

Rising costs of care make spiny chromis discerning parents

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Abstract When the costs of parental care do not scale with the number of offspring being cared for, inclusion of non-descendant young into broods can be advantageous, leading to systems of alloparental care. However, if the cost of care scales with the number of offspring, selection may act against misdirected parental care. The spiny chromis, *Acanthochromis polyacanthus*, is a marine fish with extended biparental care, and broods that increase in size over the care period strongly suggest that alloparental care occurs in this species. However, *A. polyacanthus* parents directly provision their offspring by producing ectodermal mucus for their fry to feed on. The costs of such provisioning may scale with brood size, potentially increasing the costs of parental care. Using wild *A. polyacanthus* pairs, we tested whether foreign offspring are accepted into established broods, and measured how brood defence effort and mucal feeding scale with brood size. We found that *A. polyacanthus* discriminate between their own and foreign young, vigorously expelling experimentally introduced foreign offspring. Although defensive effort did not scale with brood size, mucal feeding was strongly dependent on brood size, and this increasing cost of care likely acts as the primary selective force on parental discrimination and rejection of foreign fry in *A. polyacanthus*.

Keywords Alloparental · Parental care · Costs · Marine · Fish · *Acanthochromis polyacanthus*

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Introduction

Parental care is defined as any behaviour by an individual that improves the survival of its offspring, while carrying a fitness cost to the parent (Trivers 1972). These costs often constrain brood size by placing an upper limit on a parent's postpartum ability to care for increasing numbers of offspring (Lack 1954; Wisenden and Keenleyside 1995). However, for many species the cost of care is the same whether a parent is caring for one offspring or for many (Clutton-Brock 1991). For example, the costs of defence of offspring within the parental territory may be independent of the number of offspring being cared for, because the risk of death or injury while guarding is constant throughout time and reproductive success will typically be bounded by the physiological constraints of egg production.

When the costs of care do not scale with the offspring number, there will not be strong selection against misdirected parental care of extra young. This can lead to alloparental care systems, in which parents care for non-descendant young, either due to errors in discrimination or because there are some benefits of extending care to unrelated offspring (Solomon and French 1997). In mammals and birds, the benefits of alloparental care typically accrued by the alloparent include reciprocal cooperation, increased parental experience or improved defence of resources (Riedman 1982). The benefits for the natural offspring are generally lower, as endotherms typically have relatively small brood sizes and the offspring are generally highly dependent on parental feeding. Hence, for endothermic-related young, any benefits of being part of an augmented brood are unlikely to outweigh the direct costs of decreased parental provisioning.

In contrast, the brood sizes of some ectotherms may be one or two orders of magnitude greater than in birds and mammals, and the incorporation of extra offspring into broods comes at a lower marginal cost to existing offspring.

Alloparental care is commonly observed in fish (Wisenden 1999), where the costs of care are typically fixed (Blumer 1982; Lazarus and Inglis 1986; Smith and Wootton 1995; but may also scale with brood size, Bakker et al. 2006), and inclusion of free-swimming fry into existing broods has been documented in a number of species (reviewed by Wisenden 1999). In high-predation environments, augmenting broods with conspecific or heterospecific young can improve natal offspring survival; though mechanisms such as predation dilution (McKaye and McKaye 1977) and selfish herd effects in which adopted young are pushed to the brood periphery where they are subject to greater predation risk (Burchard 1967; McKaye et al. 1992; Johnston 1994).

The spiny chromis, *Acanthochromis polyacanthus*, is rare among marine fish in that it provides extended biparental care to its offspring (Thresher 1983; Cooper et al. 2009), and there are suggestions that it may perform alloparental care (Thresher 1985a). However, there are numerous life history parallels between *A. polyacanthus* and freshwater fish species that display alloparental behaviour, in particular neotropical cichlids, with both groups having extended biparental brood care of free-swimming young, synchronous broods and spawning territories typically less than 3 m from other brooding parents (Thresher 1983, 1985b; Kavanagh 2000). Previous studies have shown that up to 12.9 % of wild *A. polyacanthus* broods had unexplained increases of more than 20 fry between hatching and 30 days post-hatching (Thresher 1985a), strongly suggesting that some *A. polyacanthus* parents incorporate foreign fry and perform alloparental care. It has also been shown that *A. polyacanthus* parents occasionally attack their own fry, driving them away from the natal territory (Thresher 1985a), potentially as an indirect form of *farming out* their offspring to other brooding parents, as seen in some cichlids (e.g. Yanagisawa 1985). Brooding pairs that drive away their first batch of fry do so exclusively at the beginning of the breeding season and are usually rapidly able to produce another brood (Nakazono 1993; Thresher 1985a).

However, *A. polyacanthus* parents also provide a form of care that may increase the costs of parental effort and, hence, select against misdirected care. *Glancing* or *contacting* behaviour is a form of supplementary ectodermal mucous feeding in which the fry rapidly approach the parents and bite at their flanks (Kavanagh 1998). Although the function of glancing behaviour in *A. polyacanthus* is not well understood, it seems unlikely that sufficient mucus is ingested to perform a significant nutritional role, and the level of glancing by fry is not related to their nutritional state (Kavanagh 1998). However, ectodermal mucus feeding in other species may facilitate the transfer of hormones between parent and fry (Schutz and Barlow 1997), or may have some immunological function (Sin et al. 1994). This form of feeding has also been observed in some new world cichlid species. Previous observations of the Midas cichlid (*Amphilophus citrinellus*) have shown that

when fry remain with parents longer than the normal brooding period, extensive wounds on the skin of parents can occur (Barlow 2000), demonstrating a potential cost of this form of care. More generally, parental feeding of young is typically a depreciable cost of care that will scale with the number or age of young in the brood (e.g. Wisenden et al. 1995). If glancing behaviour in *A. polyacanthus* carries a cost that outweighs any benefits of inclusion of non-kin fry, we expect brooding parents to confine parental investment only to direct kin.

An apparent paradox therefore exists, wherein natural *A. polyacanthus* pairs appear to include non-descendent offspring in their broods, but provide potentially costly care that should be restricted to kin. Coupled with the observation that brooding parents occasionally drive away their own broods, this raises the question of whether brood increases in *A. polyacanthus* are voluntary or forced. If non-descendant fry successfully enter a new brood, the original donor parents could parasitise the parental effort of acceptor pairs and may further increase their own reproductive output for the season by producing a new brood. In this case, acceptor parents would bear costs of care that scale with brood size and outweigh any benefits accrued from alloparental care. Alternatively, alloparental care in *A. polyacanthus* may be a voluntary predation dilution strategy by acceptor parents, which is possible as there are no costs to fry in terms of growth or survival in larger broods (Booth and Alquezar 2002). To address these questions, we sought here to determine whether wild brooding pairs of *A. polyacanthus* voluntarily accept foreign fry into their broods. We also measured how two aspects of parental care, brood defence and glancing behaviour, scaled with brood size to determine the costs of care for differently sized broods. Specifically, we tested the predictions that (a) brooding parents accept introduced foreign fry into their existing broods, (b) brood defence scales with brood size and (c) glancing behaviour scales with brood size.

Methods

We conducted field experiments at One Tree Island, Great Barrier Reef, Australia (23°30'29"S, 152°5'30"E), during October 2009 in One Tree Island lagoon. Using floats attached to nearby rocks, we marked the location of 20 pairs of adult *A. polyacanthus* that were guarding stage 2 fry (Kavanagh 2000) measuring between 10 and 15 mm standard length, at depths between 1 and 2 m. Because of the similar size of the fry, we can be confident that all fry used in this experiment were of similar ages. We photographed all fry using an underwater digital camera and later counted the number of fry in each brood from the photos using the average from three photos of each (Nakazono 1993). *A. polyacanthus* territories in our study were between 2 and 4 m from the nearest neighbouring pair, and fry that were

exchanged between pairs were at least 10 m apart and were not nearest neighbours. For experimental manipulations of brood size, fry were removed from brooding pairs using hand nets while snorkelling. Once caught, fry were immediately transferred into holding vessels made from 40 cm lengths of 15 cm diameter PVC tubing with mesh screens on each side to permit water flow and allow fry to continue feeding. These enclosures were placed 10 m away from the parents at the same depth, away from any other *A. polyacanthus* pairs. We did not observe parents leaving their territory in search of the removed fry.

Parental aggression towards descendant and non-descendant fry

Fry taken from removal treatment pairs (see below, $n=10$) and two further pairs (such that total $n=12$) were held as described above for between 180 and 240 min. A group of five fry was then reintroduced either to their own parents ($n=6$) or a foreign pair ($n=6$) by releasing the fry at a distance of 1 m from the existing brood. In all cases, the released fry continued to swim in the direction that they left the holding chamber and attempted to join the established brood. This method of introducing a small number of fry to established groups is consistent with previous studies of alloparental care in fishes (Fraser et al. 1993; Nelson and Elwood 1997). Foreign fry were size-matched to those originally being cared for by parents by directly comparing captured fry in underwater holding chambers. The number of attacks made by the parents to the introduced fry was then recorded for a period of 1 min, after which foreign fry were again collected and returned to holding vessels until reintroduction to natal broods at the termination of experiments. Foreign fry could easily be distinguished as they were never allowed within 50 cm of the resident fry. Because familiar fry were always accepted by the parents and incorporated into the brood, these could not be re-collected.

Parental effort in modified broods

We examined the defensive behaviour of parents and the feeding behaviour of fry before and after experimental removal of approximately 90 % of the brood. Natural differences in the numbers of fry within each brood were controlled for statistical analyses (see below, [Statistical methods](#)). The original experimental design included a fry addition treatment as a comparison to the fry removal treatment, but because parents rapidly distinguished and evicted the foreign fry (see “Results”), this additional treatment was not realised. Each pair was observed for 10 min per observation from a distance of approximately 2 m by the same observer. Parents within each pair were distinguished by

body size and fin or scale damage, and separate measures were recorded for each; however, *A. polyacanthus* are sexually monomorphic, and the sex of the parents could not be determined by observation of the external morphology. We measured the number of defensive acts (chasing and biting) by parents towards heterospecifics and adult conspecifics, the average distance of the parents from the centre of their brood, and the number of glancing/contacting attempts performed by fry. Separate measures for defence against heterospecifics and conspecifics were taken because we expected that approaches by heterospecifics to the nest were likely to be primarily concerned with pre-dating the fry, whereas approaches by conspecifics may have a social function. Combining these two measures of defence into a single variable did not alter the qualitative results of statistical analyses. After initial measurements, fry were removed from pairs and transferred to the holding containers as described above. Fry from the control pairs were removed in the same manner, but returned to their parents after 3 min to control for disturbance. Four pairs were measured each day (total of $n=20$), with two pairs per treatment. Each parent within the pair was observed for 10 min, after which fry were experimentally removed. Pairs were then left undisturbed for 20 min after which a second 10-min observation was taken, such that the two behavioural observations on each group were taken approximately 1 h apart.

Statistical methods

Statistical analyses were conducted using SPSS 20. Parental aggression data towards descendant and non-descendant offspring were transformed using fourth root transformations to satisfy the assumption of normality and tested by comparing the frequency of attacks per fry using t tests with equal variances not assumed. Parental care data and their residuals were found to be normally distributed. Parental behaviour was therefore analysed using repeated measures general linear mixed models, comparing measurements before and after treatment applications with treatment (removal/non-removal) included as a main effect. Because pairs naturally had different brood sizes, causing the remaining number of fry after removal treatments to vary, we included *number of fry* in each group as a covariate in the general linear model (GLM), allowing us to directly test the influence of fry number on parental behaviours. Differences in the level of care from each parent were assessed by comparing defence and glancing behaviour of the parent nearest to the centre of the brood cloud to the parent furthest from the brood cloud during the 10-min observation period. Paired t tests were performed within each replicate brood. Pairs in which parents were equidistant from the brood were omitted from this analysis.

Results

Parental aggression towards introduced fry

A. polyacanthus parents attacked the unrelated fry significantly more frequently than their own fry after a period of separation of between 3 and 4 h (attacks per unrelated offspring introduced, $X=1.14$; attacks per related offspring introduced, $X=0.013$; t test, equal variances not assumed; $t=7.82$, $df=4.583$, $P=0.001$). In many cases, parents chased unrelated fry so far from their own territory that we had to recollect the fry before the 1 min observation period was over in order to protect them from predation. In these cases, the total number of attacks before recapture was used in analyses, providing a more conservative estimate of aggression towards foreign fry.

Parental care

Experimental removal of fry did not influence the level of parental defence against either conspecific or heterospecific intruders (Fig. 1), and there was no interaction with the number of fry within each brood (Table 1). There was no effect of experimental treatment or number of fry on the average distance parents stayed from the centre of the brood (Table 1). However, the frequency of glancing was significantly lower in experimentally reduced broods (Fig. 2), and we found a significant interaction effect with the number of

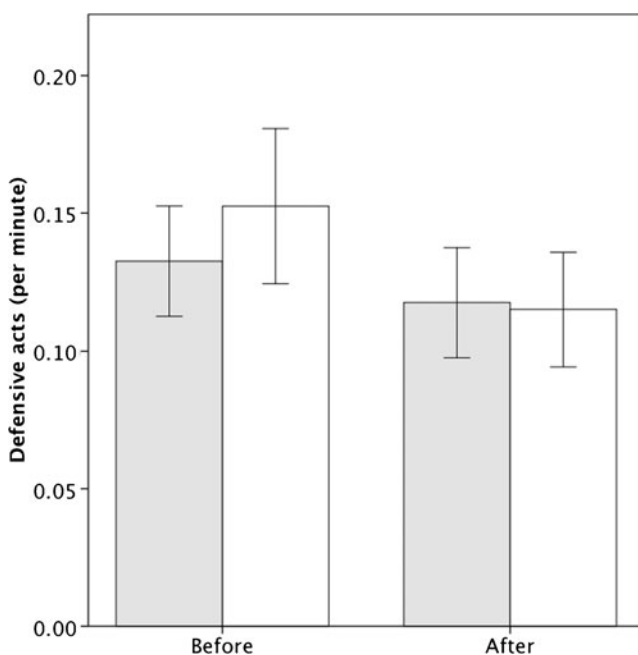


Fig. 1 The frequency of defensive acts directed towards conspecifics and heterospecifics (combined for presentation) before and after sham removal of fry (control groups, shaded bars) or 90 % reduction of brood size (treatment groups, open bars). Values are mean frequency per minute \pm SE

fry within the brood (Table 1). We found a significant linear relationship between the number of fry in each brood and the frequency of glancing received by parents ($R^2=0.746$, $F_{1,18}=52.796$, $P<0.001$; Fig. 3).

Differences in care between parents

The level of care between parents was not balanced. Before experimental manipulation of brood, the parent that was nearer to the centre of the brood engaged in more defensive acts and received more glances (defence, $t=3.900$, $df=17$, $P=0.001$; glancing $t=3.328$, $df=17$, $P=0.004$). After experimental removal of fry, the nearer parent still received significantly more glances ($t=4.405$, $df=12$, $P=0.001$); however, the differences in defensive behaviour became non-significant ($t=0.94$, $df=12$, $P=0.366$).

Discussion

Previous studies have reported rapid unexplained increases in offspring numbers of brooding pairs of *A. polyacanthus*, suggesting that brood amalgamation occurs in this species (Thresher 1985a). Combined with the ecological factors that predispose *A. polyacanthus* to brood amalgamation, (extended biparental care, synchronous broods, nearby spawning territories; Thresher 1983, 1985b; Kavanagh 2000), we expected that brooding parents would accept experimentally introduced foreign fry. However, we found that *A. polyacanthus* pairs showed a strong aversion to incorporation of foreign fry into their broods, rapidly rejecting introduced foreign fry while accepting kin offspring even if these had been kept separate for up to 4 h. Examining two facets of parental care in *A. polyacanthus*—brood defence and glancing behaviour—we found that the defence effort was not related to brood size, while the amount of glancing behaviour was dependent on brood size. Glancing is a form of somatic investment provided by brooding parents which likely increases the costs of misdirected care in *A. polyacanthus*, potentially acting as a barrier against voluntary alloparental care. Finally, we found that parental effort was not equally distributed between the parents. The nearer parent had higher levels of defence and glancing before removal of fry and continued to receive higher levels of glancing after fry removal. This imbalance potentially reflects differences in the level of care between the sexes (although this could not be determined in this sexually monomorphic species), which may influence how the potential costs of increased brood size are realised in males and females. Even if this imbalance is not sex-related, it raises the possibility that intra-pair parental conflict occurs in this species.

Rejection of fry followed a stereotypical pattern of parental aggression which has been reported previously in

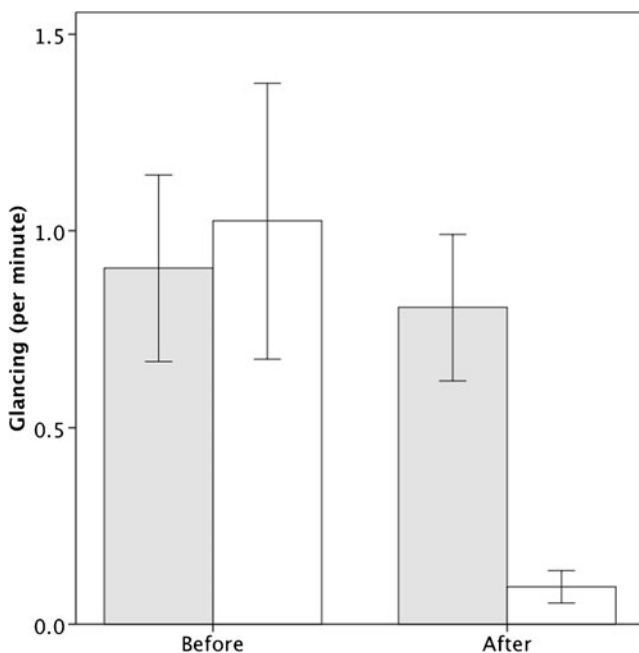
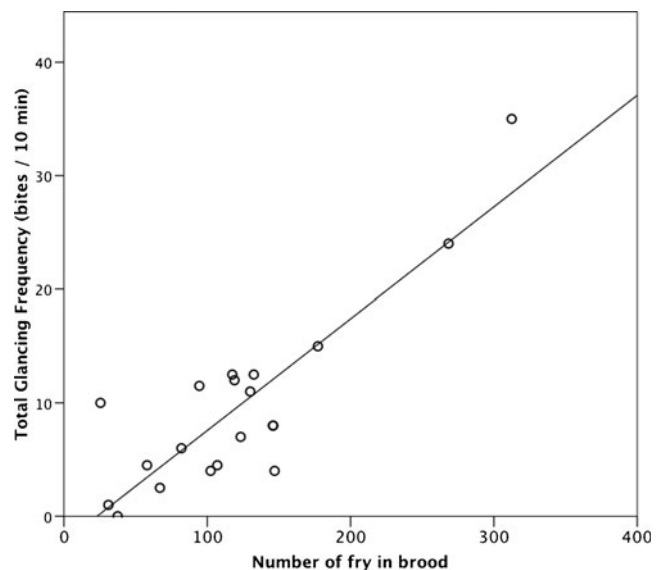
Table 1 Results from repeated measures GLM analysis on the frequency of behaviours: parental defence against heterospecifics, parental defence against conspecifics, glancing (or contacting) by fry towards parents and the average distance of parents from the centre of the territory

	Before and after removal of fry \times no. of fry			Before and after removal of fry \times treatment		
–	Wilks' λ	F_{df}	P	Wilks' λ	F_{df}	P
Defence (heterospecific)	0.917	3.338 _{1,37}	0.076	1.00	0.12 _{1,37}	0.912
Defence (conspecific)	0.981	0.702 _{1,37}	0.407	0.987	0.470 _{1,37}	0.497
Glancing	0.709	15.184 _{1,37}	0.001	0.792	9.699 _{1,37}	0.004
Average range	0.943	2.240 _{1,37}	0.143	0.993	0.249 _{1,37}	0.621

Analyses were conducted separately for each response variable

parental fish of this species towards their own brood (Thresher 1985a). In our experiments, one or both parents would rapidly approach and orient their own bodies at a 60° lateral angle to the introduced fry. Parents would then return to upright if the introduced fry were their own and allow them to return to the brood, but would remain at an angle and begin to attack and drive away foreign fry. Brooding parents commonly use olfactory cues to distinguish descendant and non-descendant young (e.g. Loiselle 1983; see also review in Wisenden 1999), and the young may orient to their parents using a combination of olfactory and visual cues (Wisenden and Pye 2009). *A. polyacanthus* parents may use olfactory cues to distinguish their own offspring, and the stereotypical angled approach to incoming fry may aid olfactory assessment of fry. It is also possible that parents assess the degree of relatedness of fry and accept closely related (though non-descendant) kin while rejecting non-kin or accept fry

from neighbouring broods which may have more similar olfactory cues (e.g. Ward and Hart 2003; Neff 2003; Mehrlis et al. 2010). In many cichlid species, parents reject foreign fry that are larger than their own while accepting fry that are of similar size or smaller size (Wisenden and Keenleyside 1992), most likely because of increased predation risk to smaller fry within groups or risk of cannibalism from larger fry (Fraser et al. 1993). However, it is unlikely that *A. polyacanthus* parents in our study were rejecting foreign fry based on size differences, as all introduced foreign fry were size-matched to the original brood. Nevertheless, there may have been small differences in the sizes of fry that we did not detect, but which were discernable to the parents and allowed them to identify foreign fry. To precisely determine the mechanism by which parents distinguish non-kin fry, experimental manipulations of the size of introduced foreign fry should be carried out to determine whether parents accept or reject foreign fry based on size differences or olfactory cues.

**Fig. 2** The frequency of glancing behaviour (a form of mucophagy by fry feeding on the flanks of parents) before and after sham removal of fry (control groups, shaded bars) or 90 % reduction of brood size (treatment groups, open bars). Values are mean frequency per minute \pm SE**Fig. 3** The total frequency of glancing behaviour per ten-minute observation period, towards both parents combined, as a function of brood size, with line of best fit. The statistical relationship between variables remains significant with the removal of the two largest values

We found that brood defence was constantly high, independent of our manipulations of the fry numbers. The high-predation environment on the reef means that undefended fry are rapidly killed, sometimes within minutes (Thresher 1985a), and even fry defended by a single parent do not survive more than a few days (Nakazono 1993). We found that parental defence was continuous and that almost all passing fish were attacked as they neared the brood. We therefore conclude that parents invest maximally in defence rather than modifying the level of defence as a function of brood size. This interpretation is consistent with the findings from a freshwater species that also performs alloparental care. In the convict cichlid, parents continue to show high levels of brood defence even when nest sites have had all fry experimentally removed and continue to defend nest sites for up to 10 min post-removal (Wisenden et al. 2008), suggesting a lag between brood loss and any subsequent behavioural modification. It is possible that *A. polyacanthus* parents in our experiments had not yet detected changes in their brood size and adjusted their behaviour accordingly, but this seems unlikely, given that our measurements of brood defence were taken an hour after fry removal.

Our finding that brood defence did not change with brood size in *A. polyacanthus*, in combination with previous studies showing that the growth, condition, and survival of *A. polyacanthus* fry is not affected by brood size (Booth and Alquezar 2002), gave us strong a priori reasons to expect alloparental care in this species. However, we found that a unique aspect of parental care in *A. polyacanthus*, glancing, linearly increased with the number of fry in the brood and may increase the costs of misdirected care. Glancing involves the offspring rapidly approaching parents and biting at their flanks, ingesting small amounts of mucus, and has been reported for fewer than 30 species of fish, almost entirely confined to neotropical cichlids (Noakes 1979). Each *A. polyacanthus* juvenile may glance as often as 12 times per day, each time removing a small amount of ectodermal mucus (Kavanagh 1998). The small amount of mucus consumed, together with the finding that glancing rate is not correlated with hunger levels, suggests that mucophagy in this species does not play a nutritional role, but may serve an immunological role (Kavanagh 1998). Because the parent glanced upon typically remains within the centre of the brood cloud, it is surrounded by fry and therefore has little control over which individual feeds from its flanks. While the parent may be able to terminate glancing completely by moving away from the brood, it is very unlikely it can control whether kin or non-kin to perform glancing if the brood contains unrelated fry.

A. polyacanthus broods typically number in the hundreds, meaning that each parent may receive thousands of bites from fry each day. We commonly observed visible damage to the mucous coat of brooding parents, and

previous observations of the Midas cichlid (*A. citrinellus*) have shown that mucal feeding by fry can lead to extensive wounds on the skin of parents (Barlow 2000), suggesting a potential cost of this form of care. Because the amount of glancing in *A. polyacanthus* is dependent on brood size, it is the most likely candidate for a cost of misdirected parental care. As such, glancing behaviour appears to be the primary selective pressure acting on parental discrimination and rejection of foreign fry in *A. polyacanthus*. However, more work is required to fully explore the relationship between the costs of glancing behaviour and increasing brood sizes. Although wild pairs did not accept foreign fry, precluding our ability to experimentally increase brood size, aquarium experiments may succeed in increasing brood sizes and examine whether costs of care become prohibitive as brood sizes increase. Further, captive experiments have the potential to directly measure the costs of parental care in this species, whether as behavioural trade-offs loss of condition (Smith and Wootton 1995), or lifetime growth costs (e.g. Jordan and Brooks 2010).

Given that we observed absolute rejection of foreign fry by brooding parents and costs of care that should preclude alloparental behaviour, how can the increases in wild brood sizes previously documented (Thresher 1985a) be explained? Although our addition of foreign fry followed established methods (Fraser et al. 1993; Nelson and Elwood 1997), it is possible that our groups of introduced fry were too small to successfully overcome parental defence. When tens or hundreds of foreign fry are driven from their own territory and enter a new territory, there may be too many fry for the resident parents to effectively deter. Once a larger group of foreign fry enter the territory, it is possible that olfactory signals become overwhelmed, preventing parents from discriminating between related and unrelated young. A similar pattern has been suggested for discrimination of foreign eggs by stickleback males (Mehlis et al. 2010). In our own pilot experiment, we found that when related fry had been kept in close proximity to unrelated fry, they were occasionally attacked when reintroduced to parents, possibly as a result of mixed olfactory signals. While *A. polyacanthus* parents have a strong aversion to accepting foreign fry due to the increased somatic costs of caring for larger broods, it is possible that brood amalgamation occurs involuntarily, with intriguing consequences for the development of alternative parental care pathways. Previous work has shown that parents who drive away their own broods typically do so early in the breeding season and are usually able to produce another brood (Nakazono 1993; Thresher 1985a). While incorporation of extra fry increases the costs of care for the accepting parents, it frees the donor parents from the costs of care. The observed increases in brood size of wild pairs may therefore be an involuntary consequence of social parasitism in this remarkable marine species.

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Ethical standards Australian ethics approval for this study was granted by the University of Sydney's Animal Ethics Committee (L04/9-2008/1/4877). After all observations were completed, the remaining fry were returned to their original parents, being accepted in all cases. Fry were in holding vessels for no longer than 300 min, and no deaths were recorded while in captivity.

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