



Plasticity and personality of parental care in the clown anemonefish

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Characterizing individual variation in parental care is critical to understanding how selection shapes and maintains patterns of care, yet little is known about how individual parents vary in their responses to the environment. Reaction norms, functions that describe how phenotypes change across an environmental gradient, provide an elegant framework for studying individual variation in behavioural responses. We use a reaction norm approach to investigate how studying plasticity, which describes variation within an individual through time, and personality, which describes repeatable variation among individuals, together explain individual variation in the parental behaviour of the anemonefish *Amphiprion percula*. More specifically, we test how resource availability influences individual parental responses to the environment and discuss the consequences for our understanding of plasticity and personality in parental care. Breeding pairs of *A. percula* were fed either a high or a low food ration and their parental behaviours were monitored. Individuals exhibited plasticity in parental behaviour across the two resource environments. Furthermore, individuals were repeatable in their behaviour through time, as evidenced by significant among-individual variation in intercept. Finally, the slope and elevation of individual reaction norms varied, revealing a level of variation not captured at the population level and providing insight into the potential mechanisms generating individual variation.

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Parental care consists of an incredible diversity of forms. Patterns of care vary within individuals through time as well as among individuals in a population (Royle, Smiseth, & Kölliker, 2012). Explanations for variation in patterns of care stem from the theory that parents face a trade-off between investing in current versus future reproductive opportunities, and therefore the benefit of care to increased offspring fitness must be balanced against its cost to residual reproductive value (Trivers, 1972). Furthermore, an individual's optimal level of care can be influenced by genes, development, social and ecological context, or a combination thereof (Dingemanse & Wolf, 2013). Therefore, the costs and benefits of providing care at any point in time can be influenced by past, current and expected future experiences, and this explains why there might be so much variation in parental care (Dingemanse & Wolf, 2013; Royle, Russell, & Wilson, 2014). A critical step towards understanding how the current environment acts on individuals to shape patterns of parental care is to characterize the individual variation in responses to the environment.

First, there can be variation within individuals over time, associated with variation in their condition or context (i.e. plasticity).

Plasticity refers to the capacity of individuals (or genotypes) to express different phenotypes in different environments (West-Eberhard, 2003). Selection may favour plasticity in parental care if plastic individuals can adaptively modify their behaviours to cope with a changing environment (Royle et al., 2014). Many studies have demonstrated average population plasticity in parental care in response to various environmental influences, including brood size and age (e.g. Westneat, Hatch, Wetzel, & Ensminger, 2011; Westneat, Mutzel, Bonner, & Wright, 2017), oxygen levels (e.g. Green & McCormick, 2005; Lissaker & Kvarnemo, 2006), sex change (Green & McCormick, 2005) and food resources (e.g. Krause, Krüger, & Pogány, 2017; Kvarnemo, Svensson, & Forsgren, 1998).

Second, there can be variation among individuals within a population (i.e. personality). Personality refers to consistent individual differences that are maintained across time and/or environmental contexts (Reale et al., 2007). Thus, plasticity and personality can refer to variation at different levels: within- and among-individuals (Westneat et al., 2011). Several explanations have been proposed to explain how selection can act to maintain among-individual variation (reviewed in Wolf & Weissing, 2010). For example, variation in past experiences can affect the optimal behavioural strategy in the current environment, which results in between-individual differences in behaviour (i.e. consistent individual differences can be a product of adaptive developmental

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plasticity; Stamps & Groothuis, 2010). Personality is a hot topic (Beekman & Jordan, 2017; Dall, Houston, & McNamara, 2004; Dingemanse & Wolf, 2010; Sih et al., 2015; Wolf & Weissing, 2012), but personality in parental care has rarely been explored. Several studies have, however, demonstrated repeatable among-individual differences in parental care across social and environmental contexts (e.g. Nakagawa, Gillespie, Hatchwell, & Burke, 2007; Schwagmeyer & Mock, 2003; Sprenger, Dingemanse, Dochtermann, Theobald, & Walker, 2012; Vallon et al., 2016).

A third possibility is that within- and among-individual variation exist simultaneously, such that individuals show repeatability in their behaviour through time but are flexible in their behaviour across contexts. We can integrate the study of plasticity and personality in parental care using the reaction norm approach (Dingemanse & Dochtermann, 2013; Dingemanse, Kazem, Réale, & Wright, 2010), which is equivalent to the character state approach in discrete environments (Via et al., 1995). Reaction norms are functions that describe how the phenotype of different genotypes changes across an environmental gradient, with each individual's phenotypic response fitted with an intercept and slope (Dingemanse & Wolf, 2013). Reaction norms can characterize the population mean response and the response of each individual through time and across environmental contexts. The study of plasticity and personality can thus be unified by quantifying variation in the slope and intercept of the population mean and individual reaction norms (Nussey, Wilson, & Brommer, 2007).

The reaction norm approach has rarely been used to study plasticity and personality in the context of parental care (Betini & Norris, 2012; Westneat et al., 2011), despite its utility in understanding how plasticity and personality explain patterns of variation in other contexts (Dingemanse et al., 2010). Here we apply the reaction norm framework to study variation in parental care in the clown anemonefish *Amphiprion percula*, within and among individuals. *Amphiprion percula* live in social groups with a larger, dominant female, a smaller, subordinate male, and up to four nonbreeding individuals (Buston & Wong, 2014). *Amphiprion* are protandrous hermaphrodites (Fricke & Fricke, 1977; Moyer & Nakazono, 1978): if the female of the group dies, then the male changes sex and assumes the position vacated by the female (Buston, 2004; Fricke, 1979; Mitchell, 2005). The breeding pair will lay a clutch of eggs up to three times per lunar month (Buston & Elith, 2011; Buston, 2004). Parents care in the form of tending, mouthing the eggs to remove debris and dead eggs, and fanning the eggs with their fins to oxygenate the clutch. In the congener *Amphiprion melanopus*, these parental behaviours are plastic and vary in response to day of development and sexual tactic of the individual (Green & McCormick, 2005). It is unknown whether there is among-individual variation in these behaviours also, but *A. percula* and its congener *Amphiprion ocellaris* exhibit consistent individual differences in activity, boldness and sociability (Medina & Buston, 2013; Schmiede, D'Aloia, & Buston, 2017; Wong et al., 2013). Our approach to studying within- and among-individual variation in *A. percula* will reveal whether and how parents vary in their responses to the environment.

Our objective was to characterize within- and among-individual variation in how *A. percula* parents respond to different resource environments. To accomplish this objective, we manipulated food resources available to pairs of *A. percula* and tested three hypotheses regarding variation in parental traits. First, we tested the hypothesis that there is plasticity in parental care (i.e. the average level of parental care varies across resource environments). If parents respond to resource availability, then we expected a main effect of environment on parental care. Second, we tested the hypothesis that there is personality in parental care (i.e. the individual level of parental care is repeatable over time). If parents

exhibit consistently different behaviour through time, then we expected repeatable among-individual differences in intercept. Third, we tested the hypothesis that individuals vary in their response to the environment, and that the level of care and their responsiveness are related. If parents vary in their responsiveness, then we expected variation in the slope of individual reaction norms, and if the magnitude of an individual's response depends on its level of care, then we expected covariance between the slope and intercept. Taken together these tests provide a comprehensive characterization of within- and among-individual variation in parental care and provide insight into the proximate and ultimate causes of individual variation.

METHODS

Laboratory Population

We conducted this study at Boston University (Boston, MA, U.S.A.) from 27 June 2014 through 22 June 2015. All experimental fish originated from natural populations of *A. percula* in Papua New Guinea and were supplied by Quality Marine. When they arrived in the laboratory, all individuals were under 30 mm standard length (SL), ensuring that they were collected as nonbreeders in the wild. Removal of nonbreeders is considered to be a sustainable practice, because they are rapidly replaced and have no impact on population growth (e.g. Buston, 2004; Planes, Jones, & Thorrold, 2009; Schlatter, Webb, & Buston, n.d.). Upon arrival in our laboratory, we randomly paired each fish with one other fish and allowed them to establish dominance on their own (Wong, Uppaluri, Medina, Seymour, & Buston, 2016). At the start of this investigation, the individual fish had been in captivity for 3–4 years.

We maintained the laboratory population of 60 pairs (120 individuals) of *A. percula* in a large, recirculating aquarium system at Boston University in accordance with Institutional Animal Care and Use protocol (IACUC number 14-006). Fish were housed in pairs in 120-litre tanks with the set of 60 tanks divided into four independent racks with 15 tanks per rack. Each of the four racks had its own pump that supplied a continuous flow of salt water recirculating at a rate of approximately 16 600 litres/h. We used a Proflux computer controller to continually monitor the pH, temperature and salinity of water in each rack. We also manually tested water samples every 2 weeks for dissolved phosphate and ammonia (Salifert test kits, Amsterdam, The Netherlands; Red Sea test kits, www.redseafish.com). We maintained abiotic conditions as constant as possible, at levels similar to those found on coral reefs in Papua New Guinea: pH = 8.30 ± 0.34 , temperature = 27.3 ± 0.19 °C, salinity = 32.5 ± 1.58 ppt. Each tank was lit with two T5 24 W bulbs whose spectra colour mimics the natural reef environment. Each tank contained 12 mm of sand on the bottom, a 15 × 15 cm ceramic tile, an anemone (*Entacmaea quadricolor*) and a small (approximately 10 × 10 cm) rock to provide habitat and substrate for egg laying. Prior to manipulation, we fed the fish approximately 24 commercial fish pellets (New Life Spectrum, New Life International, Inc., Homestead, FL, U.S.A.) per pair per day.

Feeding Manipulation

To determine how parental care varies across different environments, we conducted a feeding manipulation. Because pairs breed on a lunar schedule in the wild (Buston & Elith, 2011; Seymour, Barbasch, & Buston, 2017), the feeding manipulation ran for 12 lunar months from 27 June 2014 through 22 June 2015. Pairs were fed a high ration of food (24 fish pellets per pair per day) for 6 lunar months and a low ration of food (12 fish pellets per pair per day) for another 6 lunar months. Ten pairs received the high

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