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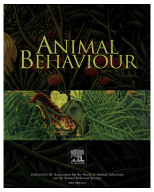

Factors influencing cannibalism in the plainfin midshipman fish

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Cannibalism of young is a common yet seemingly paradoxical phenomenon observed across a wide variety of taxa. Understanding this behaviour in the context of parental care remains a challenge for evolutionary biologists. A common adaptive explanation for the consumption of offspring is that it serves to increase the current or future reproductive success or survival of the cannibalistic parent by replenishing energy stores and facilitating continued care for any remaining young. Another explanation is that cannibalism may be a competitive response to cuckoldry or lowered certainty of parentage. We tested these ideas using the plainfin midshipman fish, *Porichthys notatus*, a species with an extended period of male-only parental care and documented offspring cannibalism. We found that the occurrence of cannibalism was not linked to the deterioration of body condition, but instead was most frequent during periods of high intrasexual competition and nest take-overs. Our results suggest that cannibalism is not driven by the energetic demands of parental care, but instead by competition among males for nests and females, and the resulting low paternity stemming from both nest take-overs and cuckoldry.

Cannibalistic behaviour has been observed in a vast range of taxa throughout the animal kingdom (Elgar & Crespi, 1992; Polis, 1981; Smith & Reay, 1991; Soulsby, 2013). Predation upon conspecific offspring has been widely documented across species, even for those that provide a high degree of parental care (Elgar & Crespi, 1992; Polis, 1981). In most caregiving species, parents invest considerable time and resources into offspring production, protection and growth, so cannibalism of offspring appears counterproductive to the goals of a caregiving parent. Evolutionary theory suggests that even with filial cannibalism, the acute loss of current reproductive success associated with the consumption of one's own offspring can be offset by future fitness benefits to the cannibal (Elgar & Crespi, 1992; Manica, 2002; Polis, 1981; Rohwer, 1978; Smith & Reay, 1991). For example, by recouping energy stores through filial cannibalism, the cannibal can prevent starvation, increase its ability to attract better or more mates, or ensure continuity of care (Rohwer, 1978; Sargent, 1992). While recouping energy presents one explanation for filial cannibalism, both empirical and theoretical studies suggest that the occurrence of offspring cannibalism across species may be driven by a variety of differing selective factors (e.g. Gray, Dill, & McKinnon, 2007; Klug & Bonsall, 2007; Klug, Lindström, & St Mary, 2006; Manica, 2002, 2004). Thus, the evolutionary function and origins of this behaviour remain an active area of study.

Starvation or dwindling energy reserves is one of the most studied driving factors for a parent to cannibalize their own offspring (Manica, 2002). This energy-based hypothesis predicts that cannibalism will increase as parental body condition deteriorates (Rohwer, 1978; Sargent, 1992). The energy recouped through filial cannibalism can be invested into future reproductive attempts, or into the continued care for the remaining offspring (Rohwer, 1978; Sargent, 1992). This hypothesis has been tested empirically in a number of different species. Kvarnemo, Svensson, and Forsgren (1998) showed that supplemental feeding in the laboratory could decrease egg cannibalism in the common goby, *Pomatoschistus microps*. However, supplemental feeding had no effect on either the number of eggs cannibalized in threespine stickleback, *Gasterosteus aculeatus* (Belles-Isles & FitzGerald, 1991), or in the fantail darter, *Etheostoma flabellare* (Lindström & Sargent, 1997). In addition, field studies have also shown that supplemental feeding cannot abolish filial cannibalism in Cortez damselfish, *Stegastes rectifraenum* (Hoelzer, 1992), or a species of Mediterranean blenny, *Aidablennius sphinx* (Kraak, 1996). Therefore, empirical support for the energy-based hypothesis is currently mixed (Klug & Bonsall, 2007; Manica, 2002).

In contrast to filial cannibalism, nonkin cannibalism of another individual's offspring can be viewed as a form of competition. For example, a male can increase his own condition and fitness at the expense of a rival's reproductive success by eating the offspring sired by a competitor (Bertram, 1975; Polis, 1981; Smith & Reay,

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1991). For numerous species of fishes, nest take-overs have been documented, wherein a competitive individual displaces a resident for its nest or territory, gaining control over it (Coleman & Jones, 2011). As offspring in a newly acquired nest or territory are typically sired by previous residents, the take-over victor will suffer no direct fitness costs by consuming them (Coleman & Jones, 2011; Sargent, 1989). In the same vein, an association between low paternal certainty and filial cannibalism has been shown in several fish species. For example, in the scissortail sergeant, *Abudefduf sexfasciatus*, the near proximity of potential cuckolder males resulted in increased cannibalism of eggs from a caregiving male's brood (Manica, 2004). Male caregivers of both bluegill sunfish, *Lepomis macrochirus* (Neff, 2003a) and threespine stickleback (Frommen, Brendler, & Bakker, 2007) are able to use direct offspring cues to assess their level of paternity over a brood and cannibalize more often when nonkin offspring are present. Even male *Telmatherina sarasinorum*, a species that does not provide parental care, will cannibalize their broods more often if cuckolders are present during spawning (Gray et al., 2007). Still other studies have been unable to show a relationship between paternal certainty and offspring cannibalism (e.g. common goby, *P. microps*: Svensson, Magnhagen, Forsgren, & Kvarnemo, 1998; sand goby, *Pomatoschistus minutus*: Svensson & Kvarnemo, 2007).

Hypotheses for cannibalism as an energy-replenishing tactic and as a competitive tactic are not necessarily mutually exclusive. However, their relative importance within a single study system has not been previously assessed. We tested these two hypotheses in the plainfin midshipman fish, *Porichthys notatus*. This species is a useful model to investigate cannibalism of offspring for a variety of reasons. First, nest-guarding males have a protracted and a presumably energetically taxing parental care period (Craig, Fitzpatrick, Walsh, Wood, & McClelland, 2014; Sisneros, Alderks, Leon, & Sniffen, 2009), which may select for cannibalism as an energy-replenishing strategy. Second, these males compete intensely with each other over nesting sites and access to mates (Cogliati, Balshine, & Neff, 2014; Cogliati, Neff, & Balshine, 2013). In combination with the expression of alternative male tactics, males consequently have surprisingly low levels of paternity in broods that they care for in the wild (on average 52%; Cogliati et al., 2013). This could select for cannibalism as a competitive strategy. Third, male midshipman fish have been documented with conspecific offspring in their digestive tracts (Cogliati, Danukarjanto, et al., 2014; Sisneros et al., 2009), however, the driving factors behind this cannibalism remain unknown.

We examined cannibalism across the long midshipman breeding period, which spans over 3 months (May–July) of care (Cogliati et al., 2013). We explored whether the prevalence of cannibalism changed across the breeding season and whether cannibalism was linked to patterns of energy loss or competition. If caregiving males cannibalize as a result of depleting energy reserves, then we predicted that cannibalism would increase over the breeding season as paternal body condition deteriorates (Sisneros et al., 2009). Alternatively, if cannibalism is a competitive tactic, then we predicted that it would be most frequent early in the season, when male–male competition is most intense (Cogliati et al., 2013). Consequently, the plainfin midshipman system provides the chance to explore cannibalism in a multifaceted way, allowing us to consider both energy-based and competition hypotheses in one species.

METHODS

Study Species

The plainfin midshipman is a marine toadfish (family Batrachoididae) distributed along the west coast of North America, from California to Alaska (Arora, 1948; Miller & Lea, 1972; Walker & Rosenblatt, 1988). Two alternative male reproductive tactics have been well described in this species (Bass, Horvath, & Brothers, 1996; Brantley & Bass, 1994; Brantley, Wingfield, & Bass, 1993; Cogliati et al., 2013; Lee & Bass, 2004). At the onset of the breeding season, large nest-guarding males (also known as type I) migrate to the intertidal zone, where they excavate a nesting cavity in the soft sediment beneath large rocks (Arora, 1948). As the tides retreat, these guarder males do not leave their nests, even as the small pools of remaining water become hypoxic (Craig et al., 2014). Males can endure these hypoxic conditions through metabolic suppression, a switch to anaerobic pathways (Craig et al., 2014) and a well-adapted system for acid–base regulation (Perry et al., 2010). The guarder males produce an acoustic signal with a specially adapted swim bladder encased in a sonic muscle capable of generating long-duration, low-frequency vibrations (Bass & Marchaterre, 1989; Sisneros & Bass, 2003) to attract gravid females to their nests (Brantley & Bass, 1994; Brantley et al., 1993; Ibara, Penny, Ebeling, van Dykhuizen, & Cailliet, 1983). Typically, the largest males acquire the largest nests and attract the most females (DeMartini, 1988; Fitzpatrick et al., n.d.). Females deposit their entire clutch of eggs (typically 150–300 eggs; A. P. H. Bose & K. M. Cogliati, personal observations; DeMartini, 1988), in a monolayer on the underside of the rock, which is the roof of the nesting cavity (Arora, 1948). Nest-guarder males care for offspring by cleaning, digging and maintaining the nest, fanning the eggs during high tide, hydrating the eggs during low tide, and defending them against egg predators and male competitors (Arora, 1948). Offspring take approximately 60 days to develop into free-swimming juveniles, but because males often continue attracting females, and care for young of various developmental stages, the care period can be longer than 60 days for males of this species (Cogliati et al., 2013), beginning in late April and continuing until early August (Cogliati et al., 2013; Crane, 1981; DeMartini, 1988).

While guarder males care for offspring and court females, sneaker males (also known as type II males) are also present in the population. These smaller males do not build nests, court or provide parental care. Instead, they attempt to fertilize eggs through stealth and sneaking behaviours, whereby they release their sperm while a guarder male spawns with a female (Brantley & Bass, 1994). Interestingly, guarder type I males are sometimes behaviourally flexible and have been observed to cuckold other guarder males (Cogliati, Balshine, et al., 2014; Cogliati et al., 2013; Lee & Bass, 2004). Presumably, this occurs when these males have no eggs in their own nest. If detected, cuckoldry attempts by type I guarder or type II sneaker males or the mere presence of other males in the nest will decrease the nest-guarding male's certainty of paternity over his brood.

Field Observations

A total of 166 plainfin midshipman nests were located between May and July 2013 in the intertidal zone of Crescent Beach (South Surrey, BC, 49°04′N, 122°88′W), a long rocky shoreline that supports a large population of spawning plainfin midshipman. It is a productive, well-sheltered spawning ground with many large rocks that are used as nesting sites, and large nearby eelgrass beds that likely serve as a nursery habitat for newly hatched juveniles. We sampled nests during three periods over the breeding season (23–26 May, 22–26 June, 19–24 July), which corresponded to the early, mid and late breeding season, respectively.

During each period, we checked nests using a short 2-day protocol (consecutive days) to minimize the likelihood of nests gaining new eggs between sampling days or losing nests from unanticipated factors such as predation. On day 1, we laid out 20 m transects parallel to the shore and located nests by overturning all suitable rocks (i.e. rocks that were sufficiently large and not too embedded into the substrate; see Cogliati, Mistakidis, et al., in press) within 2 m of either side of these transects. Each nest that contained a guarding male and offspring was considered an active nest and marked with a labelled numbered tent peg. A digital photograph was taken of such nests (Olympus digital camera TG-820, 12.0 megapixels). For each nest, we recorded the number, sex and tactic type (guarder versus sneaker) of each fish, tagged all fish with a nontoxic injectable elastomer (Northwest Marine Technology, Inc., Shaw Island, WA, U.S.A.) for future identification, and weighed (total mass to the nearest 0.1 g) and measured (total and standard length to the nearest 0.1 cm) them. On the next day, day 2, we returned to these nests, lifted the rock and took a second photograph. We noted whether the resident guarder male from the previous day was still in the nest, if the nest had been abandoned, or if a new untagged guarder male was in the nest (classified as a ‘nest take-over’). If the original guarder male from day 1 as well as a new untagged guarder male were both present, we noted the presence and position of the second male, and classified these events as ‘attempted take-overs in progress’. All digital photographs from day 1 and day 2 samplings were analysed using ImageJ software (v1.45, http://rsbweb.nih.gov/ij/) to quantify the number of offspring in each nest and the size of the nest (total surface area available for egg laying, cm^2).

We determined cannibalism by the guarder male in two ways: (1) by comparing photographs of nests taken on day 1 versus day 2 and noting whether offspring had disappeared; (2) by examining stomach contents of a sample of the fish for the presence of embryos. Thus, every fish in our data set was marked as either a cannibal (showing evidence of recent cannibalism) or a noncannibal (showing no evidence of recent cannibalism).

Data and Statistical Analyses

In total, we sampled 166 nests and collected data on the presence or absence of guarder males, sneaker males, females and any additional guarder males that appeared to be cuckolding or attempting a take-over in these 166 nests. Sample size varied between analyses depending on the measures included in the models (e.g. number of nests, number of fish of a particular sex or tactic, number of fish dissected to examine stomach contents, etc.) and the number of fish sampled (i.e. we were unable to obtain some measures from some individuals; a summary of sample sizes used in each analysis is given in Table 1).

We assessed how a number of variables changed across the breeding season, combining linear and generalized linear models for estimating parameters with permutation tests based on the same models to obtain accurate *P* values. For count responses (e.g. number of sneaker or additional cuckolding guarder males found in nests), we used a generalized linear model (GLM) with a negative binomial response, appropriate for overdispersed data (Bolker, 2008; MASS package, version 7.3.31, Venables & Ripley, 2002). For binary responses (e.g. the occurrence of nest take-over events or cannibalism), we used a binomial GLM (logistic regression). In both cases we compared the fit of the model that included a parameter for sampling time with a null model that excluded it, and repeatedly estimated the change in deviance between models (Δdev) for 1000 random permutations of the data. The *P* value was computed as the fraction of Δdev values for permuted data that were greater than or equal to the observed Δdev.

We assessed changes in body condition over the breeding season using two common indices: (1) a residual condition factor (RCF), which uses residuals from a regression of ln total body mass (g) against ln standard length (cm) (Blackwell, Brown, & Willis, 2000; Fechhelm, Griffiths, Wilson, Gallaway, & Bryan, 1995); and (2) a hepatosomatic index (HSI), calculated for all dissected fish ($N = 123$), by regressing ln liver mass (g) against ln eviscerated body mass (total body mass − digestive tract mass) and using the residuals as an approximation of the HSI. We used ANOVAs to compare body condition (RCF and HSI) across sampling periods (early, mid, late season) and binomial logistic generalized linear models (GLMs) to test for a relationship between cannibalism and body condition (RCF and HSI).

To assess how competition changed over the breeding season, we used several indicators of male–male competition. First, we used the permutation tests described above to investigate whether the number of sneaker males or additional guarder males in nests (count response variable) or the frequency of nest take-over events (binary response variable) changed over the season. Second, we explored the intensity of male competition for nests by testing the strength of the correlation between guarder male size (standard length) and nest size (surface area) within each sampling period using ordinary least squares regression. We also tested for an interaction between guarder male size and sampling period using an ANCOVA. If competition for nests is strong, as suspected, then we predicted a size-dependent distribution of males among nests.

To examine whether the incidence of cannibalism (i.e. proportion of fish within the population that show evidence of cannibalism) varied across the breeding season, we used the permutation tests described above (binary response variable). We also used binomial logistic GLMs to test for a relationship between nest take-over events and cannibalism. All analyses were performed in R version 2.15.1 (R Development Core Team, 2012) and significance was assessed at $\alpha = 0.05$.

Table 1
Summary of sample sizes used in each analysis

Analysis	Statistical test	*N*	*P*
Guarder male size vs			
Nest size across the breeding season	OLSR	164	0.004
Nest size between sampling periods	ANCOVA	164	0.001
Offspring number across the breeding season	OLSR	159	<0.0001
Body condition (residual condition factor) vs			
Time	ANOVA	185	<0.0001
Cannibalism in early season	GLM	45	0.58
Cannibalism in mid-season	GLM	52	0.009
Body condition (hepatosomatic index) vs			
Time	ANOVA	122	0.01
Cannibalism in early season	GLM	32	0.15
Cannibalism in mid-season	GLM	45	0.036
Females			
Observed across time	Permutation	166	<0.001
Sneaker males			
Observed across time	Permutation	166	<0.001
Co-occurrence with females in nests	GLM	166	<0.0001
Additional guarder males			
Observed across time	Permutation	166	<0.001
Nest			
Abandonments across time	Permutation	149	0.75
Take-over events across time	Permutation	149	<0.001
Take-overs*cannibalism	GLM	148	0.004
Offspring number			
Across the breeding season	OLSR	159	<0.0001
Between nests that were taken over vs not taken over	nGLM	139	0.02
Cannibalism			
Events across time	Permutation	148	<0.001
Early vs mid-season	MW	78	<0.0001
Between male types (take-over vs non-take-over) in mid-season	nGLM	45	0.0003

OLSR: ordinary least squares regression; ANCOVA: analysis of covariance; ANOVA: one-way analysis of variance; GLM: binomial logistic generalized linear model; nGLM: negative binomial generalized linear model; MW: Mann–Whitney *U* test.

Ethical Note

Plainfin midshipman fish are a common intertidal species and are not considered threatened or endangered. All animals were collected in accordance with the Canadian Department of Fisheries and Oceans (DFO scientific license number XR 14 2013). Marking involved injecting a nontoxic elastomer into the fin tissue between the dorsal fin rays. We also cut a small piece of fin tissue from the caudal fin to use for genetic testing in other studies, but this cut also served as an additional mark on each fish. The fin tissue regenerates in about 2 weeks, and removal of a small amount of fin tissue does not influence fish behaviour (A. P. H. Bose, K. M. Cogliati, H. S. Howe, & S. Balshine, personal observations). The fish were kept wet during handling, and marking and tissue collection procedure took no longer than 1 min. It is exceedingly unlikely that our sampling methods caused fish to abandon their nests; fewer than 4% of our sampled nests were found to be empty (a presumed abandonment) on day 2. On day 2, fish that were to be euthanized were first anaesthetized in a bath of (>0.1%) benzocaine followed by cervical severance, and their liver and digestive tracks were weighed for this study. These and other harvested tissues were used in a number of other studies. The procedures used in this study were approved by the McMaster University Animal Research Ethics Board (AUP number 10-11-70), and are in line with the guidelines set by the Canadian Council on Animal Care (CCAC).

RESULTS

Across the 166 nests sampled, we found 209 males, of which 79% were guarder males, 6% were sneaker males and 5% were additional guarder males intruding on the nest and not associated with an active nest of their own. The remaining 10% of males were take-over guarder males that had replaced a previous nest owner and had taken up residence in that nest (Table 2). Larger guarder males guarded larger nests or rocks with more surface area (cm^2; ordinary least squares regression, OLSR: $t_{162} = 2.95$, $R^2 = 0.05$, $P = 0.004$) and their nests contained more offspring (OLSR on log offspring number: $t_{157} = 5.85$, $R^2 = 0.18$, $P < 0.0001$). Nests that changed ownership (i.e. a take-over event, $N = 20$) contained fewer offspring than did nests where the original guarder male remained as resident (negative binomial GLM: $z = -2.4$, $N = 119$, $P = 0.02$).

Body Condition Decreased across the Breeding Season

Both measures of body condition showed that guarder males sampled early in the season were in better condition than those sampled late in the season (ANOVA: RCF: $F_{2,182} = 20.12$, $P < 0.0001$; HSI: $F_{2,119} = 4.64$, $P = 0.01$).

Table 2
Summary of plainfin midshipman, *Porichthys notatus*, found in nests at Crescent Beach, South Surrey, BC, in the 2013 breeding season

	Guarder tactic (type I)			Sneaker tactic (type II)	Female
	Resident	Additional	Take-over		
23–26 May	50	11	16	11	16
22–26 June	62	0	4	1	1
19–24 July	54	0	0	0	0
Total	166	11	20	12	17

The guarder tactic (type I male) has been divided into three classes. Note that, with the exception of take-over males, counts are summarized based on information collected on day 1. When two males were found in the same nest, the second male was considered the additional guarder. A take-over male could only be detected on day 2.

Competition was Most Intense Early in the Breeding Season

Females and sneaker males were more common early in the breeding season than late in the breeding season (permutation test with females: Δdev $= 24.13$, $P < 0.001$; Fig. 1a; permutation test with sneakers: Δdev $= 16.5$, $P < 0.001$; Fig. 1b). The presence of sneaker males in a nest was strongly correlated with the presence of females (binomial GLM: $z = 4.78$, $P < 0.0001$). Nests containing two or more guarder males were significantly more common early in the breeding season than late in the breeding season (permutation test: Δdev $= 23.02$, $P < 0.001$; Fig. 1c). The frequency of nest abandonment (the discovery of an empty nest on day 2 where a guarder male had originally been found on day 1) did not change over the season (permutation test: Δdev $= -0.792$, $P = 0.75$). Nest take-overs occurred more frequency early in the breeding season than late in the season (permutation test: Δdev $= -19.5$, $P < 0.001$), and all three cases of 'attempted take-overs in progress' (~2% of nests observed on day 2) were found early in the season. There was a strong positive correlation between male body size and nest size early in the season ($t_{48} = 4.88$, $R^2 = 0.33$, $P < 0.0001$; Fig. 2), and a weaker but still significant correlation in mid-season ($t_{58} = 2.85$, $R^2 = 0.12$, $P = 0.006$), but no correlation between male body size and nest size late in the season ($t_{52} = -1.32$, $R^2 = 0.03$, $P = 0.19$). This led to a significant interaction between guarder male size and sampling period (ANCOVA: $F_{2,158} = 7.16$, $P = 0.001$). Taken together these results suggest that there is more competition among males early in the season than late in the season.

Higher Prevalence of Cannibalism Early in the Breeding Season

None of the females ($N = 10$) or sneaker males ($N = 10$) internally inspected had offspring in their digestive tracts, regardless of when they were collected in the breeding season. Only guarder males ($N = 123$ males whose digestive tracks were inspected) were observed to have cannibalized offspring and cannibalism was significantly more common in the early part of the breeding season. Cannibalism declined significantly over time (permutation test: Δdev $= -49.6$, $P < 0.001$; Fig. 3a). Cannibalism was observed in 58% of sampled males in May and 27% of sampled males in June and ceased altogether at the end of the season (0% of the sampled males in July had cannibalized young).

On average, males consumed 9.3 ± 2.1 offspring (mean ± SE; range 0–53) in the early season, 3.6 ± 1.6 offspring (range 0–58) in the mid-season and 0 offspring in the late season. This decrease in number of offspring consumed was significant (Mann–Whitney *U* test: $Z = 3.99$, $N_1 = 33$, $N_2 = 45$, $P < 0.0001$). Take-over events were highly correlated with cannibalism (80% of take-over males cannibalized; binomial logistic GLM: $z = 2.85$, $P = 0.004$; Fig. 3b). Overall, take-over events accounted for 38% of all the cannibalism observed over the season. During the early season (May), cannibalistic take-over males had similar numbers of offspring in their guts (8.25 ± 2.1, range 2–17) compared to non-take-over males that cannibalized (15 ± 3.5, range 1–53; negative binomial GLM: $z = -1.58$, $P = 0.11$). However, during the mid-season (June), take-over males had significantly more offspring in their guts (23.7 ± 8.9, range 1–58) than did non-take-over males (3.0 ± 1.7, range 1–13; negative binomial GLM: $z = 3.61$, $P = 0.0003$). Cannibalism and nest take-overs did not occur in the late season (July).

Early in the season, no differences in body condition were detected between fish that cannibalized and those that did not (binomial logistic GLM on RCF: $z = 0.58$, $P = 0.56$; HSI: $z = 1.42$, $P = 0.15$). However, by the mid-season, cannibals were in better condition than noncannibals (binomial logistic GLM on RCF: $z = 2.60$, $P = 0.009$; HSI: $z = 2.09$, $P = 0.036$). No cannibalism

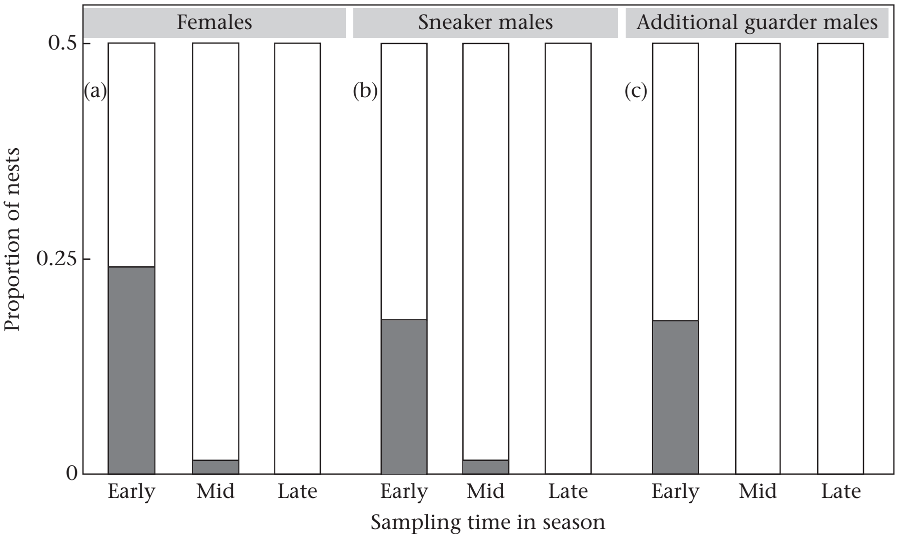

Figure 1. Proportion of plainfin midshipman (a) females, (b) sneaker males and (c) additional guarder (type I) males observed in nests of guarder males over the breeding season (early: May; mid: June; late: July). Grey bars: fish types found in the nest; white bars: fish types absent from the nest.

occurred during the late season, when recorded body conditions were lowest.

DISCUSSION

Despite a prolonged and costly period of care, our results suggest that plainfin midshipman males do not engage in cannibalism to counteract the energetic demands of parental care. Male body condition clearly deteriorated as the season progressed, and males were in the poorest condition at the end of July. Therefore, if cannibalism were a strategy used primarily to regain energy lost by prolonged parental care, then we would expect to observe an increase in cannibalism across the parental care period. Furthermore, we found that cannibals in the mid-season were in better condition than noncannibals, which is in opposition to expectations of the energy-based hypothesis. We found that prevalence of offspring cannibalism was high in the early season (observed in 58% of nesting males), but declined across sampling periods. The most frequent and severe (in terms of number of offspring consumed) cannibalism was observed in the early season, which then declined in the middle of the breeding season, and completely ceased by the end of the season. This pattern mirrors the decline in both the degree of male–male competition and the frequency of nest takeover events observed across the breeding season. Cannibalism therefore appears to be associated with a competitive environment when gravid females are more plentiful in the spawning grounds and males are still competing for nests and eggs.

Based on a number of indices, we show that mating competition is most intense early in the season. We found that guarder male size was strongly correlated with nest size early in the season, less so in the mid-season and not at all late in season. Early in the breeding season, females, sneaker males and additional ‘non-nest owner’ guarder males were more common in nests. A high level of competition will impose several costs on nesting midshipman males, including the energetic costs of defending their nest against competitors and a lowered certainty of paternity arising from more frequent cuckoldry attempts. Indeed, Cogliati et al. (2013) showed that paternity levels are lowest early in the season, further

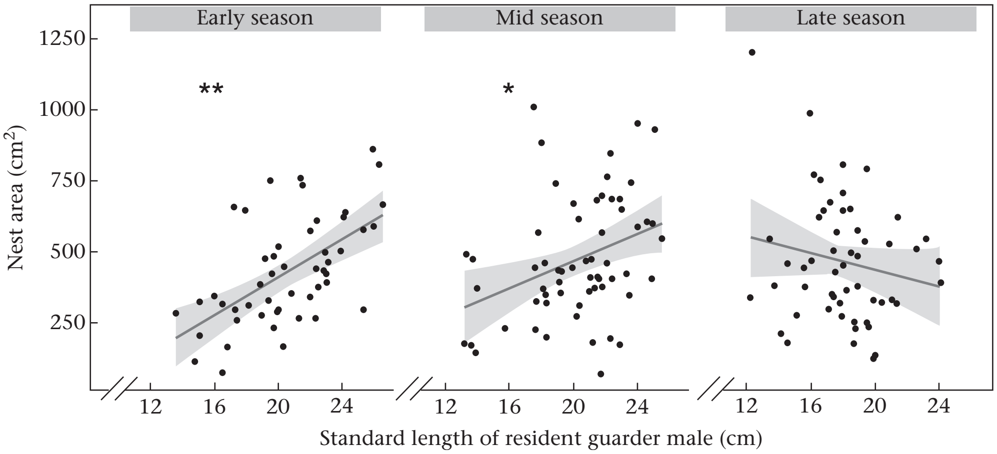

Figure 2. Standard length of plainfin midshipman guarder males plotted against nest area during the breeding season (early: May; mid: June; late: July). Confidence intervals were calculated based on the variance within each month and are presented in each panel. *$P < 0.01$; **$P < 0.001$.

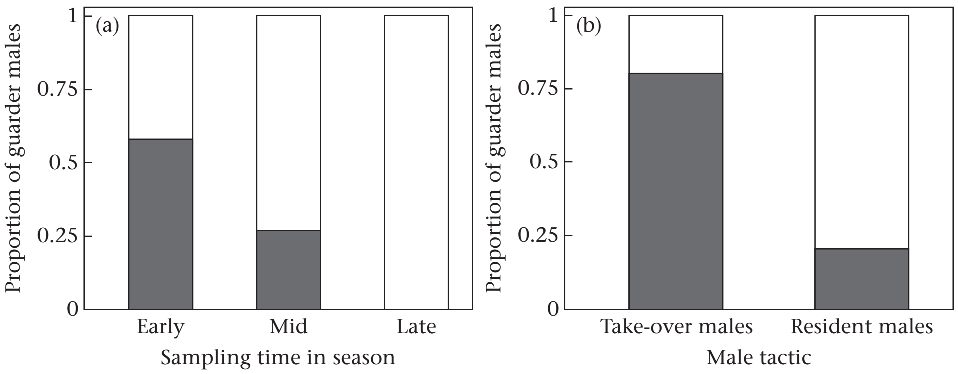

Figure 3. (a) Proportion of plainfin midshipman guarder males that cannibalized eggs in their nests plotted against time within the breeding season (early: May; mid: June; late: July). (b) Proportion of guarder males that cannibalized eggs in their nests as a function of take-over status. Grey bars: cannibalistic males; white bars: noncannibalistic males.

corroborating that there is more competition for fertilization early in the breeding season. Level of paternity is known to influence the amount of parental care provided to a brood (e.g. Neff, 2003b). Furthermore, if males are capable of kin recognition among their offspring, then selective consumption of unrelated young will incur no direct fitness costs.

While the termination of care through whole-brood cannibalism has typically been reported to occur early rather than late in the breeding period (Manica, 2002), more variation exists among species in the timing of partial-brood cannibalism (e.g. Belles-Isles & FitzGerald, 1991; Marconato, Bisazza, & Fabris, 1993; Neff, 2003a). Several additional explanations should be considered with respect to the observed seasonal decline in cannibalism that we observed in the plainfin midshipman fish. Such a seasonal decline could also arise if males place greater value on their broods as they develop from eggs into hatched embryos (Rohwer, 1978). We also found that females became scarce or absent late in the season, leading to an increasingly male-biased operational sex ratio. Therefore, early in the season, if a male cannibalized from his nest when it was at maximum capacity with offspring, he would still have a chance to acquire replacement offspring, but this would not occur late in the season. In the convict cichlid, *Cichlasoma nigrofasciatum*, experimental reductions in brood size can incite filial cannibalism, but only early in the breeding cycle when parents are still able to prepare for a subsequent brood (Lavery & Keenleyside, 1990). Increased brood investment later in the season may be favoured because alternative mating opportunities are less probable (Kondoh & Okuda, 2002), or if body condition deteriorates considerably, lowering an individual's expected future reproductive success (i.e. residual reproductive value; Pianka, 1976). Finally, density-dependent offspring survival may also influence the likelihood of cannibalism as shown in the sand goby, *P. minutus* (Klug et al., 2006), where cannibalism is used to reduce brood density, thereby improving the survival of the remaining offspring in the nest. While such impacts of offspring density on survival have not been studied in the plainfin midshipman, we think that it is an unlikely driver of cannibalism in this system. Midshipman females deposit new eggs in the nest in a single tightly packed monolayer (Arora, 1948) and will fill in any gaps among the offspring already present on the nest surface even when free space is accessible elsewhere in the nest (A. P. H. Bose, K. M. Cogliati, H. S. Howe, & S. Balshine, personal observations). Finally, cannibalism may reflect selective consumption of dead or unhealthy eggs and so may be adaptive if it protects the remaining offspring within a brood from spread of infection (Kraak, 1996). Although we did not explicitly test this idea in the present study, visual inspection and DNA testing of consumed offspring suggest that guarder males do not specifically engage in cannibalism of dead or unfertilized eggs (Cogliati, Danukarjanto, et al., 2014).

We also observed more frequent changes in nest ownership (more take-over events) early in the breeding season. This, combined with the strong tendency for take-over fish to be cannibalistic, could also contribute to our observation of more frequent cannibalism early in the season. By being cannibalistic, the new take-over guarder male can gain an energy benefit at the expense of the previous nest owner. Take-over males can also be more certain that they are not related to the eggs in their newly acquired nest compared to a nest owner who has occupied the nest for a long time. As the season progressed, we found that take-over males had on average more offspring in their guts than did non-take-over males. It is possible that our brief 2-day sampling methodology underestimated the rate of take-over events. It is entirely possible that certain males in our data set had taken over a nest prior to our sampling, yet were categorized as resident, non-take-over males. If this is the case, then competitive cannibalism of unrelated offspring, as facilitated by nest take-overs, could have driven an even larger proportion of overall cannibalism than the 38% we allocated above. However, the extent to which take-over events contribute to overall rates of cannibalism has yet to be tested explicitly.

Furthermore, nests that experienced a take-over event contained, on average, fewer offspring than nests where the original nest owner remained, indicating that small broods might have lower value to original male caregivers. If a small brood results in a lowered motivation to defend for a caregiver, this could lead to an increased likelihood of abandonment if challenged by another male. Brood size is typically a strong predictor of parental expenditure (Gross, 2005). For example, bluegill sunfish, *L. macrochirus*, vary their parental effort according to brood size (Coleman, Gross, & Sargent, 1985), and Galilee St Peter's fish, *Sarotherodon galilaeus*, caregivers are more likely to abandon small broods than large ones (Balshine-Earn & Earn, 1998).

More nest take-overs were observed early in the midshipman breeding season. For a number of reasons, we do not think that the temporal patterns of cannibalism, take-overs and abandonment were the result of sampling-related nest disturbance. First, we sampled in an identical fashion across the breeding season, but the rate of take-overs ceased. Second, we observed more, presumably, cuckolder or take-over males in nests early in the season than later in the season. Third, Cogliati et al. (2013), used microsatellite paternity analyses to reveal a genetic signature of nest take-overs occurring early in the season. Taken together these results suggest that it is unlikely that our disturbance caused undue nest abandonment. Available nesting sites are limited (DeMartini, 1988;

A. P. H. Bose, K. M. Cogliati, H. S. Howe, & S. Balshine, personal observations) and, therefore, are a valuable resource for a guarder male, making abandonment a costly act. Indeed, abandonment occurred at an extremely low frequency of less than 4% of all our sampled nests.

All incidences of cannibalism observed in the present study involved partial-brood cannibalism. Cannibals in our sample never consumed all of the offspring in a nest, even if they had taken over a nest and were presumably not related to any of the offspring. In fact, both take-over males and cuckolded males have been shown to provide alloparental care to unrelated offspring (Cogliati, Balshine, et al., 2014; Cogliati et al., 2013). Several potential explanations exist for why alloparental care is observed in the plainfin midshipman. First, parental care in the plainfin midshipman is largely nondepreciable with the possible exception of egg fanning (Cogliati et al., 2013). Thus, the costs of caring for a larger brood may not be much higher than caring for a small brood, promoting alloparental care (Wisenden, 1999). Second, males may be willing to care for unrelated offspring if these eggs serve to attract more mates. In many fish species females engage in mate choice copying (Dugatkin, 1992). For example, female blennies, *A. sphinx* (Kraak, 1996), threespine sticklebacks, *G. aculeatus* (Ridley & Rechten, 1981), and sailfin mollies, *Poecilia latipinna* (Witte & Ryan, 2002) all prefer to nest with males that have already obtained eggs from another female. Third, unrelated offspring may serve as a potential ‘insurance policy’, providing an accessible food source for the guarder male distinct from his own offspring. These explanations are not mutually exclusive and have yet to be tested empirically.

Collectively, our study has described cannibalism in a system with intense male–male competition and prolonged costly parental care. While the energy-based hypothesis of offspring cannibalism has received the most attention across animal taxa, in plainfin midshipman, we show that poor parental body condition does not correlate with cannibalism. Instead the prevalence of cannibalism was related to the degree and timing of intense male intrasexual competition. We suggest that cannibalism may help a male remain in excellent competitive condition at a time when females are readily available for spawning and the fitness rewards are likely greatest. Cannibalism may also be a product of compromised paternity resulting from prevalent cuckoldry by both guarder and sneaker males, although whether guarder males are capable of differentiating kin and nonkin offspring remains to be tested. Cannibalism may in fact be selected for by high certainty of nonpaternity that would accompany a nest take-over event. In addition, we acknowledge that we did not directly observe egg-eating behaviour by type I guarder males, a gap that future work should strive to fill. Eggs loosened in the process of fanning and caring for the brood may contribute to the levels of cannibalism we report here, but the extent to which this occurs also remains to be investigated. Future work should also focus on experimentally manipulating body condition, degree of mating competition and brood paternity to further test our findings. It would also be valuable to assess the extent to which cannibalism of offspring can augment body condition, affect competitive abilities, facilitate continued parental care, or enhance offspring survival through density-dependent effects. Finally, the present work highlights the importance of monitoring cannibalistic behaviours across an entire breeding season, as ecological driving forces for this behaviour may change temporally.

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