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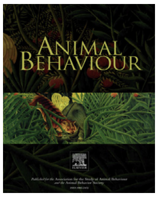

The fitness consequences of plastic responses to adult sex ratio in a paternal care fish

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Plastic behavioural strategies may help individuals maximize reproductive success in varying environments, but it cannot be assumed a priori that behavioural responses to environmental changes are adaptive. To quantify the fitness consequences of plastic behavioural strategies in a paternal care fish, we observed the intrasexually competitive and intersexually solicitous behaviours of male fantail darters, *Etheostoma flabellare*, under varying adult sex ratios (ASR) for six observational periods over the course of two full mating seasons. At the end of each observational period, eggs present in each male's nest were counted. Behavioural and egg count data were used to construct linear and generalized linear mixed models predicting male reproductive success by two proxies: presence and number of eggs in the nest. Lower adult sex ratios (the ratio of males to females) and greater male length positively predicted egg presence. Greater intrasexual aggression increased a male's chances of having eggs in high ASR groups. Intrasexual aggression and solicitation of females positively predicted final egg count regardless of ASR. Our results support the hypothesis that some behavioural responses to changing adult sex ratio are adaptive, and that other traits, such as larger male size and high mate solicitation rates, may increase reproductive success regardless of ASR.

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Theory predicts that the operational sex ratio (OSR), or the relative abundance of reproductively available male and females, is one of the key factors driving sex-specific competitiveness for mates (Andersson, 1994; Emlen & Oring, 1977). Because scarcity and abundance lie along a spectrum, the intensity of competition for mates among individuals of the abundant sex (usually males) may shift even without a full reversal of the OSR (Kvarnemo & Ahnesjö, 1996). As the limiting sex becomes scarcer, the abundant sex may become more intrasexually competitive (Kvarnemo & Ahnesjö, 1996). In support of the hypothesis that individuals may exhibit plastic behavioural responses to shifts in the OSR, numerous studies have observed a response in mating behaviour to a naturally developing or manipulated adult sex ratio (ASR) or OSR (e.g. Bretman, Westmancoat, Gage, & Chapman, 2012; Enders, 1993; Forsgren, Amundsen, Borg, & Bjelvenmark, 2004; Silva, Vieira, Almada, & Monteiro, 2010).

When investigating plastic behavioural responses to an environmental variable, a frequently made assumption is that the observed response is adaptive and thus selected for. However, the observation of a response, even where that response is predicted by an adaptationist hypothesis, is not sufficient to determine that the response is adaptive. For example, male field crickets, *Teleogryllus oceanicus*, respond to a recent female encounter with an increased, but apparently nonadaptive, propensity for intrasexual courtship (Bailey & French, 2012), and in newts of the genus *Triturus*, predator cues induce apparently nonadaptive, yet repeatable, stunting of larval development (Orizaola & Braña, 2004). Additionally, for predictor variables that are inherently correlated with other variables (e.g. ASR and the density of at least one sex), there is need for caution in interpreting proximate causation. For example, the courtship rate of male zebrafish, *Danio rerio*, changes in response to ASR only when population density is high, suggesting that this behaviour responds to an interaction of the two predictor variables rather than to ASR alone (Spence & Smith, 2005). Finally, plasticity, like any other trait, may persist in lineages in which it was once, but is no longer, selected for (e.g. Lizé, Doff, Smaller, Lewis, & Hurst, 2012). Perhaps more than most traits, plasticity lends itself to adaptationist interpretations, and therefore additional caution must be applied when determining both the proximate mechanisms of plasticity and the benefits of a plastic response.

Over the course of the mating season, the adult sex ratio of breeding populations of *Etheostoma flabellare* (fantail darters) becomes increasingly female biased (Lake, 1936; O'Rourke & Mendelson, 2013b). Under laboratory conditions, male fantail

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darters respond to changes in the ASR (increased male density relative to females) with increased rates of intrasexual aggression and intersexual solicitation (O'Rourke & Mendelson, 2013b). These increases in intrasexually competitive behaviours hypothetically represent adaptive responses to an increasing number of competitors.

To test whether behavioural responses to variation in ASR positively impacts reproductive success, we compared estimates of reproductive success with behavioural data collected for a previous study (O'Rourke & Mendelson, 2013b), in which we placed males and females in artificial streams under low, moderate and high male ASRs at time points spanning the mating season. For the present analyses, we considered individual male behaviours over 5-day trial periods as well as the number of eggs present in each male's nest at the end of those trial periods. We then used an information-theoretical approach to determine predictors of two measures of male reproductive success: (1) the presence or absence of eggs in the male's nest at the end of the trial period and (2) the total number of eggs present. The high male ASRs previously studied exceeded the natural range in ASR observed for these populations (O'Rourke & Mendelson, 2013b). Because we were interested in the adaptive nature of behavioural responses to ASR, we did not include these supernormal ASR groups in this study. Therefore, we hereafter refer only to 'low male/low ASR' and 'high male/high ASR' streams, which represent the 'low' and 'moderate' ASR streams, respectively, from our previous paper, and do not exceed the natural observed ASR range for this population. We previously observed an increase in both male intrasexual aggression and male intersexual solicitation in response to an increase from a low ASR to a high ASR (O'Rourke & Mendelson, 2013b). We therefore predicted that both aggression towards other males and solicitation of females should be more strongly associated with male reproductive success in a high ASR.

METHODS

Study System

Etheostoma flabellare is a benthic fish found throughout eastern North America that spawns in the riffles of streams and small rivers during the nuptial season (Lake, 1936; Page, 1983). Males develop orange and black nuptial coloration, with fleshy 'egg mimic' knobs at the tips of their anterior dorsal fins, and aggressively defend nests in which females deposit eggs. Females prefer males with egg mimics and possibly larger males, and egg mimic size is correlated with male length (Knapp & Sargent, 1989; Moretz & Rogers, 2004). Males provide additional paternal care by cleaning and aerating the eggs (Lake, 1936; Page, 1983), and egg cannibalization by both males and females has been observed (Knapp & Sargent, 1989; Lindström & Sargent, 1997). Allopaternal care has been observed in some members of the genus *Etheostoma* (e.g. Constanz, 1985; Porter, Fiumera, & Avise, 2002), but has not been reported in this species. Instead, egg mimics may be an alternative to alloparental care (egg adoption); both serve to attract females to the nest (Knapp & Sargent, 1989). Preliminary microsatellite data failed to indicate any incidence of egg adoption in the present study (O'Rourke & Mendelson, 2012). The species is polygynandrous; both males and females may have multiple mates within one nuptial season.

Collections and Housing

In March, April and May of 2010 and 2011, fish were collected via kick-seine from two streams in central Maryland, U.S.A. (Meadow Branch, 39°36′36″N, 77°6′36″W and Cabbage Run, 39°29′24″N, 77°19′12″W) and transported in aerated coolers to the University of Maryland, Baltimore County (UMBC) greenhouse (39°15′36″N, 76°42′36″W) within 5 h of collection. At no other point in the following procedures were the subjects housed in unnaturally high densities. Subjects were sedated with MS-222 to allow for elastomer tagging to aid in the identification of individuals. After recovery, subjects were placed in one of six artificial streams. We manipulated male numbers in the streams to create ASRs ranging from 0.33 to 0.83 males per female, with females numbering six per stream and males numbering either two (low ASR), three (low ASR) or five (high ASR) (Supplementary material, Table S1). Each stream was outfitted with seven nest tiles of equal size, and no stream held more than five males. The density of males (maximum = 6.67/m^2), the density of females (8/m^2) and the sum density of the fish (maximum = 14.67/m^2) were within the density ranges observed for natural mating grounds in the focal streams (average density = 7 fish/m^2; maximum density = 15.14 fish/m^2, particularly in shallow, cobble-rich side-channels). In these experiments, we selected males on the basis of nuptial coloration and we selected females based on maximum ripeness (abdominal roundness and protrusion of ovipositor) for each seasonal point. When dissected, all of the females had multiple clutches of oocytes in varying degrees of ripeness, as is typical of darter females in the mating season. By using only streams in which eggs were found, we hope to have controlled for variation in female readiness to some degree; we know that at least one fully ripe female was present in every stream sampled. Because we used the same methods to select females for each stream, regardless of ASR, and because female number was fixed, variation in female ripeness was controlled for between ASR treatments.

To mimic natural conditions, water flow (0.19 m/s) through each 1.25 × 0.6 × 0.6 m stream was created using Little Giant™ WPG-80-PW pond pumps, and pea gravel was used to create riffles over most of each stream, with a small 'pool' area near the downstream drainage. Every pump and hence water source was shared by two streams with different ASR treatments in a randomized block design. Water temperatures approximated the water temperatures of the collection source for each experimental cohort (range 11–19 °C), and photoperiods were natural and thus similar to the nearby collection locations. Fish were fed twice daily with live blackworms and frozen chironomid larvae in 2010 and frozen chironomid larvae in 2011. Mortalities were rare and were immediately replaced with individuals from the same collection cohort, and only males that were present in the stream throughout the trial period were used in this analysis. All other aspects of fish care were attended to in accordance with UMBC Institutional Animal Care and Use Committee (IACUC) protocol TM010240811.

Behavioural Observations

After an initial 24 h acclimation period, each of the six streams was observed for 1 h per day between the hours of 0500 and 1800 hours for 5 consecutive days. Observation order was semi-randomized, so that each individual stream was observed once each day but at different times of the day. The observer (C.O.) remained motionless in front of a viewing window spanning most of the length of the stream, only moving to record behaviours, individual actors and apparent intended audiences on a keyboard out of sight of the subjects. The observer tallied 10 types of interactive behaviours (e.g. chase, nudge, bite) occurring within 15 cm of any nest opening, and recorded, where possible, the individual identities of both the actor and the apparent audience(s).

We measured intrasexual and intersexual aggression and intersexual solicitation as suites of behaviours, derived using

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