipulated population

A total of 156 brood cycles by 33 males were observed during the study (mean no. of cycles per male ± SE= 4.6±0.3; range = 1–7). Due to harsh weather that prevented diving, the outcome of 17 cycles could not be determined, and these were excluded from the analysis. The mating phase of most cycles lasted for 2 (74.3%) or 3 days (19.0%), with a few males mating for 1 (4.7%) or 4 days (2.0%) during one cycle. The parental phase lasted either 4 (72.9%) or 5 days (27.1%).

The average size of the broods obtained by a male in all the cycles with a mating phase of given length was used in all the following comparisons. Only mating phases of 2 or 3 days were considered, due to the low number of shorter and longer cycles. All males had at least one mating phase of 2 days, and 16 males also had at least one mating phase of 3 days. There was a significant decrease in the number of eggs acquired per day by a male during the mating phase (Fig. 1; cycles with a 2-day mating phase: paired t_{32}=6.95, P<0.001; cycles with a 3-day mating phase: repeated-measures ANOVA $F_{2,\,30}$=11.42; P<0.001).

Total size of the brood at the end of the mating phase did not differ between cycles with a mating phase of 2 or 3 days (Fig. 1; paired t_{15}=0.70; P=0.5). At the end of the second day of mating, broods from 2-day phases were significantly larger than those from 3-day phases (907±45.0 vs 745.7±58.9; paired t_{15}=2.16, P=0.047). This difference developed over the first day of mating, since first-day broods were significantly larger in 2-day phases than in 3-day phases (Fig. 1; paired t_{15}=3.55; P=0.003), but there was no significant difference between broods obtained on the second day (Fig. 1; paired t_{15}=0.23; P=0.8). No relationship was found between the length of the parental phase and the size of the current brood (paired t_{24}=-1.74; P=0.1).

Eleven out of 139 broods (7.9%) were cannibalised by eight of the males. All cannibalised broods were consumed during the first day of the parental phase. The size of the cannibalised broods was significantly smaller than that of the broods which were cared for by the same male (Fig. 2; paired t_7 on average broods= 4.25; P=0.004).

Brood reduction experiments

Following brood reduction, males spent on average less time guarding the nest, made fewer chases to predators and took fewer nips to the eggs than controls (Wilcoxon sign-rank test on pooled data: $Z \leq -2.95$; n=40; $P \leq 0.003$; Table 1). However, no difference could be found in the

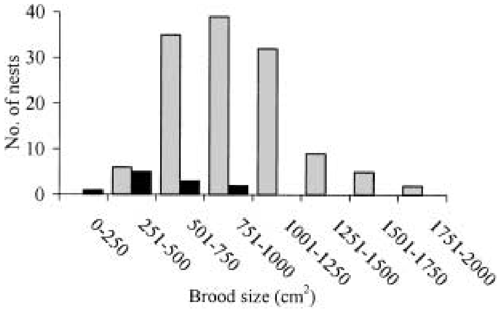

Fig. 2 Distribution of total brood sizes at the beginning of the parental phase, divided into "cared for" (*grey*) and "cannibalised" (*black*) broods.

Table 2 Number of males that cannibalised the brood or reverted to the mating phase following brood reduction. When the brood was manipulated on day 1, one of the males that reverted to mating also cannibalised his brood

Day of manipulation		*n*	Cannibalised the brood	Reverted to mating phase
1	Control	20	0**	1*
	Treatment	20	7	8
2	Control	10	0	0
	Treatment	10	2	0
3	Control	10	0	0
	Treatment	10	0	0

Fisher exact test: * *P* 0.05; ** *P* 0.01

number of intrusions by other fish (Wilcoxon sign-rank test on pooled data: Z=–0.14; n=40; P=0.89; Table 1). Control fish never cannibalised their broods, but males with broods reduced on the first or second day of the parental phase consumed their eggs on several occasions (Table 2). Males were less likely to cannibalise the eggs when the brood was reduced at a later stage of the parental phase than at the beginning (binary logistic regression: G=5.586; df=1; P=0.018). Within the treatment males with a reduced brood on the first day, there was no difference in standard length between individuals that cannibalised and those that did not (t_{16}=0.07, P=0.95). Males with the brood reduced during the first day of parental phase were more likely to revert to the mating phase than the controls (Table 2; Fisher exact test; n=40; P=0.02). No difference in standard length was detected between treatment males that attempted to remate and those that did not (t_{16}=0.54, P=0.6). When the males reverted to the mating phase, attempts to court females only lasted for the first day following the manipulation. Only two of the eight males that reverted to the mating phase were successful at obtaining further eggs. Yet, of the unsuccessful males, only one cannibalised his reduced brood, whereas the other five resumed brooding. Individuals whose brood was reduced on the second and third day never attempted to re-mate (Table 2).

Discussion

The data are consistent with the hypothesis that brood cycling in *A. sexfasciatus* is directly influenced by brood size and brood age. The shift from the mating to the brood phase occurred naturally when an appropriate number of eggs was obtained. When the brood was artificially reduced on the first day of the parental phase, courtship resumed in several males. Resumed courtship was never observed when manipulations occurred later in the mating phase, confirming that egg age limits the duration of the mating phase. These results are in accord with the early observations by van Iersel (1953) on sticklebacks. Kraak et al. (1999) also detected a significant effect of both brood size and age on the duration of the mating phase, but the latter disappeared when two outliers were removed. The results from the manipulation experiments confirm the theoretical predictions of Sargent et al. (1995) and Perrin (1995), based on trade-offs. Sargent et al. (1995) and Perrin (1995) adopted different assumptions regarding the trade-off between mating and caring in their models. Sargent et al. (1995) suggested that mating might increase predation risk for the existing brood, whereas Perrin (1995) postulated that the cost of fanning increases with brood size, and thus a male should stop collecting new eggs when the benefit of a larger brood is offset by the increased cost of parental care. The two models are not mutually exclusive as both mechanisms may operate simultaneously. No information is available on the costs of parental care in *A. sexfasciatus* and it is not possible to determine which model is most appropriate for this species.

During each brood cycle, the number of additional eggs obtained by a male decreased during the mating phase. A similar trend was observed by Kraak et al. (1999) in sticklebacks. Such a decline could be explained by a decrease in the mating effort of the male, as suggested by van Iersel (1953) for sticklebacks, or by female choice. Females in several species prefer to spawn in nests with young eggs (e.g. DeMartini 1987; Sikkel 1989; Reynolds and Jones 1999). This behaviour has been interpreted as a strategy to avoid the high risk of partial filial cannibalism faced by the youngest eggs in the nest. The two explanations are not mutually exclusive, and future studies on the dynamics of brood cycling will have to test specific predictions to distinguish between these two hypotheses.

The frequency of total filial cannibalism in *A. sexfasciatus* is well within the range found in other damselfishes (Hoelzer 1995). As expected from theoretical considerations, males consumed broods of low current reproductive value. Total filial cannibalism only occurred in smaller than average broods, and artificial brood reduction confirmed that this behaviour is a direct response to the number of eggs in the nest. Similar results had been obtained in a diverse array of fish species [another damselfish with paternal care (Petersen and Marchetti 1989), a maternal mouthbrooder (Mrowka 1987) and a biparental substrate-guarding cichlid (Lavery and

Keenleyside 1990a)]. I also provide the first evidence from a manipulative experiment in the field that the likelihood of cannibalism decreases as clutch age increases. The data obtained with *A. sexfasciatus* are analogous to those collected by Lavery and Keenleyside (1990a) on convict cichlids in the laboratory.

Filial cannibalism was elicited by the same conditions (low clutch size and age) that also favour an extension of the mating phase. Thus, the key question that remains to be answered is why parents with the same number of eggs chose different strategies. The answer probably resides in the nutritional status of the male, which was not controlled in my experiments. The relationship between filial cannibalism and energetics has proven very difficult to unravel (Sargent 1997), but Hoelzer (1992) and Kvarnemo et al. (1998) provide field and laboratory evidence that fed males eat fewer eggs than starved fathers.

The manipulation experiment on *A. sexfasciatus* emphasises the link between brood cycling and filial cannibalism, as expected from Sargent et al.'s model (1995). Despite the close match between theoretical predictions and empirical data, real fish are not constrained to a few alternative strategies. Filial cannibalism and the effort devoted to mating and caring for the brood can vary over a continuous range. *A. sexfasciatus* responded to brood reduction by decreasing parental effort, and a correlation between brood size and parental effort has been shown in several species (e.g. Carlisle 1985; Coleman et al. 1985; Sargent 1988; Ukegbu and Huntingford 1988; Lavery and Keenleyside 1990b). As suggested by Sargent (1992), dynamic resource allocation models, which take into account variable effort, would probably provide further insights in the dynamics of filial and brood cycling.

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