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IN FOCUS

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Personality and pace-of-life: Ecological lessons learnt from free-ranging lemon sharks

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Abstract

In Focus: Dhellemmes, F., Finger J.S., Smukall M.J., Gruber S.H., Guttridge T.L., Laskowski K.L., & J. Krause. (2020) Personality-driven life-history trade-offs differ in two subpopulations of free-ranging predators. *Journal of Animal Ecology*, *90*, 260–272. Life-history theory predicts that explorative individuals live-fast-but-die-young as they take risks to rapidly accumulate resources. Dhellemmes et al. (2020) show that fast-exploring sharks forage in risky habitats, where they grow-fast-but-die-young. In higher risk environments, however, this personality-related pace-of-life-syndrome does not exist because neither fast- nor slow-exploring types venture out into risky areas. The study thereby reveals the key role of ecology as a mediator of personality-related pace-of-life-syndromes in the wild.

KEYWORDS

animal personality, cross-validation, exploration, growth-mortality trade-off, life-history, pace-of-life, predation risk, risk-taking

The role of behaviour in the evolution of optimal life histories has become a forefront of research in contemporary behavioural ecology (Westneat & Fox, 2010). This is not surprising as behaviour represents the primary interface between individuals and their environment (Duckworth, 2009). Over the past two decades, a suite of adaptive theory has been developed to predict the ecological conditions favouring the adaptive integration of behaviour and life history (reviewed by Mathot & Frankenhuis, 2018). The functional integration of 'risk taking' and life history has been a particular focus of research (Luttbeg & Sih, 2010; Wolf et al., 2007). Risk-taking behaviour is functionally defined as any behaviour that facilitates resource acquisition at the cost of increased risk of predation, parasitism or starvation, and may therefore represent a behavioural 'mediator' of life-history trade-offs. Dhellemmes et al. (2020) firmly put this idea to the test in a longitudinal study of free-ranging lemon sharks *Negaprion brevirostris*.

Research focussing on the adaptive integration of behaviour and life history has been gaining momentum primarily due to the discovery that behavioural traits are both repeatable and heritable within single populations (meta-analyses: Bell et al., 2009; Dochtermann et al., 2019), and the quest for revealing the ecological conditions that may favour the adaptive emergence of repeatable behaviour (aka 'animal personality'; Dall et al., 2004). Theoreticians have addressed this issue by proposing that an individual's future fitness expectations (residual reproductive value) can be viewed as a state variable affecting the balance of costs and benefits of risk taking (as defined above), causing those with few reproductive 'assets' to boldly acquire resources but those with many to shyly protect them instead; 'bold' individuals therefore should live-fast-but-die-young (Wolf et al., 2007). More recently, behavioural ecologists have integrated ecological theory developed to understand variation in pace-of-life among populations and species (Ricklefs & Wikelski, 2002), focusing on the functional integration of phenotypic traits and life history into "pace-of-life-syndromes" among individuals of the *same* population (Dammhahn et al., 2018; Réale et al., 2010). Many empirical tests of theory, however, either failed

to support the existence of a predicted "personality-related pace-of-life syndrome", or otherwise at best provide ambiguous support (meta-analyses: Moiron et al., 2020; Royaute et al., 2018), leaving the field in crisis (Dammhahn et al., 2018). Dhellemmes et al. (2020) demonstrate how this impasse may be resolved by firmly testing two major explanations for the mismatch between theory and empirical data.

Both explanations imply that most empirical tests of theory are, in fact, inappropriate (Carter et al., 2013; Montiglio et al., 2018; Niemelä & Dingemanse, 2018). First, most studies of personality-related pace-of-life syndromes *assume* rather than demonstrate variation in pace-of-life. Dhellemmes et al. (2020) firmly put this key assumption to the test by estimating whether growth rate is under negative survival selection in the wild. Using a longitudinal dataset spanning 23 years, they demonstrate that this is indeed the case in both of two subpopulations under study, thereby firmly demonstrating the existence of the predicted growth–mortality trade-off (Stamps, 2007). Second, the integration between pace-of-life and individual behaviour is expected for behaviours facilitating resource acquisition and growth at the cost of increased predation risk. Researchers commonly subject animals to standardized behavioural assays under semi-natural conditions, and (again) *assume* rather than demonstrate that the focal risk-taking assay predicts risk-taking behaviour in the wild (Archard & Braithwaite, 2010; Niemelä & Dingemanse, 2014). Dhellemmes et al. (2020) measured exploration behaviour (ranging from slow to fast) during short-term captivity, after which they used acoustic telemetry to establish whether exploration also represented a 'proxy' for risk-taking during foraging in the wild. Lemon sharks can forage either in mangrove edges where predators cannot enter or away from cover in more productive seagrass patches. The lemon shark system also passes this test as faster explorers were more likely to forage away from the coast. Altogether, this study system is therefore extremely suitable for testing whether personality mediates the trade-off between growth and mortality, resulting in a personality-related pace-of-life syndrome.

While the verification of these two major assumptions demonstrates the scientific scrutiny required for convincingly testing personality-related ecological theory (Niemelä & Dingemanse, 2014, 2018), its foremost major contribution lies in the demonstration of the key role of ecology (Montiglio et al., 2018). Specifically, Dhellemmes et al. (2020) studied two adjacent subpopulations of lemon sharks: one was predator-poor (North Sound) while the other was predator-rich (Sharkland; Figure 1). As expected, in Sharkland, sharks of either personality type were, on average, observed much closer to mangrove edges. As a consequence, the relationship between exploration behaviour and risk taken during foraging did not exist in the predator-rich subpopulation; explorative sharks only took foraging risks in the predator-poor subpopulation. This finding explains why a personality-related pace-of-life-syndrome existed solely in an ecological context where it actually mediated the growth–mortality trade-off: the predator-poor subpopulation.

An interesting twist to the story is that the growth–mortality trade-off characterized *both* subpopulations, despite the fact that a personality-related pace-of-life syndrome existed *only* in the predator-poor environment. Did risk-taking not mediate the trade-off in the predator-rich environment, where fish primarily stayed on safe grounds? This is indeed possible. For example, ecological contexts where personality predicts how individuals resolve the growth–mortality trade-off may represent situations where *extrinsic* sources of mortality (sensu Medawar, 1952; Williams, 1957)

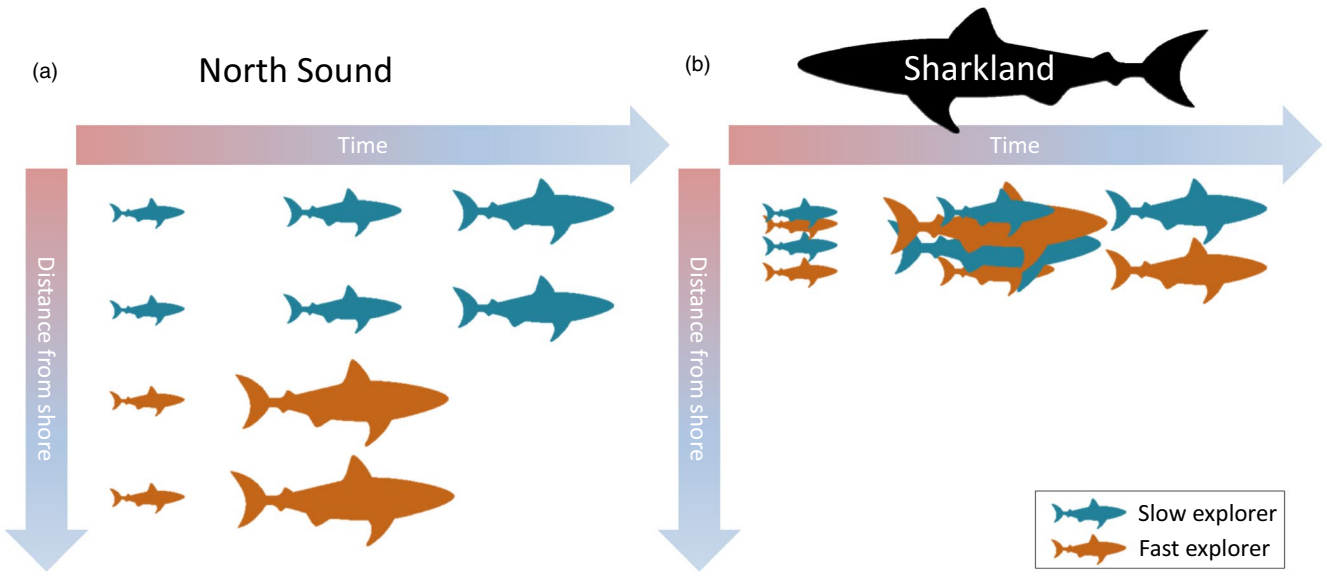

FIGURE 1 (a) Slow explorers (blue) grew slower than fast explorers (orange) but also lived longer in North Sound, a subpopulation of lemon sharks with relatively low predation risk. (b) By contrast, in Sharkland, a predator-richer environment, both types of shark stayed closer to mangrove edges, where predation risk is lower in both sites. Exploration behaviour mediated the trade-off between growth and mortality only in North Sound because only here fast-exploring sharks took more foraging risks by venturing out more into the open [Colour figure can be viewed at wileyonlinelibrary.com]

have an overriding effect. This may be the case in the North Sound subpopulation, where faster explorers exposed themselves to predation risk. By contrast, in Sharkland, where lemon sharks did not forage in open water, other mechanisms, such as *intrinsic* sources of mortality (Williams, 1957), may have shaped the growth–mortality trade-off. Variation in the relative contributions of intrinsic versus extrinsic mortality may therefore explain apparent disagreements, for example, between field and laboratory tests of pace-of-life syndromes (Moiron et al., 2020; Santostefano et al., 2017). The findings of Dhellemmes et al. (2020), therefore, call for a firm integration of ecological context in both theoretical and empirical research on pace-of-life and other life-history syndromes in nature.

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