

## Paternal investment with an uncertain future: effects of predator exposure on filial cannibalism and nesting behaviour



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### ARTICLE INFO

#### Article history:

Received 9 November 2016

Initial acceptance 12 December 2016

Final acceptance 21 June 2017

MS. number: 16-00977R

#### Keywords:

brood care

filial cannibalism

nest predator

parental investment

predation risk

residual reproductive value

Owing to trade-offs between investment in current and future reproduction, factors that diminish a parent's survival prospects, such as predation threat, are expected to increase investment in existing young. Nevertheless, effects of predation risk on parental investment have only rarely been examined, and not at all within the context of filial cannibalism (parental consumption of their own offspring). We examined filial cannibalism and nest characteristics in a small fish with paternal egg care, the sand goby, *Pomatoschistus minutus*, both when exposed to a common piscivore, the perch, *Perca fluviatilis*, and in the absence of predators. We found that when males consumed only some of their eggs (partial filial cannibalism), the number of eaten eggs did not depend on predation threat, possibly indicating that partial clutch consumption is largely motivated by benefits to existing young. Total filial cannibalism (whole clutch consumption) was marginally less common under predator exposure, while its strongest predictor was small clutch size. This suggests that the return on parental investment has a greater influence on total filial cannibalism than the likelihood of future breeding. Regarding nest architecture, males that consumed their entire brood after exposure to a predator built larger nest entrances, possibly to facilitate predator evasion. Males that cared for at least part of their brood, however, maintained small nest entrances regardless of predation threat. Furthermore, more elaborate nests were not associated with greater egg consumption, suggesting that filial cannibalism is not employed to sustain nest building. © 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Parental care confers important fitness benefits to parents by improving the survival of their offspring (Alonso-Alvarez & Velando, 2012; Clutton-Brock, 1991). However, looking after young can be costly (Alonso-Alvarez & Velando, 2012; Clutton-Brock, 1991). It can be time consuming (e.g. Thomson et al., 2014), energetically demanding (e.g. Gravel & Cooke, 2013), and expose parents to predation (e.g. Li & Jackson, 2003) or disease (e.g. Nordling, Andersson, Zohari, & Lars, 1998). As a result, parents may have to trade off investment in existing young against investment in future reproduction (Clutton-Brock, 1991; Trivers, 1972). In this regard, a range of factors can alter the optimal balance of investment in these two fitness components (Klug, Alonzo, & Bonsall, 2012). For instance, a parent may benefit from providing greater care to its current brood when prospects of future reproduction are bleak, as shown, for example, in eiders, *Somateria mollissima*, in

which immune-challenged mothers spend more time incubating their eggs and are less likely to abandon their ducklings (Hanssen, 2006). On the other hand, when there are abundant opportunities to breed in the future, parents may be more inclined to reduce or even terminate investment in existing young to mitigate the costs of current reproduction (Gross, 2005; Klug et al., 2012; Magnhagen, 1992; Sargent & Gross, 1985; Williams, 1966a, 1966b). To this end, one way in which parents can reduce or terminate investment in the current brood is to consume their own young.

Apart from preventing the costs of parental care from impinging on future reproduction, consuming one's own offspring, known as filial cannibalism, can also provide energy and nutrition to parents (Manica, 2002). In the case of partial filial cannibalism, where only some of the young under a parent's care are eaten, resources acquired from offspring consumption may be used to support the parent in caring for uneaten young, as seen in river bullheads, *Cottus gobio*, and cardinalfish, *Apogon lineatus* (Kume, Yamaguchi, & Taniuchi, 2000; Marconato, Bisazza, & Fabris, 1993). In these cases, filial cannibalism may simply be an investment in current reproduction. However, if resources acquired from consuming young are

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used to promote further breeding, filial cannibalism is, at least partially, an investment in future reproduction. In acts of total filial cannibalism especially, that is, when parents consume all young under their care, the motivation is likely to be solely investment in future reproduction (Manica, 2002). Accordingly, parents are expected to commit more filial cannibalism when the potential for future reproduction is high (Rohwer, 1978). However, not all empirical evidence supports this prediction. For example, elevated levels of filial cannibalism are not usually reported to occur early in the breeding season (e.g. Lissåker, 2007; Marconato et al., 1993; Okuda & Yanagisawa, 1996; but see Mehliis, Bakker, Engqvist, & Frommen, 2010; Okuda, Takeyama, & Yanagisawa, 1997; Takeyama, Okuda, & Yanagisawa, 2002), and only occasionally occur in response to heightened access to mates (Bjelvenmark & Forsgren, 2003; Okuda, Ito, & Iwao, 2004; Pampoulie, Lindström, & St Mary, 2004; reviewed in Deal & Wong, 2016), even though both these conditions may increase the prospects of future reproduction. Meanwhile, the effects of other factors that could predict the likelihood of future breeding remain rarely tested. For example, despite theoretical models that suggest that the likelihood of parents being preyed upon (hereafter referred to as 'parental predation risk') is one of the most significant factors determining the occurrence of brood abandonment (Steinhart, Dunlop, Ridgway, & Marschall, 2008), the effects of parental predation risk are, to our knowledge, untested within the context of filial cannibalism, and largely also that of parental care in general (for exceptions, see Arundell, Wedell, & Dunn, 2014; Fox & McCoy, 2000; Javoš & Tammaru, 2004).

The sand goby, *Pomatoschistus minutus*, is a small marine and brackish water fish that performs both total and partial filial cannibalism (Forsgren, Karlsson, & Kvarnemo, 1996). In this species, uniparental egg care by the male takes place within a nesting chamber that he excavates underneath a rock or empty mussel shell, onto which he piles sand (Lindström, 1988). The nest then serves as a protective location for the eggs, with some evidence suggesting that nests with narrow entrances and those covered with large sand piles provide concealment and protection from egg predators (Lissåker & Kvarnemo, 2006; see also Jones & Reynolds, 1999; Lehtonen, Lindström, & Wong, 2013; Svensson & Kvarnemo, 2003). The nest may also play a role in mate attraction. In particular, sand piled above the nest amplifies male vocalizations (Lugli, 2013) and females appear to prefer to spawn in nests covered by larger sand piles, at least under a subset of conditions (Lehtonen & Lindström, 2009; Lehtonen & Wong, 2009; Lehtonen, Wong, & Lindström, 2010; Svensson & Kvarnemo, 2005). Within the nest, males can care for the eggs of multiple females, either contemporaneously or in sequence (Jones, Walker, Lindström, Kvarnemo, & Avise, 2001). However, individuals generally do not survive to participate in multiple breeding seasons (Fonds, 1973; Healey, 1971).

Partial filial cannibalism can benefit male sand gobies, for example by improving the survivorship of eggs within crowded nests (Klug, Lindström, & St Mary, 2006; Lehtonen & Kvarnemo, 2015a, 2015b; Lindström, 1998). Males may also use energy from egg consumption to improve their body condition (Klug et al., 2006; Lindström, 1998; Lissåker, Kvarnemo, & Svensson, 2003). However, whether energy acquired through egg consumption is used to improve predominantly future or current reproduction is at present unclear. Moreover, total filial cannibalism in sand gobies appears to be a facultative strategy employed when the costs of providing care to young are high and the potential benefits low (Chin-Baarstad, Klug, & Lindström, 2009; Klug et al., 2006). However, certain factors that should promote increased future reproductive potential for male sand gobies, such as heightened access to gravid females, have not been found to be linked with higher rates

of total filial cannibalism (Pampoulie et al., 2004). These findings suggest that responsiveness of male filial cannibalism to determinants of future reproduction are not yet well understood and further investigations are therefore warranted.

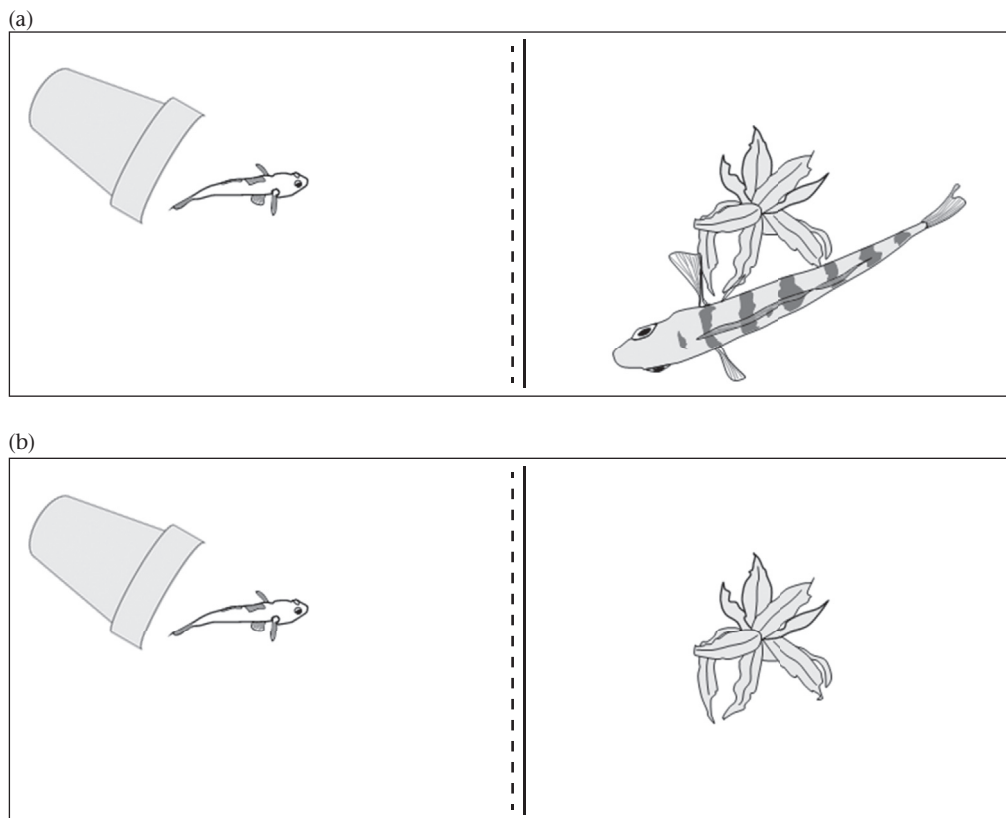
Throughout their life span, sand gobies are vulnerable to a range of predators, especially birds (Lindström & Ranta, 1992) and fish (Hansson, Arrhenius, & Nellbring, 1997; Koli, Rask, & Aro, 1985; Lappalainen, Rask, Koponen, & Vesala, 2001). Indeed, it is likely that the level of this predation pressure will influence the prospects of future reproduction of parental male gobies. This is not only because falling victim to predators prevents further reproduction, but also because attempting to remain inconspicuous to predators may restrict the courtship and spawning activities of sand gobies (Forsgren & Magnhagen, 1993; Wong, Järvenpää, & Lindström, 2009; see also: Magnhagen, 1990; Magnhagen & Forsgren, 1991). Therefore, under a higher risk of predation, the potential to reinvest resources gained via filial cannibalism may be particularly limited. We can thus predict that sand gobies that perceive a relatively high risk of predation will be less likely to engage in total filial cannibalism and, in cases of partial filial cannibalism, eat fewer of their eggs, especially if filial cannibalism is performed primarily to improve future rather than current reproductive success.

In this study, we set out to examine the effect of perceived predation risk on filial cannibalism in the sand goby by comparing the behaviour of egg-tending males exposed to a perch, *Perca fluviatilis*, a common predator of sand gobies (Koli et al., 1985; Lappalainen et al., 2001), with that of males guarding eggs in a comparatively safe environment. We also examined the effect of predation threat on nest construction. This could elucidate the motives behind any adjustment of the level of filial cannibalism and test whether filial cannibalism is employed to acquire energy for nest maintenance and construction as suggested by earlier findings showing that good body condition and supplemental feeding in sand gobies promote higher quality or more extensive nest building (Lehtonen & Wong, 2009; Lindström, 1998; Olsson, Kvarnemo, & Svensson, 2009).

## METHODS

Experimentation took place during the sand goby breeding season (May–July 2014) at the Tvärminne Zoological Station (59°50.7'N, 23°15.0'E) on the Baltic Sea's coast. Gobies were collected within the nearby nature reserve using a hand trawl (Evans & Tallmark, 1979; Lehtonen & Kvarnemo, 2015a) and dip-nets, while a gillnet was used to capture perch. After capture, all fish were brought to the station and placed in single-species stock aquaria within a semi-outdoor laboratory facility where experimentation occurred. Within this facility, all aquaria received sea water flow-through and were exposed to natural light and temperature conditions. Sand gobies housed in stock aquaria were segregated by sex and fed daily on frozen chironomid larvae and live *Neomysis* shrimp. Perch remained unfed for the duration of the experiment.

To initiate a replicate, a male and female sand goby were selected and their wet mass and standard length were measured. Females were chosen based on the presence of a distended abdomen, indicating gravidity (Kvarnemo, 1997). Males were selected haphazardly but those under 30 mm standard length were avoided, as larger males dominate nesting sites in this species (Lindström, 1988; Lindström & Pampoulie, 2005; Magnhagen & Kvarnemo, 1989), with smaller males often prevented from spawning or resorting to sneak spawning tactics (Takegaki, Svensson, & Kvarnemo, 2012). After selection, each male–female pair of gobies was added to an experimental aquarium (Fig. 1). Each of these aquaria contained a pair of plastic barriers, one opaque and



**Figure 1.** Top-view schematic layout of experimental aquaria for the (a) 'predator' treatment and (b) 'control' treatment. Dashed lines are used to depict clear aquarium dividers, while solid lines represent opaque dividers. Schematic is not to scale.

one clear, which divided them into a 'nesting compartment' and an 'exposure compartment' (Fig. 1). The male–female pair was introduced to the nesting compartment, which had been provided with a sand substrate and an artificial nesting site. The nesting site comprised a flowerpot half (diameter of the mouth: 8 cm) with its interior lined with a thin acetate sheet, upon which females attached their eggs during spawning. Initially, the male was released directly into the nesting compartment, whereas the female was held in a clear plastic receptacle in front of the nesting site to encourage the male to begin nest construction. This involved the male piling sand directly on top of the flowerpot and excavating a nesting chamber underneath it, leaving a single entry passageway which varied in size from a completely open flowerpot mouth (indicating a low level of nest construction) to a sand-enclosed passageway just large enough for the male to pass through (which is found only in thoroughly constructed nests). The following day, the female's receptacle was removed releasing her into the nesting compartment to spawn. The pair was left for 1 more day to spawn, and then the female was removed and released back into the sea. In some cases ( $N = 44$ ), no spawning occurred within this timeframe and so the replicate was aborted and the male was also released. For pairs that did spawn ( $N = 79$ ), we removed and photographed the sheet lining the nest, to which their eggs were attached, in order to later count the eggs spawned (Pampoulie et al., 2004). Care was taken to ensure the sheet and eggs remained submerged in a shallow tray of water during this procedure, after which they were quickly returned to the nest.

After the eggs were returned to the nest-holding male, he was randomly assigned to either the 'predator' ( $N = 40$ ) or 'control' ( $N = 39$ ) treatment. In the predator treatment, we then added a perch (standard length:  $176 \pm 31$  mm [mean  $\pm$  SD],  $N = 40$ ) and a plastic plant to the aquarium's exposure compartment, with the

plastic plant providing refuge for the perch. In the control treatment, only a plastic plant was added to the exposure compartment. This ensured that all fish were subject to novel stimuli. In both treatments, we then removed the opaque barrier dividing the nesting and exposure compartments, leaving only the transparent barrier in the tanks. To prevent other cues disturbing the fish after this, we wrapped the exterior vertical walls of the aquaria in black plastic and left the males to brood their eggs. We did not offer any food to males during this brooding period, as opportunities to forage are restricted during brood care (Lindström & Hellström, 1993; Salgado, Cabral, & Costa, 2004).

There is some evidence that dissolved oxygen levels may influence filial cannibalism rates (Klug et al., 2006; but see Lissåker et al., 2003). To account for this in our analysis, we measured the dissolved oxygen in each nesting compartment using a dissolved oxygen meter (model: YSI ProODO; YSI Inc., Yellow Springs, OH, U.S.A.) 7 days after the male had been left to brood. At this point, sand goby eggs are close to hatching (Kvarnemo, 1994). After measuring the dissolved oxygen, we then measured the height and width of the nest entrance and the amount of sand piled on the nest (assessed as the height of sand piled on the nest, as measured from the base of the tank; see Lehtonen, Wong, & Kvarnemo, 2016). We then immediately removed the lining sheet from the male's nest and photographed it using the same procedure as for the initial photograph. This enabled us to estimate how many eggs were consumed by males by counting the eggs on the photographs of their nest-lining sheets from the beginning and end of the brooding period using the manual cell counter plugin of ImageJ (Rasband, 1997–2015). This measure of filial cannibalism follows previously published studies (e.g. Klug & Lindström, 2008; Lehtonen & Lindström, 2007), with male consumption of eggs being the only plausible explanation for egg disappearance, whereas egg viability

at the point of consumption could not be ascertained in this study. Finally, male sand gobies were removed from their tanks and reweighed before we returned them, and any perch used in the trial, back to the sea. Some males ( $N = 14$ ) died during the brooding period, and one control male was accidentally removed from his tank too early. Measurements from these replicates were not used for our analyses (except in determining the relationship between male length and weight for body condition calculations). The final sample size was thus 33 predator treatment males and 31 control males. No sand gobies were used across multiple replicates, and perch were only reused when the first male to which they were exposed died during brooding.

### Statistical Analyses

#### Filial cannibalism

All analyses were conducted using *R* (R Core Team., 2016). Since total filial cannibalism and partial filial cannibalism are thought to be distinct phenomena (Manica, 2002), we modelled each of these separately. A probit regression model was used to analyse the occurrence of total filial cannibalism and an ordinary least squares (OLS) regression model was used to analyse the number of eggs eaten in cases of partial filial cannibalism. For our analyses we classified males that consumed all of their eggs, as well as one male that consumed all but eight of the eggs in his brood (>99%), as total filial cannibals. Observations from these males were truncated from the data set for the partial filial cannibalism model. Furthermore, we performed a natural logarithm transformation on the number of eggs consumed for this model to achieve approximately normally distributed residuals. Both models of filial cannibalism were fully additive with predation threat treatment, prespawning male body condition and dissolved oxygen level used as predictors. Furthermore, the initial number of eggs spawned was used as a predictor for the total filial cannibalism model only, since we believe that the weight of the existing empirical evidence supports the assumption that, for sand gobies, the occurrence of total filial cannibalism is influenced by initial clutch size (Andr n & Kvarnemo, 2014; Forsgren et al., 1996; Klug et al., 2006; Liss aker & Svensson, 2008; Pampoulie et al., 2004; but see Chin-Baarstad et al., 2009), whereas the number of eggs consumed in cases of partial filial cannibalism is not (Andr n & Kvarnemo, 2014; Kvarnemo, 1997; Liss aker & Kvarnemo, 2006; see also: Lindstr m, 1998; Pampoulie et al., 2004). Inclusion of male body condition in our analyses allowed us to account for the possibility that individuals might adjust their egg consumption based on their body condition if filial cannibalism is performed to acquire energy (Manica, 2002). As a proxy of male body condition, we used the scaled mass index, which we calculated following the procedure described by Peig and Green (2009) using the *smatr* R package for the necessary standardized major axis regression (Warton, Duursma, Falster, & Taskinen, 2012). Measurements from all 79 males that spawned in this experiment were used to calculate the value of the scaling coefficient and exponent of the power law assumed to describe the relationship between male standard length and prespawning body mass in these gobies. The use of dissolved oxygen level as a predictor can account for the possibility that oxygen saturation might have been affected by perch in the predator treatment. However, this was a cautious approach, given that the dissolved oxygen levels dealt with in this experiment (predator treatment:  $99 \pm 14\%$  [mean  $\pm$  SD],  $N = 33$ ; control treatment:  $103 \pm 8\%$ ,  $N = 31$ ) far exceed the hypoxic conditions where it is thought filial cannibalism and nest building may be influenced (Klug et al., 2006; Liss aker & Kvarnemo, 2006; Liss aker et al., 2003). For all the presented regression models, we draw inference based on Wald *t* tests of coefficients.

One potential issue with our OLS model of partial filial cannibalism is that the sample we examined was no longer random as a result of total filial cannibals being excluded from this analysis. To address this, we also fitted a Heckman sample selection model (Tobit-2 model) to the data, but since this revealed qualitatively similar results to the OLS model with minimal bias in parameter estimates, we elected to focus on the simpler OLS analysis here, with the sample selection model presented in the Appendix.

#### Male weight change

To determine whether the consumption of eggs influenced the change in male weight over the duration of the brood care period, we used two general linear models each with male weight change as the response variable. First, we tested whether mode of filial cannibalism (partial or total) in isolation influenced weight change. Second, we included the mode of filial cannibalism, the number of eggs consumed and the interaction between these two terms as predictors, to test whether the effects of filial cannibalism mode could be attributed to the different number of eggs eaten by males that engaged in these two modes of filial cannibalism.

#### Nest construction and maintenance

We constructed three separate general linear models, each examining one nest architecture parameter (nest opening width, nest opening height and nest sand pile height) as a response variable. The included predictor variables, which were the same for each model, were predation treatment, male standard length, prespawning male body condition, oxygen saturation level, the number of eggs consumed by the male, and whether or not the male engaged in total filial cannibalism. We also included terms for the two-way interactions between the mode of filial cannibalism and each of the other predictors. This was done because we wanted to account for the possibility that total and partial filial cannibals alter the construction of their nests in response to environmental variables differently.

#### Ethical Note

Experiments were approved by the Biological Sciences Animal Ethics Committee of Monash University (BSCI/2014/01) and complied with the laws of Finland, where the procedures met the standards of 'ELLA' (the Finnish Animal Experiment Board) for noninvasive animal experiments. Some sand gobies died during brooding as part of this study ( $N = 14$ ), which probably reflects natural mortality where most adults do not survive for multiple breeding seasons (Fonds, 1973; Healey, 1971). All surviving fish from this experiment were returned to the sea after the experiment.

## RESULTS

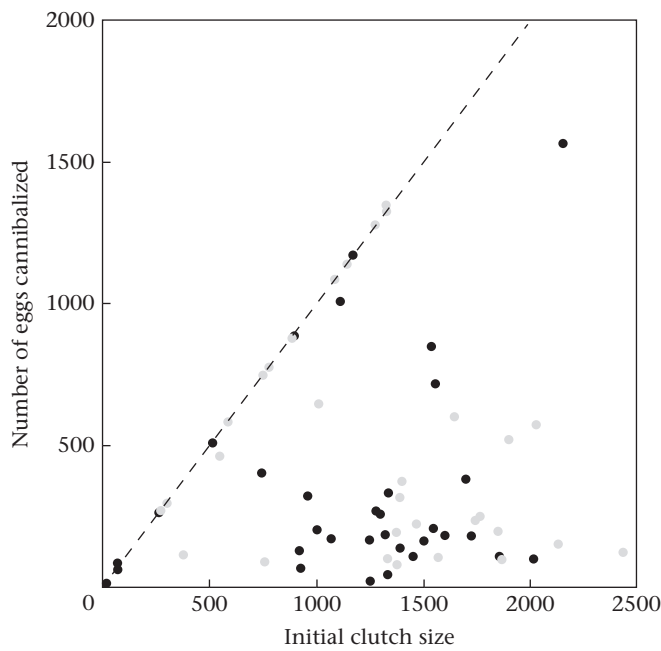
### Filial Cannibalism

After spawning, males had  $1226 \pm 545$  (mean  $\pm$  SD) eggs ( $N = 64$ ), with  $414 \pm 388$  of these typically being consumed by the end of the trial. All males consumed at least some eggs (minimum consumed = 12 eggs) and 18 of the 64 males in the final sample engaged in total filial cannibalism. Males with small initial clutches were significantly more likely to engage in total filial cannibalism (Table 1, Fig. 2). Exposure to a perch also tended to decrease the likelihood of a male engaging in complete clutch cannibalism, occurring in seven of 33 (21%) perch-exposed males compared to 11 of 31 (35%) unexposed males, although this effect was marginally nonsignificant (Table 1, Fig. 2). Neither prespawning male body

**Table 1**  
Parameter estimates from models of filial cannibalism

Predictor	Total filial cannibalism (Probit model)			Partial filial cannibalism (OLS regression model)		
	$\beta_S$ (SE)	$\beta$ (SE)	$t$ (P)	$\beta_S$ (SE)	$\beta$ (SE)	$t$ (P)
Intercept	-0.909 (0.240)	-0.909 (0.240)	-3.785 (<0.001)	5.357 (0.124)	5.371 (0.123)	43.507 (<0.001)
Initial clutch size	-2.448 (0.595)	-0.002 (0.001)	-4.117 (<0.001)	—	—	—
Prespawning male body condition (g)	-0.226 (0.477)	-1.642 (3.458)	-0.475 (0.635)	-0.350 (0.247)	-2.540 (1.793)	-1.417 (0.164)
Perch exposure	-0.808 (0.442)	-0.808 (0.442)	-1.828 (0.068)	-0.038 (0.251)	-0.038 (0.251)	-0.153 (0.879)
Dissolved oxygen levels (%)	-0.035 (0.481)	-0.002 (0.021)	-0.072 (0.942)	-0.012 (0.223)	-0.001 (0.010)	-0.052 (0.959)

Perch exposure was dummy coded with 'predator' treatment as 0.5 and 'control' as -0.5, and all other predictor variables were mean centred. Regression coefficients based on raw predictor values ( $\beta$ ) as well as rescaled regression coefficients ( $\beta_S$ ) from scaling nonbinary inputs by two standard deviations are reported following Gelman (2008).



**Figure 2.** Plot of the number of eggs cannibalized by males during brooding against the initial clutch size for males exposed to a perch in the 'predator' treatment (black dots) and males in the 'control' treatment that did not encounter a predator (grey dots). Points lying on the diagonal ( $N = 18$ ), where the initial clutch size is equal to the number of cannibalized eggs, represent cases of total filial cannibalism. Two data points that fall on the diagonal have been displaced upwards by 20 units to prevent overplotting.

condition nor the level of dissolved oxygen had significant effects on total filial cannibalism (Table 1).

For partial filial cannibalism, none of the potential predictors we examined (predation treatment, prespawning male body condition and dissolved oxygen levels) had significant effects on the number of eggs eaten (Table 1).

**Male Weight Change**

Males, on average, lost weight between the start of spawning and the completion of brooding (Wald test:  $t_{62} = -3.734, P < 0.001$ ; see also Table 2). Total filial cannibals lost significantly less weight than partial filial cannibals ( $t_{62} = 3.116, P = 0.003$ ). However, once we took the effect of the number of eggs eaten by each male and its interaction with filial cannibalism mode into account by including them in the model, the marginal effect of filial cannibalism mode was no longer significant (Table 2). The interaction between the number of eggs eaten and mode of filial cannibalism was also not significant but males lost significantly less weight with an increased number of eggs consumed (Table 2).

**Nest Construction and Maintenance**

There was a positive correlation between nest entrance height and width at the end of the brooding period ( $r_S = 0.791, t_{62} = 10.195, P < 0.001$ ). Both dimensions were negatively correlated with the amount of sand piled above the nest, and while the relationship regarding nest entrance height was marginally nonsignificant, that involving nest entrance width was significant (nest entrance height:  $r_S = -0.225, t_{62} = -1.818, P = 0.074$ ; width:  $r_S = -0.294, t_{62} = -2.421, P = 0.018$ ).

For both nest entrance height and width, there was a significant interaction between the effects of predation treatment and whether or not males engaged in total filial cannibalism (Table 3). Specifically, the height and width of nest entrances was unrelated to the predation treatment among partial filial cannibals (nest entrance height:  $\beta_S = -1.024 \pm 1.117, t_{52} = -0.917, P = 0.364$ ; width:  $\beta_S = 2.718 \pm 3.29, t_{52} = 0.826, P = 0.412$ ), whereas among total filial cannibals, exposure to a perch was associated with significantly taller and wider nest entrances (nest entrance height:  $\beta_S = 4.500 \pm 2.133, t_{52} = 2.109, P = 0.040$ ; Fig. 3a; width:  $\beta_S = 19.217 \pm 6.279, t_{52} = 3.061, P = 0.003$ ; Fig. 3b). For both nest entrance height and width, the mode of filial cannibalism did not interact significantly with prespawning male body condition, male length, number of eggs consumed or dissolved oxygen level (Table 3). Similarly, nest entrance height and width were not significantly affected by prespawning male body condition, male length, number of eggs consumed or dissolved oxygen level, although there was a marginally nonsignificant tendency for longer males to build taller nest entrances (Table 3).

The height of sand piled on the nest was not affected by perch exposure or dissolved oxygen, with total and partial filial cannibals behaving similarly in this regard (Table 3). Longer males piled significantly more sand on their nests regardless of the mode of filial cannibalism (Table 3). The relationship between the number of eggs eaten and the height of the sand piled on a male's nest depended on the mode of filial cannibalism (Table 3, Fig. 4). Specifically, for partial filial cannibals, there was no significant relationship between the number of eggs consumed and the height of

**Table 2**  
Parameter estimates from model of change in male wet mass (mg) over the brooding period

Predictor	$\beta_S$ (SE)	$\beta$ (SE)	$t$ (P)
Intercept	-25.584 (5.622)	-25.584 (5.622)	-4.551 (<0.001)
Number of eggs eaten	62.042 (12.554)	0.080 (0.016)	4.942 (<0.001)
Total filial cannibalism	5.901 (13.073)	5.901 (13.073)	0.451 (0.653)
Number of eggs eaten * Total filial cannibalism	21.861 (23.168)	0.028 (0.030)	0.944 (0.349)

Predictor variables were mean centred. Regression coefficients based on raw predictor values ( $\beta$ ) as well as rescaled regression coefficients ( $\beta_S$ ) from scaling nonbinary inputs by two standard deviations are reported.

**Table 3**  
Parameter estimates for models of nest architecture at the completion of brooding

Predictor*	Nest entrance height (mm)			Nest entrance width (mm)			Nest sand pile height (mm)		
	$\beta_s$ (SE)	$\beta$ (SE)	$t$ (P)	$\beta_s$ (SE)	$\beta$ (SE)	$t$ (P)	$\beta_s$ (SE)	$\beta$ (SE)	$t$ (P)
Intercept	10.837 (0.523)	10.837 (0.523)	20.709 (<0.001)	39.253 (1.540)	39.253 (1.540)	25.487 (<0.001)	67.070 (1.008)	67.070 (1.008)	66.513 (<0.001)
Total filial cannibalism	4.236 (1.228)	4.236 (1.228)	3.449 (0.001)	10.679 (3.615)	10.679 (3.615)	2.954 (0.005)	0.097 (2.367)	0.097 (2.367)	0.041 (0.967)
Perch exposure	0.530 (1.002)	0.530 (1.002)	0.528 (0.600)	7.358 (2.950)	7.358 (2.950)	2.494 (0.016)	-0.335 (1.932)	-0.335 (1.932)	-0.174 (0.863)
Number of eggs eaten	0.090 (1.185)	0.000 (0.002)	0.076 (0.940)	5.408 (3.488)	0.007 (0.004)	1.550 (0.127)	-2.594 (2.284)	-0.003 (0.003)	-1.136 (0.261)
Pre-spawning male body condition	-0.818 (0.963)	-5.934 (6.985)	-0.850 (0.399)	-0.711 (2.834)	-5.160 (20.558)	-0.251 (0.803)	-1.163 (1.855)	-8.440 (13.460)	-0.627 (0.533)
Male length (mm)	1.862 (0.976)	0.182 (0.096)	1.907 (0.062)	4.661 (2.874)	0.456 (0.281)	1.622 (0.111)	5.102 (1.881)	0.500 (0.184)	2.712 (0.009)
Dissolved oxygen levels (%)	0.610 (1.072)	0.027 (0.047)	0.569 (0.572)	-2.353 (3.155)	-0.102 (0.137)	-0.746 (0.459)	0.760 (2.066)	0.033 (0.090)	0.368 (0.714)
Perch exposure*Total filial cannibalism	5.524 (2.408)	5.524 (2.408)	2.294 (0.026)	16.499 (7.088)	16.499 (7.087)	2.328 (0.024)	-3.497 (4.641)	-3.497 (4.641)	-0.754 (0.455)
Number of eggs eaten*Total filial cannibalism	1.186 (2.313)	0.002 (0.003)	0.513 (0.610)	4.623 (6.808)	0.006 (0.009)	0.679 (0.500)	-10.904 (4.457)	-0.014 (0.006)	-2.446 (0.018)
Pre-spawning male body condition*Total filial cannibalism	-2.437 (2.254)	-0.177 (0.164)	-1.081 (0.285)	-5.034 (6.633)	-36.519 (48.126)	-0.759 (0.451)	7.689 (4.343)	55.782 (31.510)	1.770 (0.083)
Male length (mm)*Total filial cannibalism	0.068 (2.371)	0.007 (0.232)	0.029 (0.977)	-0.523 (6.978)	-0.051 (0.683)	-0.075 (0.941)	3.486 (4.569)	0.341 (0.447)	0.763 (0.449)
Dissolved oxygen levels (%)*Total filial cannibalism	4.063 (2.935)	0.177 (0.128)	1.384 (0.172)	5.993 (8.639)	0.261 (0.376)	0.0694 (0.491)	0.151 (0.246)	0.151 (0.246)	0.612 (0.543)

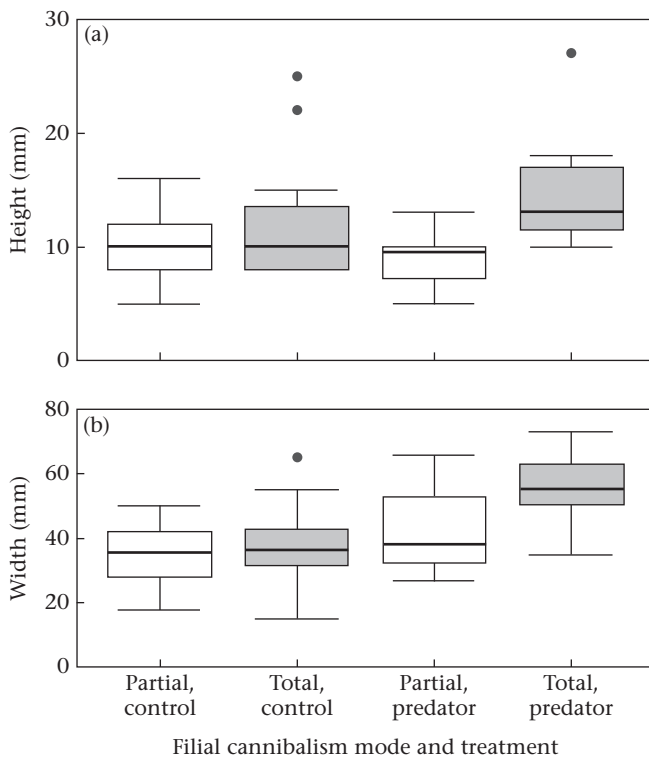
Perch exposure was dummy coded with 'predator' treatment as 0.5 and 'control' as -0.5, and all other predictor variables were mean centred. Regression coefficients based on raw predictor values ( $\beta$ ) as well as rescaled regression coefficients ( $\beta_s$ ) from scaling nonbinary inputs by two standard deviations are reported.

the sand pile ( $\beta_s = 0.473 \pm 2.886$ ,  $t_{52} = 0.164$ ,  $P = 0.871$ ; Fig. 4). By contrast, for total filial cannibals, consumption of more eggs was associated with piling less sand above the nest ( $\beta_s = -10.431 \pm 3.397$ ,  $t_{52} = -3.071$ ,  $P = 0.003$ ; Fig. 4). There was also a marginally nonsignificant tendency for the effect of pre-spawning male body condition on nest sand pile height to differ between partial and total filial cannibals but the main effect of body condition was not significant (Table 3).

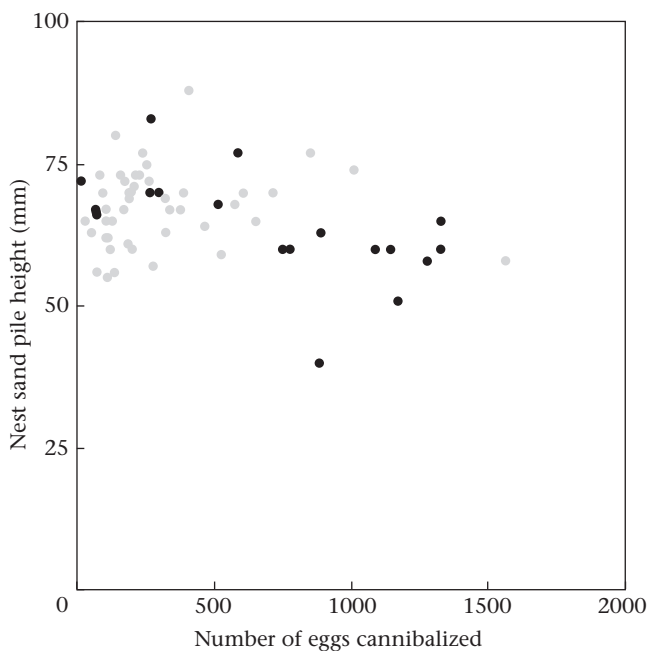
## DISCUSSION

We predicted that exposure to a predator would result in increased investment in the existing young, since the perceived likelihood of surviving to engage in future reproduction should be diminished by a seemingly risky environment. However, we found that partial filial cannibalism was not influenced by the presence of a predatory perch. For total filial cannibalism, males tended to consume their entire brood less often in the presence of a perch, although this result was marginally nonsignificant. Therefore, there is currently insufficient evidence to show that parental predation risk influences filial cannibalism. Future research addressing total filial cannibalism should thus consider predation risk. First, our results suggest that threat of predation may have a more prominent effect on this form of filial cannibalism. Second, total filial cannibalism is only thought to be adaptive if parents can survive to reproduce again (Manica, 2002), which is contingent on avoiding predation. By contrast, partial filial cannibalism may be less (or not at all) influenced by predation risk because it can benefit parents in ways that do not depend on further reproduction, such as through improved survival of existing young (Klug et al., 2006; Lehtonen & Kvarnemo, 2015a, 2015b; see also Klug & Lindström, 2008).

As far as we are aware, the influence of parental predation risk has not previously been specifically investigated within the context of filial cannibalism. However, in contrast to our findings, some studies on other forms of parental investment have shown increased investment in existing young in response to predation threat. For example, in the side-blotched lizard, *Uta stansburiana*, and shaded broad-bar moth, *Scotopteryx chenopodiata*, females that have been injured, and are thus less able to evade predators, appear to elevate their level of parental expenditure on current offspring (Fox & McCoy, 2000; Javoš & Tammaru, 2004). Thus, injury may have a more direct bearing on parents' perception of predation risk and, as a result, their current reproductive decisions. Similarly, the timing of predator cues may be important especially for total filial cannibalism, which typically occurs soon after spawning (Forsgren et al., 1996; reviewed in Manica, 2002). However, while pre-spawning exposure to predators may elicit a stronger effect on filial cannibalism, such patterns could be confounded by the potential of predator exposure to also affect courtship and spawning (Forsgren & Magnhagen, 1993; Wong et al., 2009). It also remains possible that filial cannibalism is not selected to be sensitive to predation threat in sand gobies. However, sand gobies should at least have the capacity for plasticity of filial cannibalism, because the behaviour is modulated by other environmental factors (Chin-Baarstad et al., 2009; Pamplouie et al., 2004). Similarly, other behaviours in sand gobies can respond to predation threat (foraging: Magnhagen, 1988; courtship and spawning: Forsgren & Magnhagen, 1993; Wong et al., 2009), suggesting that variation in predation risk is present and perceived by sand gobies. Finally, it remains feasible that filial cannibalism behaviour is retained during periods of elevated predation risk despite reduced parental expectation of future reproduction due to yet unknown benefits of offspring consumption during such circumstances. For example, if predation threat restricts the ability of individuals to forage (Magnhagen, 1988), parents may be selected to exploit their own young as a



**Figure 3.** Tukey box plots showing the distribution of nest entrance (a) heights and (b) widths for male sand gobies that committed total or partial filial cannibalism and were either exposed to a perch in the predator treatment or nothing in a control treatment. The internal line of each box represents the median value and the edges the first and third quartiles. The whiskers denote the lowest and highest data points that are within one step of the first and third quartiles, respectively, where one step is 1.5 times the interquartile range. Values greater than one step above the third quartile are denoted with black dots.



**Figure 4.** Plot of nest sand pile heights against the number of eggs consumed by the nest-holding male during the brooding period. Data points from total filial cannibals are black and those from partial filial cannibals are grey.

safe energy source (cf. McNamara, 1990). Therefore, further research exploring how predation risk relates to specific activities, such as nest tending and foraging, is necessary.

Previous studies indicate that consuming eggs can reduce weight loss by males, suggesting energetic benefit from this activity (Klug et al., 2006; Lindström, 1998; Lissåker et al., 2003). In the current study, our results suggest that any such energetic advantage enjoyed by total filial cannibals is not a direct result of avoiding caring for young. In particular, although total filial cannibals lost less weight than partial filial cannibals (which cared for the young over the full duration of the brood care phase), this difference appears to be explained by the greater number of eggs consumed by total filial cannibals, even without considering the reduced parental expenditure of total cannibals. Furthermore, we found that nest structure was unrelated to the number of eggs consumed by male gobies except for total filial cannibals, in which males that consumed more eggs piled less sand on their nests. Thus, there is no evidence to suggest that energy from egg consumption was used for nest construction. Finally, our finding that neither form of filial cannibalism was related to male body condition is in contrast with the idea that males in poor condition use filial cannibalism to replenish energy reserves. While such a result is in accordance with earlier work on sand gobies (Chin-Baarstad et al., 2009; Forsgren, 1997; Klug et al., 2006; Lissåker et al., 2003), the situation in other taxa might be different (Neff, 2003; Okuda et al., 2004 see also: Candolin, 2000; Kvarnemo, Svensson, & Forsgren, 1998; Manica, 2004; Marconato et al., 1993; Takahashi & Kohda, 2004). For example, in the mouthbrooding cardinalfish, *Apogon doederleini*, males tend to engage in greater amounts of filial cannibalism towards the end of the breeding season when their body condition has deteriorated as a result of restricted foraging opportunities during earlier breeding attempts (Okuda & Yanagisawa, 1996; Takeyama et al., 2002).

The factor that most strongly influenced the occurrence of total filial cannibalism was clutch size. In line with findings from previous work on both sand gobies (see Methods section), as well as other species (see Manica, 2002 for a review) such as the fantail darter, *Etheostoma flabellare* (Lindström & Sargent, 1997) and bluegilled sunfish, *Lepomis macrochirus* (Neff, 2003), males were more likely to engage in total filial cannibalism when their initial clutch size was small. This suggests that the benefits of total filial cannibalism outweigh the costs of offspring consumption when brood size is small. Moreover, our finding that consumption of a large number of eggs among total filial cannibals was associated with piling less sand onto the nest suggests that those males that totally consume larger clutches may be less motivated to maintain the nest site or are inherently less capable of doing so.

We found that among total filial cannibals, males that were exposed to predatory perch constructed larger nest entrances than other males. This could be adaptive if small nest entrances inhibit predator evasion, or if nest construction incites predation, as suggested by Magnhagen and Forsgren (1991). Alternatively, nest maintenance may be reduced as a strategy to renest at a safer time or location (but see Magnhagen, 1990; Magnhagen & Forsgren, 1991). Curiously though, the amount of sand piled on the nest was not similarly affected. This may reflect the importance of the sand pile in concealing the nest from predators (Lindström & Ranta, 1992), or the potential greater value of a large sand pile in attracting mates (Lehtonen & Lindström, 2009; Lugli, 2013; Svensson & Kvarnemo, 2005; cf. Lehtonen & Wong, 2009) compared to a small nest entrance (Svensson & Kvarnemo, 2005, 2007). Intriguingly, unlike total filial cannibals, for males that cared for at least some of their eggs, predator exposure was unrelated to nest architecture. Perhaps, the possibility of increased vulnerability to egg predators associated with larger nest entrances (Lissåker &

Kvarnemo, 2006) explains why predator-exposed parental males still built small nest entrances. In other words, males that are committed to rearing at least some of their brood appear not to compromise care even when doing so could jeopardize their own survival.

In conclusion, our results indicate that partial filial cannibalism was not affected by the perceived threat of predation to the parent, possibly because this type of cannibalism is performed to benefit the current brood. Our results with regard to total filial cannibalism were less clear-cut, with a nonsignificant tendency for males to avoid total filial cannibalism when predation threat was high, suggesting that further research into this area could be informative. With regard to nest construction, we showed that consumption of a larger clutch was not linked to more elaborate nest construction, which may indicate that males do not consume eggs for the purpose of nest maintenance. Moreover, we found that aspects of nest architecture were influenced by the presence of a predatory perch only in total filial cannibals, suggesting that care-giving males do not compromise nest maintenance when confronted by a predator. Predator presence was linked to large nest entrances among total filial cannibals, possibly due to reluctance to re-nest in the vicinity of a predator or because large-entrance nests may be safer to build or occupy. Overall, the findings of this study highlight the importance of considering the effect of adult predation risk on parental effort decisions.

## Acknowledgments

We thank the staff of the Tvärminne Zoological Station for their assistance in the field and provision of an excellent writing environment; Jessica Åsbacka, Isaac Gravalin, Tamás Kopcsányi and William Sowersby for help collecting fish; Ulrika Candolin and Charlotta Kvarnemo for fruitful discussions on experimental design; two anonymous referees and Marie Herberstein for providing helpful feedback on the manuscript; and Anmei Vuong for formatting assistance. We also acknowledge financial support from The Holsworth Wildlife Research Endowment – ANZ Trustees Foundation (to N.D.S.D.) and The Australian Research Council (to B.B.M.W.).

## References

- Alonso-Alvarez, C., & Velando, A. (2012). Benefits and costs of parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 40–61). Oxford, U.K.: Oxford University Press.
- Andrén, M. N., & Kvarnemo, C. (2014). Filial cannibalism in a nest-guarding fish: Females prefer to spawn in nests with few eggs over many. *Behavioral Ecology Sociobiology*, *68*, 1565–1576.
- Arundell, K. L., Wedell, N., & Dunn, A. M. (2014). The impact of predation risk and of parasitic infection on parental care in brooding crustaceans. *Animal Behaviour*, *96*, 97–105.
- Bjelvenmark, J., & Forsgren, E. (2003). Effects of mate attraction and male-male competition on paternal care in a goby. *Behaviour*, *140*, 55–69.
- Candolin, U. (2000). Changes in expression and honesty of sexual signalling over the reproductive lifetime of sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, *267*, 2425–2430.
- Chin-Baarstad, A., Klug, H., & Lindström, K. (2009). Should you eat your offspring before someone else does? Effect of an egg predator on filial cannibalism in the sand goby. *Animal Behaviour*, *78*, 203–208.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Deal, N. D. S., & Wong, B. B. M. (2016). How mate availability influences filial cannibalism. *Quarterly Review of Biology*, *91*, 47–67.
- Evans, S., & Tallmark, B. (1979). A modified drop-net method for sampling mobile epifauna on marine shallow sandy bottoms. *Holarctic Ecology*, *2*, 58–64.
- Fonds, M. (1973). Sand gobies in the Dutch Wadden Sea (*Pomatoschistus*, Gobiidae, Pisces). *Netherlands Journal of Sea Research*, *6*, 417–473.
- Forsgren, E. (1997). Female sand gobies prefer good fathers over dominant males. *Proceedings of the Royal Society B: Biological Sciences*, *264*, 1283–1286.
- Forsgren, E., Karlsson, A., & Kvarnemo, C. (1996). Female sand gobies gain direct benefits by choosing males with eggs in their nests. *Behavioral Ecology Sociobiology*, *39*, 91–96.
- Forsgren, E., & Magnhagen, C. (1993). Conflicting demands in sand gobies: Predators influence reproductive behaviour. *Behaviour*, *126*, 125–135.
- Fox, S. F., & McCoy, J. K. (2000). The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. *Oecologia*, *122*, 327–334.
- Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, *27*, 2865–2873.
- Gravel, M. A., & Cooke, S. J. (2013). Does nest predation pressure influence the energetic cost of nest guarding in a teleost fish? *Environmental Biology of Fishes*, *96*, 93–107.
- Gross, M. R. (2005). The evolution of parental care. *Quarterly Review of Biology*, *80*, 37–45.
- Hanssen, S. A. (2006). Costs of an immune challenge and terminal investment in a long-lived bird. *Ecology*, *87*, 2440–2446.
- Hansson, S., Arrhenius, F., & Nellbring, S. (1997). Diet and growth of pikeperch (*Stizostedion lucioperca* L.) in a Baltic Sea area. *Fisheries Research*, *31*, 163–167.
- Healey, M. C. (1971). Gonad development and fecundity of the sand goby, *Gobius minutus* Pallas. *Transactions of the American Fisheries Society*, *100*, 520–526.
- Javois, J., & Tammara, T. (2004). Reproductive decisions are sensitive to cues of life expectancy: The case of a moth. *Animal Behaviour*, *68*, 249–255.
- Jones, J. C., & Reynolds, J. D. (1999). The influence of oxygen stress on female choice for male nest structure in the common goby. *Animal Behaviour*, *57*, 189–196.
- Jones, A. G., Walker, D., Lindström, K., Kvarnemo, C., & Avise, J. C. (2001). Surprising similarity of sneaking rates and genetic mating patterns in two populations of sand goby experiencing disparate sexual selection regimes. *Molecular Ecology*, *10*, 461–469.
- Klug, H., Alonso, S. H., & Bonsall, M. B. (2012). Theoretical foundations of parental care. In N. J. Royle, P. T. Smiseth, & M. Kölliker (Eds.), *The evolution of parental care* (pp. 21–39). Oxford, U.K.: Oxford University Press.
- Klug, H., & Lindström, K. (2008). Hurry-up and hatch: Selective filial cannibalism of slower developing eggs. *Biology Letters*, *4*, 160–162.
- Klug, H., Lindström, K., & St Mary, C. M. (2006). Parents benefit from eating offspring: Density-dependent egg survivorship compensates for filial cannibalism. *Evolution*, *60*, 2087–2095.
- Koli, L., Rask, M., & Aro, E. (1985). Growth, age distribution and year class strength of perch, *Perca fluviatilis* L., at Tvärminne, northern Baltic Sea. *Aqua Fennica*, *1*, 161–167.
- Kume, G., Yamaguchi, A., & Taniuchi, T. (2000). Filial cannibalism in the paternal mouthbrooding cardinalfish *Apogon lineatus*: Egg production by the female as the nutrition source for the mouthbrooding male. *Environmental Biology of Fishes*, *58*, 233–236.
- Kvarnemo, C. (1994). Temperature differentially affects male and female reproductive rates in the sand goby: Consequences for operational sex ratio. *Proceedings of the Royal Society B: Biological Sciences*, *256*, 151–156.
- Kvarnemo, C. (1997). Food affects the potential reproductive rates of sand goby females but not of males. *Behavioral Ecology*, *8*, 605–611.
- Kvarnemo, C., Svensson, O., & Forsgren, E. (1998). Parental behaviour in relation to food availability in the common goby. *Animal Behaviour*, *56*, 1285–1290.
- Lappalainen, A., Rask, M., Koponen, H., & Vesala, S. (2001). Relative abundance, diet and growth of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) at Tvärminne, northern Baltic Sea, in 1975 and 1997: Responses to eutrophication? *Boreal Environment Research*, *6*, 107–118.
- Lehtonen, T. K., & Kvarnemo, C. (2015a). Density effects on fish egg survival and infections depend on salinity. *Marine Ecology Progress Series*, *540*, 183–191.
- Lehtonen, T. K., & Kvarnemo, C. (2015b). Infections may select for filial cannibalism by impacting egg survival in interactions with water salinity and egg density. *Oecologia*, *178*, 673–683.
- Lehtonen, T. K., & Lindström, K. (2007). Mate compatibility, parental allocation and fitness consequences of mate choice in *Pomatoschistus minutus*. *Behavioral Ecology Sociobiology*, *61*, 1581–1588.
- Lehtonen, T. K., & Lindström, K. (2009). Females decide whether size matters: Plastic mate preferences tuned to the intensity of male–male competition. *Behavioral Ecology*, *20*, 196–199.
- Lehtonen, T. K., Lindström, K., & Wong, B. B. M. (2013). Effect of egg predator on nest choice and nest construction in sand gobies. *Animal Behaviour*, *86*, 867–871.
- Lehtonen, T. K., & Wong, B. B. M. (2009). Should females prefer males with elaborate nests? *Behavioral Ecology*, *20*, 1015–1019.
- Lehtonen, T. K., Wong, B. B. M., & Kvarnemo, C. (2016). Effects of salinity on nest-building behaviour in a marine fish. *BMC Ecology*, *16*, 7.
- Lehtonen, T. K., Wong, B. B. M., & Lindström, K. (2010). Fluctuating mate preferences in a marine fish. *Biology Letters*, *6*, 21–23.
- Li, D., & Jackson, R. R. (2003). A predator's preference for egg-carrying prey: A novel cost of parental care. *Behavioral Ecology Sociobiology*, *55*, 129–136.
- Lindström, K. (1988). Male-male competition for nest sites in the sand goby, *Pomatoschistus minutus*. *Oikos*, *53*, 67–73.
- Lindström, K. (1998). Effects of costs and benefits of brood care on filial cannibalism in the sand goby. *Behavioral Ecology Sociobiology*, *42*, 101–106.
- Lindström, K., & Hellström, M. (1993). Male size and parental care in the sand goby, *Pomatoschistus minutus*. *Ethology Ecology and Evolution*, *5*, 97–106.
- Lindström, K., & Pampoulie, C. (2005). Effects of resource holding potential and resource value on tenure at nest sites in sand gobies. *Behavioral Ecology*, *16*, 70–74.
- Lindström, K., & Ranta, E. (1992). Predation by birds affects population structure in breeding sand goby, *Pomatoschistus minutus*, males. *Oikos*, *64*, 527–532.
- Lindström, K., & Sargent, R. C. (1997). Food access, brood size and filial cannibalism in the fantail darter, *Etheostoma flabellare*. *Behavioral Ecology Sociobiology*, *40*, 107–110.



- Lissåker, M. (2007). Does time of the season influence filial cannibalism in the sand goby, *Pomatoschistus minutus*? *Environmental Biology of Fishes*, 80, 69–75.
- Lissåker, M., & Kvarnemo, C. (2006). Ventilation or nest defense—parental care trade-offs in a fish with male care. *Behavioral Ecology Sociobiology*, 60, 864–873.
- Lissåker, M., Kvarnemo, C., & Svensson, O. (2003). Effects of a low oxygen environment on parental effort and filial cannibalism in the male sand goby, *Pomatoschistus minutus*. *Behavioral Ecology*, 14, 374–381.
- Lissåker, M., & Svensson, O. (2008). Cannibalize or care? The role of perceived paternity in the sand goby, *Pomatoschistus minutus*. *Behavioral Ecology Sociobiology*, 62, 1467–1475.
- Lugli, M. (2013). Sand pile above the nest amplifies the sound emitted by the male sand goby. *Environmental Biology of Fishes*, 96, 1003–1012.
- Magnhagen, C. (1988). Changes in foraging as a response to predation risk in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*. *Marine Ecology Progress Series*, 49, 21–26.
- Magnhagen, C. (1990). Reproduction under predation risk in the sand goby, *Pomatoschistus minutus* and the black goby, *Gobius niger*: The effect of age and longevity. *Behavioral Ecology Sociobiology*, 26, 331–335.
- Magnhagen, C. (1992). Parental care and predation risk in fish. *Annales Zoologici Fennici*, 29, 227–232.
- Magnhagen, C., & Forsgren, E. (1991). Behavioural responses to different types of predators by sand goby *Pomatoschistus minutus*: An experimental study. *Marine Ecology Progress Series*, 70, 11–16.
- Magnhagen, C., & Kvarnemo, L. (1989). Big is better: The importance of size for reproductive success in male *Pomatoschistus minutus* (Pallas) (Pisces, Gobiidae). *Journal of Fish Biology*, 35, 765–763.
- Manica, A. (2002). Filial cannibalism in teleost fish. *Biological Reviews of the Cambridge Philosophical Society*, 77, 261–277.
- Manica, A. (2004). Parental fish change their cannibalistic behaviour in response to the cost-to-benefit ratio of parental care. *Animal Behaviour*, 67, 1015–1021.
- Marconato, A., Bisazza, A., & Fabris, M. (1993). The cost of parental care and egg cannibalism in the river bullhead, *Cottus gobio* L. (Pisces, Cottidae). *Behavioral Ecology Sociobiology*, 32, 229–237.
- McNamara, J. M. (1990). The Policy which maximises long-term survival of an animal faced with the risks of starvation and predation. *Advances in Applied Probability*, 22, 295–308.
- Mehlis, M., Bakker, T. C. M., Engqvist, L., & Frommen, J. G. (2010). To eat or not to eat: Egg-based assessment of paternity triggers fine-tuned decisions about filial cannibalism. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2627–2635.
- Neff, B. D. (2003). Paternity and condition affect cannibalistic behavior in nest-tending bluegill sunfish. *Behavioral Ecology Sociobiology*, 54, 377–384.
- Nordling, D., Andersson, M., Zohari, S., & Lars, G. (1998). Reproductive effort reduces specific immune response and parasite resistance. *Proceedings of the Royal Society B: Biological Sciences*, 265, 1291–1298.
- Okuda, N., Ito, S., & Iwao, H. (2004). Mate availability and somatic condition affect filial cannibalism in a paternal brooding goby. *Behaviour*, 141, 279–296.
- Okuda, N., Takeyama, T., & Yanagisawa, Y. (1997). Age-specific filial cannibalism in a paternal mouthbrooding fish. *Behavioral Ecology Sociobiology*, 41, 363–369.
- Okuda, N., & Yanagisawa, Y. (1996). Filial cannibalism by mouthbrooding males of the cardinal fish, *Apogon doederleini*, in relation to their physical condition. *Environmental Biology of Fishes*, 45, 397–404.
- Olsson, K. H., Kvarnemo, C., & Svensson, O. (2009). Relative costs of courtship behaviours in nest-building sand gobies. *Animal Behaviour*, 77, 541–546.
- Pampoulie, C., Lindström, K., & St Mary, C. M. (2004). Have your cake and eat it too: Male sand gobies show more parental care in the presence of female partners. *Behavioral Ecology*, 15, 199–204.
- Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, 118, 1883–1891.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Rasband, W. S. (1997–2015). *ImageJ*. Bethesda, MD: U. S. National Institutes of Health. <http://imagej.nih.gov/ij/>.
- Rohwer, S. (1978). Parent cannibalism of offspring and egg raiding as a courtship strategy. *American Naturalist*, 112, 429–440.
- Salgado, J. P., Cabral, H. N., & Costa, M. J. (2004). Feeding ecology of the gobies *Pomatoschistus minutus* (Pallas, 1770) and *Pomatoschistus microps* (Krøyer, 1883) in the upper Tagus estuary. *Portugal. Scientia Marina*, 68, 425–434.
- Sargent, R. C., & Gross, M. R. (1985). Parental investment decision rules and the Concorde fallacy. *Behavioral Ecology Sociobiology*, 17, 43–45.
- Steinhart, G. B., Dunlop, E. S., Ridgway, M. S., & Marschall, E. A. (2008). Should I stay or should I go? Optimal parental care decisions of a nest-guarding fish. *Evolutionary Ecology Research*, 10, 351–371.
- Svensson, O., & Kvarnemo, C. (2003). Sexually selected nest-building – *Pomatoschistus minutus* males build smaller nest-openings in the presence of sneaker males. *Journal of Evolutionary Biology*, 16, 896–902.
- Svensson, O., & Kvarnemo, C. (2005). The importance of sperm competition risk and nest appearance for male behavior and female choice in the sand goby, *Pomatoschistus minutus*. *Behavioral Ecology*, 16, 1042–1048.
- Svensson, O., & Kvarnemo, C. (2007). Parasitic spawning in sand gobies: An experimental assessment of nest-opening size, sneaker male cues, paternity, and filial cannibalism. *Behavioral Ecology*, 18, 410–419.
- Takahashi, D., & Kohda, M. (2004). Courtship in fast water currents by a male stream goby (*Rhinogobius brunneus*) communicates the parental quality honestly. *Behavioral Ecology Sociobiology*, 55, 431–438.
- Takegaki, T., Svensson, O., & Kvarnemo, L. (2012). Socially induced tactic change in 2 types of sand goby sneaker males. *Behavioral Ecology*, 23, 742–750.
- Takeyama, T., Okuda, N., & Yanagisawa, Y. (2002). Seasonal pattern of filial cannibalism by *Apogon doederleini* mouthbrooding males. *Journal of Fish Biology*, 61, 633–644.
- Thomson, R. L., Pakanen, V. M., Tracy, D. M., Kvist, L., Lank, D. B., Rönkä, A., et al. (2014). Providing parental care entails variable mating opportunity costs for male Temminck's stints. *Behavioral Ecology Sociobiology*, 68, 1261–1272.
- Toomet, O., & Henningsen, A. (2008). Sample selection models in R: Package sampleSelection. *Journal of Statistical Software*, 27, 1–23.
- Trivers, R. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection & the Descent of Man, 1871–1971* (pp. 136–179). Chicago, IL: Aldine Press.
- Vance, C., & Ritter, N. (2014). Is peace a missing value or a zero? On selection models in political science. *Journal of Peace Research*, 51, 528–540.
- Warton, D. I., Duursma, R. A., Falster, D. S., & Taskinen, S. (2012). smatr 3—an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, 3, 257–259.
- Williams, G. C. (1966a). *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton, NJ: Princeton University Press.
- Williams, G. C. (1966b). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100, 687–690.
- Wong, B. B. M., Järvenpää, M., & Lindström, K. (2009). Risk-sensitive mating decisions in a visually compromised environment. *Biology Letters*, 5, 600–602.
- Wooldridge, J. M. (2002). *Sample selection, attrition, and stratified sampling. Econometric analysis of cross section and panel data*. Cambridge, MA: The MIT Press.

## APPENDIX. SAMPLE SELECTION MODELLING

As an alternative approach to examine what influences the number of eggs eaten during partial filial cannibalism, we fitted a Heckman sample selection model (Tobit-2 model) to our data using full information maximum likelihood estimation with the sampleSelection R package (Toomet & Henningsen, 2008). This model had two parts. First, a probit regression model was used to estimate the effect of predictors upon the likelihood of the occurrence of partial (rather than total) filial cannibalism. Just like the probit model of the occurrence of total filial cannibalism presented in the main text, we used prespawning male body condition, oxygen saturation level, predation treatment and initial number of eggs spawned as predictors. This first part of the Heckman selection model was thus identical to the probit model in the main text, except that the sign of all regression coefficients was reversed since the occurrence of partial filial cannibalism is effectively the opposite of the occurrence of total filial cannibalism (as all males ate some eggs). Accordingly, we do not present the results of this selection part of the model.

The second part of the Heckman selection model determined the effects of predictors on the response variable, in this case, the natural logarithm of the number of eggs consumed during partial filial cannibalism. This is analogous to the ordinary least squares (OLS) model of the same response variable presented in the main text except this model corrects for biases in the estimates of independent variable effects on egg consumption during partial filial cannibalism that may have arisen as a result of males nonrandomly engaging in total filial cannibalism (see Wooldridge, 2002). We also used the same predictors here as the OLS model (male body condition, oxygen saturation levels and predation treatment). Beyond the empirical justification for not including initial number of eggs spawned as a predictor of the extent of partial filial cannibalism discussed in the main text there is also a practical benefit to this choice: that model identification is improved when a variable is used to predict the occurrence of an event but not the extent of the response when the event occurs (Vance & Ritter, 2014).

The results of the Heckman selection model were qualitatively similar to those of the OLS model (Table A1, cf. Table 1). Specifically, we found no significant effect of male body condition, oxygen saturation level or predation treatment on the number of eggs

eaten in cases of partial filial cannibalism (Table A1). Furthermore, there was no significant correlation between the errors of the selection equation (describing the occurrence of total filial cannibalism) and outcome equation (describing the number of eggs eaten during partial filial cannibalism) in the Heckman selection model ( $r_S = 0.028$ ,  $t_{52} = 0.056$ ,  $P = 0.955$ ). The interpretation of this is that after taking into account a male's body condition, clutch size, oxygen saturation level and predator exposure level his propensity to engage in total filial cannibalism does not influence the number of eggs he will consume when he engages in partial filial cannibalism. In other words, there is no evidence that selection bias arising from nonrandom occurrence of total filial cannibalism was a serious problem in this experiment (see Vance & Ritter, 2014).

**Table A1**

Parameter estimates from Heckman sample selection model of partial filial cannibalism outcome equation

Predictor	$\beta_S$ (SE)	$\beta$ (SE)	$t$ ( $P$ )
Intercept	5.363 (0.165)	5.363 (0.165)	32.513 (<0.001)
Prespawning male body condition (g)	-0.347 (0.241)	-2.521 (1.748)	-1.442 (0.149)
Perch exposure	-0.043 (0.256)	-0.043 (0.256)	-0.170 (0.865)
Dissolved oxygen levels (%)	-0.012 (0.219)	-0.001 (0.010)	-0.053 (0.958)

Perch exposure was dummy coded with 'predator' treatment as 0.5 and 'control' as -0.5, and all other predictor variables were mean centred. Regression coefficients based on raw predictor values ( $\beta$ ) as well as rescaled regression coefficients ( $\beta_S$ ) from scaling nonbinary inputs by two standard deviations are reported.