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Nest tending increases reproductive success, sometimes: environmental effects on paternal care and mate choice in flagfish

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Parents should adjust parental care if the costs and benefits of that care vary. Traditionally, the benefit of care has been assumed to be increased offspring fitness, yet increasing evidence indicates that care can also increase mating success. We examined male behaviour and reproductive success across environments in flagfish, *Jordanella floridae*, a pupfish found across a range of salinities in Florida, U.S.A. Care may be more beneficial to offspring in freshwater habitats than in brackish ones. If so, female preferences for care-giving males should be stronger in fresh water. We quantified male behaviour in fresh and brackish water for four populations and examined whether male behaviour influenced the probability of spawning or the number of eggs spawned. A male's behaviour influenced his reproductive success, but did so differently in fresh and brackish water. In fresh water, the male's behaviour prior to spawning was a strong predictor of whether or not he would spawn, whereas in brackish water, postspawning behaviour of males predicted additional spawning success. These results suggest that the traits that females use to assess potential mates differ depending on the salinity of the environment. Despite the importance to a male's spawning success of different activities in different salinities, male behaviour did not differ consistently between salinities. We discuss possible benefits to females of a phenotypically plastic mate choice criterion and examine explanations for why male behaviour does not covary with the strength of sexual selection across environments.

Keywords: behavioural plasticity; courtship; flagfish; *Jordanella floridae*; mate choice; mating; parental care; parental investment; sexual conflict; sexual selection

The optimal amount of care to provide one's young reflects a balance between the benefits of care to young and the costs to the parent's residual reproductive value (e.g. Williams 1966; Sargent & Gross 1993; Webb et al. 2002). Consistent with this model, parents often reduce the care that they provide their offspring when the costs of caring are high (e.g. Brommer et al. 2000; Weimerskirch et al. 2001) and increase care when the benefits are high (Dale et al. 1996; Listøen et al. 2000). These natural selection pressures are not the only factors influencing parental investment decisions, as an increasing body of work demonstrates that female mating preferences can select for male activity that is likely to improve offspring fitness (Møller & Thornhill 1998; Tallamy 2000; Pampoulie et al. 2004). For example, mating success can be associated with the quality of a potential mate's nest (Reynolds & Jones 1999), the care that he will provide young (Forsgren 1997; Östlund & Ahnesjö 1998; Lindström et al. 2006) and whether he is caring for a current brood (Petersen et al. 2005). Thus, natural and sexual selection can simultaneously influence optimal care.

Natural and sexual selection may favour different amounts of care in species in which the choosy sex (e.g. females) is not the care-giving sex (e.g. males) (reviewed in Clutton-Brock 1991), as is the case for many invertebrates, fish and birds (reviews in Andersson 1994; Tallamy 2000).

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Specifically, imposing sexual selection on paternal care predicts an increase in care above the natural selection optima (Kirkpatrick 1985; Hoelzer 1989; Iwasa & Pomiankowski 1999), which can create conflict between the interests of males and females (reviewed in Arnqvist & Rowe 2005). Females should favour males that provide the greatest fitness benefits to offspring, whereas males should balance benefits to offspring against the costs of providing care (e.g. Trivers 1972; Westneat & Sargent 1996).

For species distributed across a range of environmental conditions, the strength of this conflict can vary across environments if environmental conditions influence the benefits of care to offspring (Dale et al. 1996). If the strength of female preferences for parental males is correlated with the expected benefit of care to young, then preferences should be stronger in the environments in which care is most beneficial. Variation in care across environments, then, should reflect the changes in benefits to offspring as well as changes in the strength of mating preferences.

We examined variation in parental care both within and between populations of flagfish, *Jordanella floridae*. Care in flagfish is provided entirely by males, who defend nesting territories and guard, clean and fan eggs from multiple females. Male parental behaviour is variable both within (St Mary et al. 2001; Hale et al. 2003) and between (C. M. St Mary, unpublished data) populations, and a component of this variation can be attributed to variation in salinity (St Mary et al. 2001). The benefits of parental care under various salinities are currently unknown. However, previous work suggests that care may be more beneficial in fresh water. Specifically, an increased rate of fungal infection in fresh water appears to reduce survival of unattended embryos (St Mary et al. 2004). Consequently, egg cleaning may be more beneficial in fresh than in brackish water. Furthermore, if egg cleaning is more beneficial to offspring in fresh water, then the strength of mating preferences for nest-tending males should be stronger in fresh water.

We examined the effects of salinity on male activity before and after spawning in four populations of flagfish. Flagfish are native to both freshwater and brackish habitats, so we examined the effect of native habitat type on behavioural responses to salinity by observing males from both coastal and inland habitats. Behaviour may differ between populations native to different habitat types because of genetic drift resulting from reproductive isolation. Alternatively, behaviour may differ consistently between habitat types, suggesting adaptation to local conditions. In flagfish, the amount of gene flow across the salinity gradient is unknown. However, the proximity of freshwater habitats in Florida to coastal salt marsh may facilitate gene flow across the salinity gradient within drainages. An effect of native habitat type on behaviour would indicate that gene flow is restricted and that selection regimes differ between salinities.

We also examined female mating preferences by determining whether male pre- and postspawning activity was associated with reproductive success. Male flagfish perform nest-tending activities, such as fanning and nest cleaning, prior to spawning (Bonnevier et al. 2003), and these activities may serve as signals to potential mates of the quality of care that a male will provide young (Tallamy 2000). In addition, females often mate repeatedly with the same male and a male's behaviour once he has eggs in his nest may influence whether a female will mate with him again (Tallamy 2000). Therefore, we examined male behaviour both before and after spawning, with respect to his initial and subsequent reproductive success. An effect of salinity on reproductive success would indicate that mating tendencies of males and/or females are plastic in response to salinity. An effect of male behaviour on reproductive success would suggest that females dynamically adjust their spawning activity in response to male behaviour. We expected female preferences based on male activity to vary in strength and direction across salinity treatments and populations, and a male's preference for a particular female and his interest in mating to be similarly correlated with his activity across all treatments in much the same way that we expect courtship to be similar in all treatments. Indeed, field observations indicate that courtship T-circling (Mertz & Barlow 1966) precedes spawning in both inland and coastal populations (R. Hale, personal observation). As a result, we further expected variation across salinities and populations in the association between male behaviour and reproductive success to indicate variation in female mating preferences.

METHODS

Collection and Transportation

Fish were collected from four sites in Florida between May and July of 2003 under Florida Fish and Wildlife Conservation Commission Scientific Collector's Permit number FNC-03-015 U.S. and Fish and Wildlife Service Special Use Permit numbers 58875 and 03008 for St Marks National Wildlife Refuge and number 03 SUP 59 for Merritt Island National Wildlife Refuge. Seine nets, minnow traps and dip nets were used to collect animals. Otter Creek (OC, Levy County) and Miccosukee (MC, Miami-Dade County) are inland and freshwater. St Marks (SM, St Marks National Wildlife Refuge, Wakulla County) and Merritt Island (MI, Merritt Island National Wildlife Refuge, Brevard County) are coastal, with freshwater areas in close proximity to brackish areas. Animals were transported to the Florida State University (FSU) campus in Tallahassee, where the experiments were conducted, in insulated coolers. Fish were transferred to 1-m diameter wading pools at the FSU Mission Road Greenhouse, where they experienced the natural daylight cycle. All animals were returned to their native sites within 4 months of collection.

Acclimation and Experiments

Responses to salinity in each of the four populations were examined in a factorial design with two native habitat types (coastal and inland) crossed with two salinity treatments (fresh and brackish). Two populations were nested within each native habitat type. Males and females