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

Nicholas D. S. Deal a,*, Topi K. Lehtonen a, b, c, Kai Lindström b, Bob B. M. Wong a

a School of Biological Sciences, Monash University, Victoria, Australia
b Environmental and Marine Biology, Åbo Akademi University, Turku, Finland
c Department of Biology, 2004 University of Turku, Finland

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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.

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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. Lissäker, 2007; Marconato et al., 1993; Okuda & Yanagisawa, 1996; but see Mehlis, 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 inDeal & 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; Javois & 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 (Lissäker & 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; Lindström, 1998). Males may also use energy from egg consumption to improve their body condition (Klug et al., 2006; Lindström, 1998; Lissäker, 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-Baarsstad, 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, Jarvenpää, & Lindström, 2009; see also: Magnhagen, 1996; 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 Tvarminne 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 seawater 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 graviparity (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
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 ± 31 mm [mean ± SD], N = 40) and a 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 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 Lissáker 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 weighed 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 (>98%), 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 (Andrén & Kvarnemo, 2014; Forsgren et al., 1996; Klug et al., 2006; Lissäker & 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 (Andrén & Kvarnemo, 2014; Kvarnemo, 1997; Lissäker & Kvarnemo, 2006; see also: Lindström, 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 ± 14% [mean ± SD], N = 33; control treatment: 103 ± 8, N = 31) far exceed the hypoxic conditions where it is thought filial cannibalism and nest building may be influenced (Klug et al., 2006; Lissäker & Kvarnemo, 2006; Lissäker 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 nonintrusive 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 ± 545 (mean ± SD) eggs (N = 64), with 414 ± 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
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 1
<table>
<thead>
<tr>
<th>Predictor Variable</th>
<th>Total filial cannibalism (Probit model)</th>
<th>Partial filial cannibalism (OLS regression model)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>$b_0$ (SE)</td>
<td>$\beta$ (SE)</td>
</tr>
<tr>
<td>Initial clutch size</td>
<td>$-0.909$ (0.240)</td>
<td>$-0.909$ (0.240)</td>
</tr>
<tr>
<td>Prespawning male body condition (g)</td>
<td>$-2.448$ (0.595)</td>
<td>$-0.002$ (0.001)</td>
</tr>
<tr>
<td>Dissolved oxygen levels (%)</td>
<td>$-0.226$ (0.477)</td>
<td>$-1.642$ (3.458)</td>
</tr>
<tr>
<td>Perch exposure</td>
<td>$-0.808$ (0.442)</td>
<td>$-0.808$ (0.442)</td>
</tr>
<tr>
<td>Perch exposure</td>
<td>$-0.035$ (0.481)</td>
<td>$-0.002$ (0.021)</td>
</tr>
</tbody>
</table>

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 ($b_0$) from scaling nonbinary inputs by two standard deviations are reported following Gelman (2008).

### Table 3
<table>
<thead>
<tr>
<th>Predictor Variable</th>
<th>Parameter estimates from model of change in male wet mass (mg) over the brooding period</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>$b_0$ (SE)</td>
</tr>
<tr>
<td>Number of eggs eaten</td>
<td>$-25.584$ (5.622)</td>
</tr>
<tr>
<td>Total filial cannibalism</td>
<td>$26.042$ (12.554)</td>
</tr>
<tr>
<td>Number of eggs eaten</td>
<td>$5.901$ (13.073)</td>
</tr>
<tr>
<td>Total filial cannibalism</td>
<td>$21.861$ (23.168)</td>
</tr>
</tbody>
</table>

Predictor variables were mean centred. Regression coefficients based on raw predictor values ($\beta$) as well as rescaled regression coefficients ($b_0$) from scaling nonbinary inputs by two standard deviations are reported.
Parameter estimates for models of nest architecture at the completion of brooding

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Nest entrance height (mm)</th>
<th>Nest entrance width (mm)</th>
<th>Nest sand pile height (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>b (SE)</td>
<td>t (P)</td>
<td>b (SE)</td>
</tr>
<tr>
<td>Male length (mm)</td>
<td>4.063 (2.935)</td>
<td>0.177 (0.128)</td>
<td>1.384 (0.172)</td>
</tr>
<tr>
<td>Perch exposure was dummy coded</td>
<td>as predator treatment as</td>
<td>0.075 (0.941)</td>
<td>3.486 (4.569)</td>
</tr>
</tbody>
</table>
|                                  | 0.5 and all other predictor variables were mean centred. Regression coefficients based on raw predictor values (b) as well as rescaled regression coefficients (S) from scaling multicollinearity impact by two standard deviations are reported.

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, Scopteryx 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; Javoir & 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; Pampoulie 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

the sand pile (\(\beta_S = 0.473 \pm 2.886, t_{S2} = 0.164, P = 0.871\); Fig. 4). By contrast, for total filial cannibals, consumption of more eggs was associated with piling less sand above the nest (\(\Delta S = -10.431 \pm 3.397, t_{S2} = -3.071, P = 0.003\); 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, Scopteryx 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; Javoir & 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; Pampoulie 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
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; Lissäker 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; Lissäker 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 deederleini, 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 blue-gilled 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 larger 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 (Lissäker &
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 canibials, possibly due to reluctance to renest 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.

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References


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 ($t_5 = 0.028$, $t_{52} = 0.056$, $P = 0.955$). 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

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\beta$ (SE)</th>
<th>$\beta$ (SE)</th>
<th>t (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>5.363 (0.165)</td>
<td>5.363 (0.165)</td>
<td>32.513 (&lt;0.001)</td>
</tr>
<tr>
<td>Prespawning male body condition (g)</td>
<td>-0.347 (0.241)</td>
<td>-2.521 (1.748)</td>
<td>-1.442 (0.149)</td>
</tr>
<tr>
<td>Perch exposure</td>
<td>-0.043 (0.256)</td>
<td>-0.043 (0.256)</td>
<td>-0.170 (0.865)</td>
</tr>
<tr>
<td>Dissolved oxygen levels (%)</td>
<td>-0.012 (0.219)</td>
<td>-0.001 (0.010)</td>
<td>-0.053 (0.958)</td>
</tr>
</tbody>
</table>

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.