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

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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.

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 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 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; Javoiš & 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