



The impact of predation risk and of parasitic infection on parental care in brooding crustaceans



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Parental care is common in vertebrates, but less common in invertebrates, tending to occur in species that have relatively few young that can be protected from the physical or biotic environment. Individuals will be selected to trade off current and future reproductive success, leading to adaptive changes in brood care behaviour in response to predation risk. Investment in brood care may also be reduced as a result of costs of parasitic infection. Here we investigated the impact of predator cues and of parasite infection on brood care behaviour in amphipod crustaceans. We found no evidence for any reduction in brooding behaviour or reproductive success in response to infection by vertically transmitted microsporidian parasites. This may reflect the mechanism of parasite transmission, as vertically transmitted parasites rely on host reproduction to pass to the next generation. However, we found evidence for changes in brood care behaviour in response to increased risk of predation. Larger *Crangonyx pseudogracilis* females, with higher oxygen demands for their broods, showed a reduction in active brood care when exposed to predator cues. Additionally, *Gammarus duebeni* were found to reduce brooding duration in response to predator cues; we suggest that this earlier release of juveniles is likely to enhance survival of the brood, by spreading the risk of predation on juveniles.

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In its broadest sense, parental care is defined as any form of parental behaviour that increases the fitness of offspring (Clutton-Brock, 1991). Forms of parental care are very diverse, ranging from selection of oviposition sites and provisioning embryos via yolked eggs, to guarding embryos, carrying hatchlings on the body and feeding offspring (Davies, Krebs, & West, 2012; Wilson, 1975). Parental care is a common trait in vertebrates, and universal among birds and mammals (Trumbo, 2012). By contrast, in invertebrates, which commonly produce large numbers of offspring, parental care is less common (Kokko & Jennions, 2003) and tends to occur in species that have relatively few young that can be protected from the physical or biotic environment, such as predators (Davies et al., 2012). None the less, diverse species and forms of care are reported in invertebrates, including egg guarding (Agrawal, Combs, & Brodie, 2005; Gilbert, Thomas, & Manica, 2010) and offspring protection and provisioning (Gillespie, 1990; Nakahira, Tanaka, & Kudo, 2013; Suzuki, 2010) in insects and spiders, and brooding (Baeza & Fernández, 2002; Logerwell & Ohman, 1999; McCabe & Dunn,

1994) and active aeration (Baeza & Fernández, 2002; Dick, Bailey, & Elwood, 2002; Tarutis, Lewis, & Dyke, 2005) of embryos in aquatic crustaceans.

Investment in care is costly to the parent, and trade-offs between the costs and benefits of parental care are important in shaping life history patterns throughout the animal kingdom (Clutton-Brock, 1991; Davies et al., 2012). Animals that reproduce multiple times throughout their lifetime face a trade-off between current and future reproductive success (Trivers, 1972). The energetic demands of care may lead to a reduction in brood size or quality of care in the future (Buzatto, Requena, Martins, & Machado, 2007; Miller & Zink, 2012; Ward, Cotter, & Kilner, 2009; but see Suzuki, 2014). Additionally, mortality risks increase during parental care, because of increased energetic expenditure, trade-offs with foraging time and increased exposure to predation (e.g. Lewis & Loch-Mally, 2010; Liker & Székely, 2005; Reguera, 1999; Smith & Wootton, 1995).

As parental care may increase both energetic expenditure and exposure to predation, there are likely to be trade-offs between parental care and predator avoidance behaviours. This selects for adaptive behavioural responses; for example, parent birds often decrease offspring provisioning rate when the perceived risk of nest predation is high (Fontaine & Martin, 2006; Ghalambor, Peluc,

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& Martin, 2013). In the freshwater turtle *Emydera macquarii*, risk of predation on the mother affects nest site selection and reproductive success. In areas of high predation risk to the mother, females position nests closer to the water, which reduces offspring survival through increased risks of drowning and nest predation (Spencer, 2002). Similarly, female water striders select oviposition sites based upon predation risk to both the mother (Hirayama & Kasuya, 2013) and the eggs (Hirayama & Kasuya, 2009), with frequency of oviposition decreasing when predators are present.

In addition to predation risk, parental care strategies may also be influenced by parasite infection. Parasitism imposes fitness costs and energetic costs (e.g. Dobson & May, 1987; Møller, Allander, & Dufva, 1990), which are often associated with reduced reproductive output (Forbes, 1993) and host life history responses (Agnew, Koella, & Michalakis, 2000; Milinski, 1990). The energetic costs of parasitism may lead to reduced parental care. For example, experimental increase of mite loads in nests was found to reduce the food provisioning rates of barn swallows, *Hirundo rustica*, most probably because of reduced efficiency of infected parents (Møller, 1994). Conversely, Stott and Poulin (1996) reported an increase in ventilating egg-fanning behaviour in male upland bullies, *Gobiomorphus breviceps*, infected by the digenean trematode *Telogaster opisthorchis*. This is attributed to compensation for loss of future reproductive success, as heavily infected individuals suffer reduced physical condition and impaired antipredator responses (Stott & Poulin, 1996).

One strategy for protecting young from the external environment is to carry the embryos after laying and fertilization (Clutton-Brock, 1991), a form of parental care that is common among noninsect invertebrates (Trumbo, 2012). A number of species of crustacean passively brood their offspring, carrying the embryos on their body (e.g. Baeza & Fernández, 2002) or in an external brood pouch (marsupium; e.g. Borowsky, 1983; Dick, Faloon, & Elwood, 1998), until they emerge as juveniles. Wilson (1975) highlighted four main pressures that select for more extensive parental care, of which predation and extreme environmental conditions, in particular oxygen availability (Dick et al., 1998, 2002; Fernández, Bock, & Pörtner, 2008; Fernández, Calderón, Cifuentes, & Pappalardo, 2006; Thiel, 1999), pose the greatest threats to aquatic crustaceans. Active brood care has been observed in several species of amphipod crustacean, including adjustment of embryo position in the brood pouch (Shillaker & Moore, 1987), retrieval of lost embryos (Borowsky, 1983; Patterson, Dick, & Elwood, 2008; Shillaker & Moore, 1987) and aeration of embryos via specialized flexing motions and rapid pleopod beating (Dick et al., 1998, 2002; Dick & Elwood, 2006; Tarutis et al., 2005). These behaviours are plastic and it has been shown that females can adjust levels of ventilation behaviour in response to temperature and oxygen availability (Dick et al., 1998, 2002; Tarutis et al., 2005). However, it is not known how biotic factors, such as predation and parasitism, might affect parental care strategies in brooding crustaceans.

Here we investigated the impact of predation risk and of parasitic infection on brood care behaviour in two species of amphipod: *Gammarus duebeni*, which brood the young in the marsupium for ca. 3 weeks, during which time embryos hatch and are released as juveniles at the next moult (Sutcliffe, 1992), and *Crangonyx pseudogracilis*, which similarly brood the young in the marsupium, but also actively ventilate/aerate the young via specialized behaviours (Dick et al., 1998). Amphipods are iterative breeders; hence investment in brood care is likely to represent a trade-off between current and future reproductive success.

For amphipods with active brood care the motion generated by active egg ventilation may pose an increased predation risk (Lewis & Loch-Mally, 2010; Thiel, 1998). Hence the amount of brood care performed by females is likely to be the result of a trade-off

between maximizing reproductive success and avoiding predation. In *C. pseudogracilis*, which performs active brood care (Dick et al., 1998), we tested the hypothesis that females will minimize predation risk by reducing their iconic flexing and pleopod-beating behaviours in response to olfactory cues from the three-spined stickleback, *Gasterosteus aculeatus*. Additionally, we investigated changes in brooding duration and reproductive success in response to three-spined stickleback cues in *Gammarus duebeni*, which show passive brood care.

Amphipods are hosts to several species of feminizing, microsporidian parasites, for which prevalence is high in many host populations and species (e.g. Slothouber Galbreath, Smith, Terry, Becnel, & Dunn, 2004; Terry et al., 2004). These parasites are maternally inherited, and so feminization increases the rate of parasite transmission (Bandi, Dunn, Hurst, & Rigaud, 2001; Dunn, Terry, & Smith, 2001). The effect of parasitic infection cannot be neglected in parental care, because parasitism imposes energetic and fitness costs (e.g. Dobson & May, 1987; Møller et al., 1990). The impact of microsporidian parasites on amphipod brood care behaviour will depend on the metabolic burden imposed by the parasite, but may also reflect selection on the parasite to maximize host reproduction, and hence parasite transmission. These parasites cause some reduction in host fitness; for example, *Nosema granulosis*-infected *G. duebeni* release fewer juveniles from their marsupium than uninfected females, despite having comparable initial brood sizes (Ironsides et al., 2003). Hence we predicted that reduced brood care behaviour would underlie this reduced juvenile survival. However, as these parasites are vertically transmitted via the oocyte, they will be selected to minimize their impact on host reproduction (Bandi et al., 2001; Dunn et al., 2001), or even promote increased investment in reproduction in their hosts (e.g. Haine et al., 2004; Haine, Motreuil, & Rigaud, 2007). Therefore an increase in brood care might alternatively be predicted in infected females. Here we investigated the impact of infection by *Fibrillanosema crangonycis* (Slothouber Galbreath et al., 2004) on active brood care in *C. pseudogracilis*, and by *N. granulosis* and *Dictyocoela duebenum* (Terry et al., 2004) on brooding duration and reproductive success in *G. duebeni*.

METHODS

Animal Collection and Husbandry

In October 2011, *C. pseudogracilis* were collected from a small pond in Middleton Park, Leeds, U.K. (53°75'N, 1°55'W) and *G. duebeni* were collected from Budle Bay, Northumberland, U.K. (55°40'N, 1°43'W), using a fine mesh net. Amphipods in both stock tanks and experimental pots were maintained in aerated water at 14 °C, under long day conditions (16:8 h light:dark). *Crangonyx pseudogracilis* were maintained in fresh dechlorinated tap water, with rotted sycamore, *Acer pseudoplatanus*, leaves and duckweed (Lemnoideae) provided for food and shelter. *Gammarus duebeni* were kept in brackish water (made by dissolving Instant Ocean sea salt in dechlorinated tap water at a concentration of 7 g/litre, to match field salinity) and supplied with rotted sycamore leaves and algae (*Enteromorpha* spp.) for food and shelter. Both the water and food supplies were replaced regularly, to ensure the welfare of the animals.

Three-spined sticklebacks were collected from Saltfleet, Lincolnshire, U.K. (53°25'59.55'N, 0°10'49.41'W) by seine netting and transported in 20-litre commercial fish transport bags (maximum density five fish/litre), one-quarter filled with water from the source. These were packed into plastic boxes and transported by car to the housing facilities in Leeds, with no mortality. The sticklebacks were maintained in the laboratory for 18 months, at a density

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