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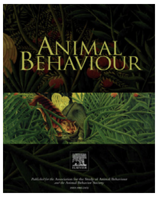

Is there a pace-of-life syndrome linking boldness and metabolic capacity for locomotion in bluegill sunfish?

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The concept of behavioural syndromes (i.e. correlations between behavioural traits) has provided an important framework for understanding individual variation in animal behaviour and its link to individual variation in physiology and life-history traits. The pace-of-life syndrome concept posits that behavioural, physiological and life-history traits coevolve in response to correlated selection pressures, and therefore predicts a positive correlation between boldness (i.e. exploration and risk taking) and metabolic capacity for locomotor performance in individuals. We tested for a pace-of-life syndrome linking boldness and metabolic capacity for locomotor activity in juvenile bluegill sunfish, *Lepomis macrochirus*. Individual fish were screened and classified as bold or shy using an established refuge emergence test. Subsequently, the aerobic and anaerobic metabolisms of bold and shy individuals were quantified using respirometry and by measuring the metabolic by-products of white muscle anaerobic glycolysis following exhaustive exercise, respectively. Bold fish demonstrated 25% greater metabolic scope for activity (i.e. aerobic capacity) than shy fish, which was attributable to a 15% greater maximum metabolic rate. However, there was no significant difference in resting metabolic rate or anaerobic energy expenditure (i.e. anaerobic capacity) between bold and shy fish. These results partially support a pace-of-life syndrome linking boldness and aerobic metabolism in juvenile bluegill sunfish, but did not reveal a link between boldness and anaerobic metabolism. Our findings suggest that aerobic and anaerobic capacities may be subject to different selection pressures, and that physiological processes governing maximum anaerobic performance in fishes are independent from behavioural and physiological traits related to boldness.

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Understanding the origins and maintenance of interindividual variation in behaviour within populations has received considerable attention among behavioural and evolutionary ecologists over the past two decades (Foster & Endler, 1999; Wilson, 1998) because of its importance for the evolution of behavioural adaptations (Dingemanse & Réale, 2005; Smith & Blumstein, 2008). The concept of behavioural syndromes provides a conceptual framework for understanding individual variation in animal behaviour (Sih, Bell, & Johnson, 2004; Wilson & McLaughlin, 2007). Behavioural syndromes are suites of correlated behaviours that exist across situations, such that the absolute expression of a particular behavioural trait (e.g. aggression) by individuals may vary across situations, but the relative expression (i.e. rank order) of that behaviour among individuals remains consistent (Sih et al., 2004). Behavioural syndromes can be expressed at the individual, population or species level (Atwell et al., 2012; Ingley, Rehm, & Johnson, 2014; Sih et al., 2004). Although behavioural syndromes can be influenced by experience (Bell & Sih, 2007; Brown, Burgess, & Braithwaite, 2007; Frost, Winrow-Giffen, Ashley, & Sneddon, 2007), be domain specific (e.g. feeding, mating, antipredator; Coleman & Wilson, 1998; Wilson & Stevens, 2005) and covary with ecological conditions (Dingemanse et al., 2007), persistence of individual behavioural differences across situations implies that behaviour is not infinitely plastic; that is, not all individuals are capable of expressing the optimum behaviour in all situations (Sih et al., 2004).

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One ecologically important axis of behavioural variation is the shy–bold continuum (Wilson, Clark, Coleman, & Dearstyne, 1994). Boldness may be defined as an animal's willingness to take risks and explore novel objects or environments, such that bolder individuals tend to behave normally or become actively exploratory when confronted with novel situations, whereas shyer individuals retreat or become vigilant (Wilson et al., 1994; Wilson & McLaughlin, 2007). Boldness has been linked to several ecologically important behaviours, including learning (Dugatkin & Alfieri, 2003; Guillette, Reddon, Hurd, & Sturdy, 2009; Sneddon, 2003), aggression (Huntingford, 1976; Riechert & Hedrick, 1993; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004), mate choice (Godin & Dugatkin, 1996), locomotor activity (Sneddon, 2003; Wilson & Godin, 2009) and dispersal or migratory tendency (Chapman et al., 2011; Fraser, Gilliam, Daley, Le, & Skalski, 2001). A number of studies (Ariyomo, Carter, & Watt, 2013; Brown, Burgess, et al., 2007; Mazué, Dechaume-Moncharmont, & Godin, 2015; van Oers, Drent, De Goede, & Van Noordwijk, 2004; Sinn, Apiolaza, & Moltschaniwskyj, 2006) suggest that boldness has a genetic basis and may be a heritable trait in some species. However, which behavioural trait leads to greater fitness depends on the specific environment, with bold individuals typically faring better in low-risk, stable environments, and shy individuals faring better in high-risk, variable environments (Sih et al., 2004).

Boldness and certain physiological traits in individual animals may be intercorrelated, thereby forming behaviour–physiology syndromes. Previous investigations of physiological correlates of boldness have focused primarily on sex differences (Ariyomo et al., 2013; Harris, Ramnarine, Smith, & Pettersson, 2010; Ingley et al., 2014), growth rate (Brown, Jones, & Braithwaite, 2007; Mas-Muñoz, Komen, Schneider, Visch, & Schrama, 2011; Ward, Thomas, Hart, & Krause, 2004), the glucocorticoid stress response (Atwell et al., 2012; Raynaud & Schradin, 2014; Thomson, Watts, Pottinger, & Sneddon, 2011) and resting metabolic rate (Careau, Thomas, Humphries, & Réale, 2008; Finstad, Forseth, Ugedal, & NæSje, 2007; Lantová, Zub, Koskela, Šíchová, & Borowski, 2011; Väätäinen, 2013). Resting metabolic rate (RMR; often used synonymously with basal metabolic rate in endotherms, or standard metabolic rate in ectotherms) is the minimum energy required for an animal to maintain physiological homeostasis (Careau et al., 2008). Two competing cause-and-effect models have emerged to explain observed relationships between boldness and resting metabolic rate (Careau et al., 2008). The ‘performance model’ states that a higher RMR is needed to maintain the digestive and metabolic machinery that supports boldness-related behaviours (e.g. higher levels of activity and aggression), and thus predicts that RMR will be positively correlated with boldness. In contrast, the ‘allocation model’ states that animals with finite energy resources must manage a limited energy budget, such that available energy should be allocated either to RMR or to boldness-related behaviours (Careau et al., 2008). Consequently, the allocation model predicts a negative correlation between RMR and boldness. To date, most empirical studies have favoured the performance model over the allocation model (Biro & Stamps, 2010), but depending on the system the two principles may act concurrently and cancel each other out, resulting in no net phenotypic correlation (Careau, Killen, & Metcalfe, 2014).

Related to the performance model described above, the pace-of-life syndrome concept posits that behavioural, physiological and life-history traits coevolve in response to correlational selection pressures (Réale et al., 2010), and thus, in addition to predicting a positive relationship between boldness and RMR, it also predicts a positive relationship between boldness (i.e. exploration and risk taking) and metabolism supporting aerobic and anaerobic locomotor activity (Le Galliard, Paquet, Cisel, & Montes-Poloni, 2013). Curiously, despite the observation that boldness has been linked to increased locomotor activity (Sneddon, 2003; Wilson & Godin, 2010) and greater predation risk (Dugatkin, 1992; Milinski, Lüthi, Eggler, & Parker, 1997), few studies have examined the relationship between boldness and locomotor performance (Careau & Garland, 2012; Farwell & McLaughlin, 2009; Le Galliard et al., 2013). Moreover, we are unaware of any studies that have directly tested for correlations between boldness and metabolic (aerobic and anaerobic) capacity to perform locomotor activities; although, Killen et al. (2014) have shown that aerobic capacity, but not anaerobic capacity, is correlated with dominance in damselfish, *Pomacentrus amboinensis*. In vertebrates, low-intensity, sustainable locomotor activity (e.g. foraging and migration) is fuelled by oxidative phosphorylation (aerobic metabolism) and is limited by an individual's metabolic scope for activity (MSA), the difference between maximum metabolic rate (MMR) and RMR (Beamish, 1978; Bennett, 1978). In contrast, high-intensity locomotor activity (e.g. prey capture and predator evasion) is fuelled primarily by anaerobic glycolysis (anaerobic metabolism), which results in a buildup of the metabolic by-product, lactate, and is only sustainable for several seconds to a few minutes (Beamish, 1978; Bennett, 1978). The pace-of-life syndrome concept predicts that both aerobic (i.e. MSA) and anaerobic capacity (anaerobic energy expenditure; AEE) should be greater in bold individuals than in shy ones.

In the current study, we tested for a pace-of-life syndrome linking boldness and metabolic capacity for locomotor activity in wild-caught juvenile bluegill sunfish, *Lepomis macrochirus*. Juveniles of this species are an excellent organismal model for our study because (1) they have been shown to exhibit strong and consistent individual differences in boldness (Wilson & Godin, 2009), (2) boldness in this species is correlated with higher levels of activity and greater use of fast undulatory swimming over slow labriform swimming (Wilson & Godin, 2010) and (3) many aspects of their behavioural ecology have been characterized (Spotte, 2007). We hypothesized that juvenile bluegill sunfish would exhibit a pace-of-life syndrome linking boldness to both aerobic and anaerobic metabolism, and therefore, we predicted that bold fish would exhibit greater RMR, greater aerobic capacity (MSA) and greater anaerobic capacity (AEE) than shy fish.

METHODS

Experimental Animals

Juvenile bluegill sunfish ($N = 82$ in July 2009 and $N = 56$ in July 2010) were angled from near-shore, shallow habitats in Lake Opinicon, Ontario, Canada (44°33′32″N, 76°19′41″W), using small barbless hooks baited with a small piece (~1 cm) of earthworm. To minimize angling stress and injury, we used a standardized angling protocol that required all fish be landed, have the hook removed and be placed into a cooler with fresh lake water within 10 s of the hook being set (i.e. from when the fish bit down on the hook). Any angled fish with visible signs of injury (i.e. hooked somewhere other than upper or lower jaw) or disease, or that took longer than 10 s to land and free from the hook, were excluded from the study.

Captured sunfish were placed in a cooler (50.4 litres; 56 × 30 × 30 cm) containing lake water and transferred to shore-side laboratory facilities at the Queens' University Biological Station (Lake Opinicon; total transit time <30 min), where they were housed individually in shaded plastic tanks (39.5 litres; 52 × 40 × 19 cm) overnight for at least 16 h before being used in experiments the next day. Holding tanks were supplied continuously with fresh, aerated lake water, and artificial plants were added to each tank to provide refuge and minimize holding stress (Portz, Woodley, & Cech, 2006). Water temperature ranged from 20.6 to 24.4 °C in 2009 and from

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