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Rate of movement of juvenile lemon sharks in a novel open field, are we measuring activity or reaction to novelty?

J. S. Finger [a, b, c, *, 1], F. Dhellemmes [a, b, c, 1], T. L. Guttridge [b], R. H. J. M. Kurvers [c, d], S. H. Gruber [b], J. Krause [a, c]

[a] Humboldt-Universität zu Berlin, Faculty of Life Sciences, Berlin, Germany
[b] Bimini Biological Field Station Foundation, Bahamas
[c] Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany
[d] Max Planck Institute for Human Development, Berlin, Germany

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Personality differences are widespread throughout the animal kingdom and can have important ecological and evolutionary consequences. Despite a rapidly increasing body of literature, large (marine) vertebrates remain underrepresented in personality research. Given their unique life history traits (e.g. slow growth rate, slow reproduction rate, long life span) and their pivotal role in ecosystem processes, this is an important gap in our current knowledge. Here we investigated consistency and plasticity in movement behaviour of wild juvenile lemon sharks, *Negaprion brevirostris*, by repeatedly subjecting sharks to open field tests. First, we investigated the presence of interindividual differences in movement behaviour in a novel open field. Second, we investigated the effect of trial repetition on movement behaviour to understand whether movement in a novel open field reflects a reaction to novelty, or general activity. Third, we estimated individual differences in habituation/sensitization rates over trial repetition and studied how the habituation rate was predicted by the initial movement rate. We found consistent individual differences in movement behaviour during the open field tests. Sharks showed habituation in movement behaviour (i.e. decrease) over repeated trials indicating that the movement behaviour during the first trials is a reaction to novelty, and not general activity. Individuals, however, differed in their rate of habituation (i.e. plasticity) and this rate was negatively related to an individual's movement behaviour in the first open field trial. In addition to showing individual differences in consistency and plasticity in juvenile lemon sharks, our study emphasizes the importance of examining the validity of personality tests when adapting them to new species.

The discovery that individuals can show consistent behavioural differences through time (i.e. animal personality; Biro & Stamps, 2008) has shifted the traditional view of individual variation from random noises to a biologically important phenomenon. Indeed, such differences in individual behaviour can have important ecological and evolutionary consequences (Sih, Bell, & Johnson, 2004; Wolf & Weissing, 2012) and enhance management programmes (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Mittelbach, Ballew, Kjelvik, & Fraser, 2014). As a result, research on animal personality is currently booming and knowledge is rapidly accumulating on a diversity of species (Gosling, 2001; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, Johnson, & Ziemba, 2004). However, despite this rapid expansion much of our understanding comes from studies on captive animals that are easy to house and with a short life span (Archard & Braithwaite, 2010). This bias has led to an underrepresentation of large animals, especially large marine vertebrates which are usually characterized by slow growth rate and reproduction rate, long life span and a relatively high trophic position (Jennings, Pinnegar, Polunin, & Boon, 2001; Lewison, Crowder, Read, & Freeman, 2004; Romanuk, Hayward, & Hutchings, 2011; Stevens, Bonfil, Dulvy, & Walker, 2000). These characteristics make them both important to ecosystems processes and highly vulnerable to anthropogenic impact (Estes et al., 2011; Stevens et al., 2000). Furthermore, obtaining data on a wide variety of organisms with different life history and ecological conditions is warranted to understand the evolution of animal personality (Réale et al., 2007; Réale et al.,

* Correspondence: J. S. Finger, Bimini Biological Field Station Foundation, 9300 SW 99 St, Miami, FL 33176-2050, U.S.A.
E-mail address: js.finger@yahoo.fr (J. S. Finger).
[1] Shared first authorship.

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2010). Therefore, expanding personality research to animals with longer life spans is vital.

Advancing knowledge of large aquatic organisms is challenging because of logistical constraints (e.g. sample size, capture constraints, housing difficulties). However, novel technologies such as biotelemetry (radio and acoustic telemetry) and biologging (archival logger) devices now offer sophisticated means of evaluating the behaviour, spatial ecology, energetics and physiology of these animals in their natural environment (Cooke et al., 2004; Hussey et al., 2015; Krause et al., 2013). In recent years, applying these techniques has led to the discovery of individual variation in movement patterns, habitat use and feeding habits for various large marine animals, such as mammals, sharks, birds and reptiles (Hatase, Omuta, & Tsukamoto, 2007; Heithaus, Dill, Marshall, & Buhleier, 2002; Kuhn, Crocker, Tremblay, & Costa, 2009; Matich & Heithaus, 2015; Patrick et al., 2014; Rosenblatt & Heithaus, 2011; Tinker, Costa, Estes, & Wieringa, 2007; Vaudo et al., 2014). The observed individual differences, however, cannot easily be directly linked to personality due to the challenge of disentangling personality from various other factors (e.g. environmental or population differences). It is, therefore, pertinent to develop appropriate captive personality tests that complement these field data. Such experiments have been adapted successfully for sharks, identifying social personalities in catsharks, *Scyliorhinus canicula*, and showing the importance for their social structure of individual differences in the locomotion behaviour of juvenile lemon sharks, *Negaprion brevirostris* (Jacoby, Fear, Sims, & Croft, 2014; Wilson et al., 2015). However, the development of standardized tests to detect consistent individual differences in sharks' movements is still lacking. The 'open field test' has frequently been used to quantify consistent individual differences in movement and is, therefore, a promising candidate to investigate personality in sharks.

Developing and interpreting personality tests can be challenging (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013) and open field tests are no exception. In their seminal study, Réale et al. (2007) proposed five distinct personality axes: aggressiveness, sociability, shyness–boldness, exploration–avoidance (also called neophilia) and activity. Within these axes, the behaviours during open field tests have mostly been interpreted as exploration (Conrad et al., 2011; Garamszegi, Markó, & Herczeg, 2013) but also as boldness (Toms, Echevarria, & Jouandot, 2010) and, when distance moved is recorded, as activity (Carter et al., 2013). Various methods can help to interpret behaviour during personality tests. Carter et al. (2013) discussed the use of convergent (i.e. different tests measure the same personality trait) and discriminant validity tests (i.e. different tests measure different personality traits). For example, in guppies, *Poecilia reticulata*, movement activity in an open field test was not correlated with activity in a nonstressful environment (Burns, 2008), suggesting that the open field test measures reaction to novelty and not general activity (i.e. discriminant validity). However, in this study (and for large vertebrates in general) performing multiple tests was logistically difficult.

Another method to verify a reaction to novelty is to repeatedly expose individuals to the same open field (Warren & Callaghan, 1976). If the observed behaviour is a reaction to novelty, it is expected to covary with the number of exposures (i.e. habituation and/or sensitization; Groves & Thompson, 1970). Thus, when facing logistical constraints, testing habituation and/or sensitization can be a viable alternative. In addition, several studies have demonstrated high individual variation in the strength and direction of the response change, with such variations being related to an individuals' personality (Mathot, Wright, Kempenaers, & Dingemanse, 2012). Personality-related differences in plasticity (also known as behavioural reaction norms) have gained attention because of their evolutionary and ecological significance (Dingemanse, Kazem, Réale, & Wright, 2010; Dingemanse & Wolf, 2013; Martin & Réale, 2008; Mathot et al., 2012). Thus, when repeatedly exposing individuals to the open field, it is possible to also investigate the presence of individual differences in plasticity and its effect on repeatability.

In this study, we used the lemon shark, a common large coastal species in the western Atlantic whose biology, behaviour and ecology have been extensively studied (Guttridge et al., 2011; Guttridge et al., 2009; Sundström et al., 2001). At our study site in Bimini, Bahamas, juveniles (<4 years) use the mangrove-fringed shoreline which offers a shallow (<0.5 m depth) and protected habitat (Newman, Handy, & Gruber, 2007). Adjacent to the shorelines are deeper seagrass flats which older conspecifics (>120 cm total length) occupy during favourable tides to predate upon the juveniles (Guttridge et al., 2011; Morrissey & Gruber, 1993a). Despite having a home range close to the shoreline, some juvenile lemon sharks venture into these riskier habitats (Morrissey & Gruber, 1993b). Dibattista, Feldheim, Gruber, and Hendry (2007) demonstrated that sharks that were large at birth and fast growing had higher mortality rates than smaller, slower growing individuals. These findings, together with their ease of capture, abundance and robustness in captivity, make the lemon shark an excellent model species for cartilaginous fishes and large marine vertebrates to experimentally investigate individual differences in a novel open field.

Juvenile lemon sharks were observed on six occasions in an open field, with the following aims: (1) to test the repeatability of their rate of movement (ROM) to investigate the presence of interindividual differences in movement behaviour; (2) to test the variable ROM for habituation and/or sensitization with repeated exposure to the open field to understand whether the behaviour is a proxy for activity or for reaction to novelty; and (3) to investigate the presence of individual differences in the strength and/or direction of such a habituation/sensitization effect and how differences in these effects, in turn, relate to personality.

METHODS

Study Site and Experimental Set-up

This study was conducted in Bimini (20°–28°N, 72°–80°W), Bahamas, a chain of islands situated approximately 85 km east of the coast of Florida, U.S.A. In total, 28 juvenile lemon sharks (14 females and 14 males) were captured using gillnets (see Manire & Gruber, 1991 for details). Upon capture, each individual was measured for body size (mean precaudal length (PCL) $\pm$ SD = 53.23 $\pm$ 4.79 cm), sexed and equipped with a unique colour-coded tag (T-bar type, Floy Tag Inc, Seattle, WA, U.S.A.) for visual identification.

Sharks were housed in a large circular holding pen (10 m diameter) constructed just offshore in shallow (<1.5 m) sand bottom flats (see Guttridge et al., 2009 for details). Sharks were given a minimum of 2 days to acclimatize to captive conditions. During nonexperimental periods, sharks were fed to satiation every 3 days on a diet of fresh and frozen local fish (*Sphyraena barracuda*). During experimental periods, sharks were always fed the day before an observation day (see below).

Secured to the holding pen was a start box (semicircle; 1.5 m radius) that provided access to a rectangular (6 $\times$ 12 m) open field split into 18 sectors (2 $\times$ 2 m) by ground markers (Fig. 1). Sliding doors (manually operated) were used to control the movement of sharks between the three compartments, with an external exit channel attached to the test pen to facilitate the return of sharks after trial completion. Individuals had never been introduced to this pen before the trials. Behavioural observations were conducted from a 2 m high observation tower.