Physiology & Behavior 152 (2015) 68–78

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/phb

Puffed and bothered: Personality, performance, and the effects of stress on checkered pufferfish

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HIGHLIGHTS

- Wild checkered pufferfish have consistent, individual-level differences in behaviour.
- Personality, puff response, and swimming performance did not form coping styles.
- Behaviours and performance in the lab were not related to movements in the field.
- A physiological dose of cortisol did not modify personality or performance.

ARTICLE INFO

Article history:
Received 31 March 2015
Received in revised form 9 September 2015
Accepted 10 September 2015
Available online 13 September 2015

Keywords:
Cortisol
Swimming performance
Coping
Movement
Sphoeroides testudineus

ABSTRACT

Although consistent individual-level differences in behaviour are widespread and potentially important in evolutionary and ecological processes, relatively few studies focus on the physiological mechanisms that might underlie and regulate these individual-level differences in wild populations. We conducted experiments to determine whether checkered pufferfish (*Sphoeroides testudineus*), which were collected from a dynamic (in terms of depth and water temperature) tidal mangrove creek environment in The Bahamas, have consistent individual-level differences in locomotor activity and the response to a simulated predator threat, as well as swimming performance and puffing in response to stressors. The relationships between personality and performance traits were evaluated to determine whether they represented stress-coping styles or syndromes. Subsequently, a displacement study was conducted to determine how personality and performance in the laboratory compared to movements in the field. In addition, we tested whether a physiological dose of the stress hormone cortisol would alter individual consistency in behavioural and performance traits. We found that pufferfish exhibited consistent individual differences in personality traits over time (e.g., activity and the duration of a response to a threat) and that performance was consistent between the lab and the natural enclosure. Locomotor activity and the duration of startled behaviour were not associated with swimming and puffing performance. Locomotor activity, puffing performance, and swimming performance were not related to whether fish returned to the tidal creek of capture after displacement. Similarly, a cortisol treatment did not modify behaviour or performance in the laboratory. The results reveal that consistent individual-level differences in behaviour and performance were present in a population from a fluctuating and physiologically challenging environment but that such traits are not necessarily correlated. We also determined that certain individual performance traits were repeatable between the lab and a natural enclosure. However, we found no evidence of a relationship between exogenous cortisol levels and behavioural traits or performance in these fish, which suggests that other internal and external mechanisms may underlie the behaviours and performance tested.

1. Introduction

There is growing recognition that consistent individual-level differences in behaviour are widespread in natural populations and that they are important for ecological and evolutionary processes. Consistent individual-level differences in behaviour have been described in the contexts of animal personality [1], temperament [2], behavioural syndromes [3], and stress-coping styles [4], and have been documented in a wide variety of invertebrates [5] and vertebrates [6], including fishes [7]. We define animal personality as individual-level differences in behaviour that are consistent over time and between contexts [1–3],

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http://dx.doi.org/10.1016/j.physbeh.2015.09.011
0031-9384/

whereas we define behavioural syndromes as correlations between different personality traits [3]. Personality traits and physiological stress responses that form coherent sets within groups of individuals are defined as stress-coping styles [4]. A key evolutionary consequence of personalities and coping styles is that they can at times represent limited plasticity, so that an animal might not be able to express the most suitable behaviour in all contexts [8], which could incur significant fitness consequences for individuals [9,10,11]. The fitness consequences of such individual-level variation in behaviour also have the potential to influence higher-order processes such as population growth and persistence, interspecific interactions, community dynamics, and rates of evolution [11,12].

Yet, despite the potential costs of behavioural consistency, accumulating evidence suggests that diverse personalities emerge and persist within natural populations [6], possibly as a result of factors such as fluctuating environmental conditions [13] and frequency-dependent selection [14]. However, compared to captive-bred mice and rats, relatively few studies focus on the physiological mechanisms that might underpin personality [15] and coping styles in wild animals, especially ectotherms [16,17]. Furthermore, there is a paucity of studies that validate personality in the field despite concerns that personality traits observed in stressful lab conditions may not reflect personality traits expressed wild animals in natural conditions [18].

Careau and Garland [19] suggest that individual differences in performance can help elucidate the relationships between selection, physiology, and consistent behaviour. These authors describe how efforts have been made to include behaviour in the pace-of-life syndrome hypothesis [20], which posits that combinations of physiological characteristics have evolved with particular life-history traits within species [21,22]. In general, this integration appears to be supported by studies that indicate that there is a positive relationship between activity, aggressiveness, boldness, and metabolic rates [23] as well as life-history traits [10] but not in all cases, as these relationships tend to be highly context specific [19]. Given the difficulty in establishing a direct, causal relationship between metabolism and personality, and given that selection acts more directly on performance than the mechanisms that limit performance, Careau and Garland [19] advocate that researchers examine the relationships between physiology and performance as well as performance and personality to elucidate the links between physiology, personality, and selection. Despite the promise of this integrative approach and evidence that personality and individual differences in performance exist in natural environments [24–28], few studies address the ecological relevance of consistent individual differences in both stress-coping behaviours and performance.

In addition to performance capabilities, individual differences in endocrine stress responses can also be proximate causes of divergent personalities. Relationships between endocrine reactivity and the consistent stress coping behaviours of individuals suggest that, for some behaviours, consistent individual-level differences may be related to hormone levels [4,29]. When an animal's homeostasis is at risk, endocrine responses orchestrate a range of changes that help the organism cope with stress [30], including alterations in behaviour. In fish, these endocrine response systems include the brain-sympathetic-chromaffin cell axis and the hypothalamic-pituitary-interrenal axis (HPI; [31]). Catecholamines and corticosteroids are important end products of these axes which mediate changes in metabolism and ion balance, cardiovascular, respiratory, and immune functions [32] and ultimately induce changes in behaviour [33]. The activity of the HPI axis in fishes appears to have a particularly strong relationship with stress-coping behaviours, which is consistent with its analogues in other animals [4,30].

Despite evidence of a relationship between the activity of the HPI axis and behaviour, only a few studies have tested the causal link between cortisol, the primary glucocorticoid in fish, and styles of stress-coping behaviour in isolation from other parts of the stress response, such as the perception of a stressor and hormones that stimulate the production of cortisol [7]. These include studies that have explored the effects of cortisol on behaviour in fish using exogenous cortisol treatments. This approach initiates the cortisol-mediated responses to stress without activating the onset of the HPI axis and without a sensory perception of a stressor and can thus be used to isolate the cortisol-mediated effects on behaviour. Several of these studies provide evidence that cortisol is related to altered behaviour in fish. For example, an intraperitoneal cortisol implant increased the probability of social subordination in juvenile captive bred rainbow trout (*Oncorhynchus mykiss*) in size-matched pairs but this effect was abolished with the administration of the glucocorticoid receptor antagonist, RU486 [34]. In another study, a chronic cortisol treatment from an implant resulted in reduced feeding in rainbow trout but did not alter their swimming performance [35]. Other studies that explore the relationships between specific stressors, physiological characteristics, and behaviour reveal that there can also be an interaction between stressors and the effects of an individual's metabolism on behaviour (see review in [36]). Most of the studies on the effects of cortisol and stressors on behaviour have been conducted using captive-bred animals (but see examples for animals from wild populations [37–40], reviewed in [41]). Factors such as past experiences with predation threats and fluctuations in environmental conditions could affect the behavioural response of wild animals to stress [42,14].

Checkered pufferfish (*Sphoeroides testudineus*) provide a useful model to study whether animals from a fluctuating and potentially stressful environment will demonstrate consistency in behaviour and performance and whether a cortisol treatment will alter this consistency. This species is common in tropical and sub-tropical mangrove habitats throughout the Americas, with populations being found from Florida to Brazil [43]. Checkered pufferfish are well adapted to withstand frequent and drastic changes in temperature [44], water depth (tides), and salinity [45,46], and must also withstand frequent natural and anthropogenic alterations to their habitat [47]. In addition to these environmental stressors, pufferfish are subject to predation by herons (Ardeidae) [48] and fish [49], despite their defensive toxin, tetrodotoxin [50], and their ability to increase their size by pumping water or air into their stomachs [51].

In this study, we tested whether or not pufferfish exhibit consistent individual-level differences in activity and anti-predator responses (simulated aerial and aquatic predations events) as well as performance under stress (i.e., puff magnitude and duration, duration of a chase to exhaustion) over time. We also tested whether or not individual activity and performance were repeatable between a laboratory environment and a natural, enclosed environment. We conducted a displacement study to determine how activity and performance traits corresponded to individual differences in movement and recapture in the wild. Lastly, we tested whether a cortisol treatment would alter individual consistency in behaviour and performance. To do this, we injected the fish with a physiological dose of cortisol for an intermediate duration (3 days) to activate the cortisol-mediated components of the stress response (as per [52]) and compared the behaviour and performance of individuals before the cortisol treatment, during peak cortisol, and after the cortisol treatment was exhausted.

2. Methods

2.1. Study site and study animals

Checkered puffers (n = 60; January 2014) were collected in Page Creek (24°49′04.7″N, 76°18′51.6″W) (Fig. 1), a mangrove-lined creek at the south end of Eleuthera, The Bahamas, using a large (20 m) beach seine during the outgoing tide. Only fish weighing 50 g and over were retained, to prevent mortality from tagging and cortisol injection procedures. Captured fish were transported to the wetlab research facilities at the Cape Eleuthera Institute (24°50′06.70″N, 76°19′31.69″W) in coolers with frequent water changes (30% water volume every 5 min)