RESEARCH ARTICLE

Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators

Félicie Dhellemmes[1,2,3] | Jean-Sébastien Finger[3] | Matthew J. Smukall[3,4] |
Samuel H. Gruber[3†] | Tristan L. Guttridge[3,5] | Kate L. Laskowski[1,6] | Jens Krause[1,2]

[1]Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany; [2]Faculty of Life Sciences, Albrecht Daniel Thaer-Institute of Agricultural and Horticultural Sciences, Humboldt-Universität zu Berlin, Berlin, Germany; [3]Bimini Biological Field Station Foundation, South Bimini, Bahamas; [4]College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA; [5]Saving the Blue, Miami, FL, USA and [6]Department of Evolution and Ecology, University of California Davis, Davis, CA, USA

Correspondence
Félicie Dhellemmes
Email: Felicie.dhellemmes@gmail.com

Abstract

1. Consistent individual differences in behaviour (i.e. personality) can be explained in an evolutionary context if they are favoured by life history trade-offs as conceptualized in the pace-of-life syndrome (POLS) hypothesis. Theory predicts that faster-growing individuals suffer higher mortality and that this trade-off is mediated through exploration/risk-taking personality, but empirical support for this remains limited and ambiguous. Equivocal support to the POLS hypothesis suggests that the link between life history and personality may only emerge under certain circumstances. Understanding personality-driven trade-offs would be facilitated by long-term studies in wild populations experiencing different ecological conditions.

2. Here, we tested whether personality measured in semi-captivity was associated with a growth-mortality trade-off via risk-taking in the wild in two subpopulations of juvenile lemon sharks *Negaprion brevirostris* known to differ in their predator abundance. We expected stronger personality-driven trade-offs in the predator-rich environment as compared to the predator-poor environment.

3. Sharks were captured yearly from 1995 onwards allowing us to obtain long-term data on growth and apparent survival in each subpopulation. We then used a novel open-field assay to test sharks for exploration personality yearly from 2012 to 2017. A subset of the tested sharks was monitored in the field using telemetry to document risk-taking behaviours. We tested (a) if fast explorers in captivity took more risks and grew faster in the wild and (b) if natural selection acted against more explorative, faster-growing sharks.

4. In the subpopulation with fewer predators, more explorative sharks in captivity took more risks in the wild and grew faster. In turn, larger, fast-growing sharks had lower apparent survival. In the predator-rich subpopulation, despite finding

---

selection on fast growth, we found no link between exploration personality and the growth-mortality trade-off.

5. Our study demonstrates that the association between personality and life history is favoured in some ecological contexts but not in others. We identify predator and resource abundance as two main potential drivers of the personality-mediated trade-off and emphasize that future work on the POLS hypothesis would benefit from an approach integrating behaviour and life history across ecological conditions.

1 | INTRODUCTION

Within a population, individuals often exhibit consistent individual differences in behaviour, a phenomenon described as 'animal personality' (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Maintenance of such within-population variation can be explained when behaviour mediates trade-offs between important life-history traits (Réale et al., 2010; Wolf, van Doorn, Leimar, & Weissing, 2007). Life history trade-offs occur when the optimal response for one trait is reached at the expense of another (Stearns, 1989). Such trade-offs can maintain multiple phenotypes in a population by allowing individuals with different behavioural strategies to achieve comparable fitness (Mangel & Stamps, 2011). For example, individuals that explore more and take more risks may discover more new food patches than their less explorative conspecifics (Spiegel, Leu, Bull, & Sih, 2017). Consequently, they would grow faster and reproduce at a younger age but experience higher mortality via predation. In turn, less explorative, risk-averse individuals would likely conduct less extensive searches for resources, leading to lower growth and delayed reproduction but higher survival due to lower predator encounter probabilities (Lapiedra, Schoener, Leal, Losos, & Kolbe, 2018). In goldfish *Carassius auratus*, individuals that make more outings from a refuge acquire more food than their risk-averse conspecifics but suffer higher risks from avian predation (Balaban-Feld et al., 2019). In this way, individual behaviour is expected to play a critical role in mediating trade-offs between important life-history traits such as growth and mortality (Stamps, 2007). This concept is most comprehensively conceptualized by the pace-of-life syndrome (POLS) hypothesis which integrates covariations in life history, behaviour and physiology within populations (Dammhahn, Dingemanse, Niemelä, & Réale, 2018).

Despite a large literature on life history trade-offs and on animal personality, testing the link between these two phenomena has led to equivocal evidence (Montiglio, Dammhahn, Dubuc Messier, & Réale, 2018; Royauté, Berdal, Garrison, & Dochtermann, 2018). For instance, female wild cavies *Cavia aperea* that explored more in a known captive environment grew faster, in accordance with theoretical predictions. But unexpectedly, exploration in a novel open field correlated negatively with growth and no behaviour correlated with the reproductive output of the animals (Guenther, 2018). In crickets *Gryllus integer*, bolder animals were found to have stronger cellular immune functions, challenging predictions of the POLS hypothesis (Niemelä, Dingemanse, Alioravainen, Vainikka, & Kortet, 2013). More recently, a meta-analysis revealed that personality only explained a small portion of variance in survival (Moiron, Laskowski, & Niemelä, 2020). Such conflicting results could be due to the inadequacy of the testing environment to elicit trade-offs. Indeed, the need for controlled and repeated testing inherent to studies on personality has led to a predominance of captive study systems in the literature (Archard & Braithwaite, 2010). However, local ecological conditions (e.g. predator abundance, resource abundance etc.) may be necessary to drive the emergence of life history trade-offs (Moiron et al., 2020; Montiglio et al., 2018). For instance, stronger selection on risk-taking behaviours was observed in the presence of predators than in their absence in *Anole sagrei* lizards (Lapiedra et al., 2018). Furthermore, the relationship between personality, survival and reproduction was found to be habitat dependent in Eurasian red squirrels, *Sciurus vulgaris* (Santicchia et al., 2018). Therefore, the link between life history and personality might be most effectively investigated in long-term studies of free-ranging animals experiencing strong and variable ecological pressures (Jablonszky et al., 2018; Montiglio et al., 2018).

The ambiguity of evidence supporting the link between personality and life history trade-offs may also arise from the difficulty of establishing the ecological relevance of captive behavioural tests (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). Exploration of a standardized novel open field in house mice *Mus musculus domesticus* reflected exploratory behaviour in semi-natural environments (Krebs, Linnenbrink, & Guenther, 2019) and a similar test in great tits *Parus major* did not (Arvidsson, Adriaensen, van Dongen, De Stobbeleere, & Matthysen, 2017). One test might be appropriately used as a proxy for natural behaviours in some species but not in others. Researchers in that case would benefit from working in systems

in which behaviours measured in captivity can be compared to similar behaviours in the field to ensure that the captive tests' results can be expected to regulate trade-offs in the wild (as previously suggested by Réale et al., 2007).

Here we tested whether personality measured in a novel open field mediates a growth-mortality trade-off via wild risk-taking behaviour, in juvenile lemon sharks *Negaprion brevirostris*. At our study site, Bimini, Bahamas (Figure 1), juvenile lemon sharks exhibit high site-fidelity and small home-ranges, which allow for regular monitoring until they die or disperse (Chapman et al., 2009; Morrissey & Gruber, 1993). Previous work suggests that life history trade-offs are important in this system, with slower-growing and smaller-bodied individuals enjoying higher apparent survival (DiBattista, Feldheim, Gruber, & Hendry, 2007) whereas individuals that exhibit riskier foraging strategies experience higher growth rate but potentially higher predation (Hussey et al., 2017). It is unclear, however, whether individual behaviour mediates the growth-mortality trade-off in this system. Wild-caught juvenile lemon sharks from Bimini were tested yearly in a captive novel open-field assay from 2012 to 2017 ($n = 286$ individuals tested), with a subset of the tested sharks ($n = 46$) monitored in the field for up to a year using acoustic telemetry to record their distance from the shore, which is a known refuge from predators (Hussey et al., 2017). Then, using 23 years of mark–recapture data

$(n = 2,627$ individuals), the personality measures and the telemetry data, we tested the predictions (a) that faster explorers in the novel open field were found further from shore (i.e. exhibited risk-prone behaviours) and had higher growth rates and (b) that natural selection acted against explorative, fast-growing individuals in two adjacent subpopulations of juvenile lemon sharks (North Sound and Sharkland, see Figure 1). Because these subpopulations were described to differ in their predator abundance, with Sharkland having more predators (Dhellemmes, Finger, Laskowski, Guttridge, & Krause, 2020; Guttridge et al., 2012), we expected selection on exploration behaviour and fast growth to be stronger there than in North Sound.

2 | MATERIALS AND METHODS

2.1 | Shark capture and handling

In Bimini, Bahamas (Figure 1), lemon sharks are born in April and May of each year (Gruber, de Marignac, & Hoenig, 2001). They exhibit high site-fidelity and can be found for the first 2–5 years of their lives in specific areas (so-called nurseries) around the islands (Morrissey & Gruber, 1993). In this study we focus on the subpopulations inhabiting two nursery areas that are adjacent but almost totally separated with respect to emigration and immigration of sharks under 2 years of age: North Sound and Sharkland (Figure 1; Gruber et al., 2001). Sharks from both subpopulations were sampled in May and June of every year since 1995. Sampling was conducted using gillnets (180 m, length) deployed perpendicularly to the shore at three standard locations (see Figure 1) for six consecutive nights (12 hr) in each nursery. Nurseries were sampled consecutively resulting in 12 nights of sampling per year. We checked the nets every 15 min to minimize stress of sharks and bycatch. Upon capture, sharks were checked for the presence of a uniquely coded PIT (Passive Integrated Transponder, Destron Fearing), they were tagged, sexed, measured [Pre-caudal length (PCL), nearest mm] and the condition of their umbilical wound was assessed to estimate age (see below Section 2.2). Sharks were then transferred to a nearby housing pen (details on pen construction: Guttridge et al., 2009) which prevented them from being captured on multiple occasions within the sampling period. Consequently, a rapid decrease of the capture rate was observed over the six nights of sampling, providing evidence for the very high efficiency of these methods (96% of a subpopulation captured by the fourth night of fishing as estimated by Gruber et al., 2001). Since the inception of this mark–recapture program in 1995, we recorded a total of 3,419 captures of sharks under 2 years old (0 year old, $n = 2,204$; 1 year old, $n = 1,215$) which accounted for the majority of sharks captured ($n = 1,075$ captures of sharks between 2 and 5 years old).

FIGURE 1 Map of the Bimini Islands (N 25.717, W −79.283), displaying the two juvenile lemon shark nursery areas (North Sound and Sharkland), the six capture locations and the two testing sites

2.2 | Age estimations

Lemon sharks are placental viviparous and juveniles are born with an umbilical wound which closes slowly over a few months (DiBattista
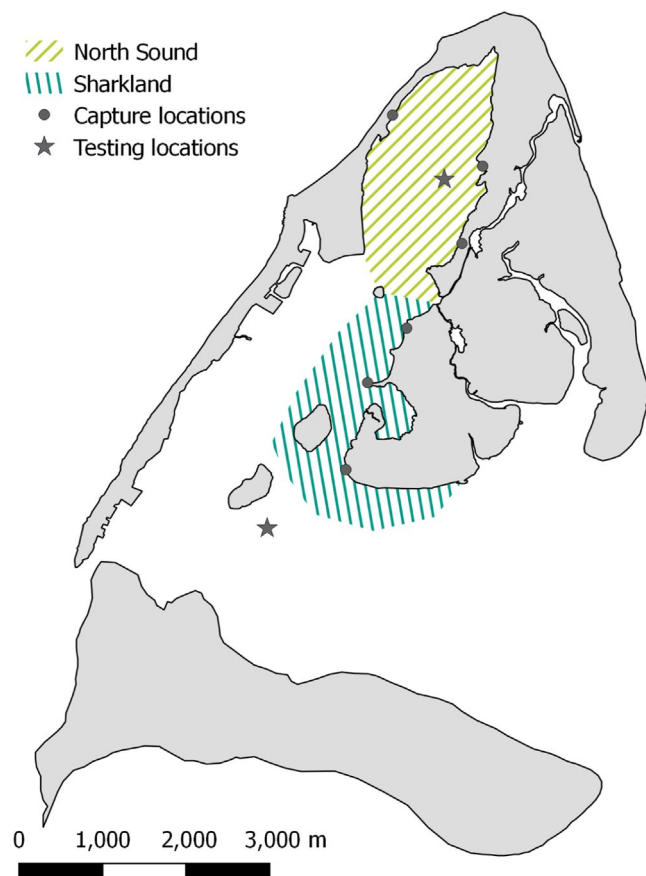
et al., 2007). As a result, newborn sharks were identified by checking the status of their umbilical wound (open to any extent: 0 year old, fully closed: imprecise age, up to 5 years old). Umbilical wound status was not recorded for $n = 1,227$ sharks. To estimate their age, we used a linear regression of age on PCL for sharks that had been precisely aged (i.e. via umbilical status) and that were under 2 years old, as we were mostly interested in 0 and 1-year old sharks for this study (Adjusted R^2: 0.66, $F_{1,3,312} = 6,627$, $p < 0.0001$). We predicted the age of the sharks based on the linear model, rounding the estimated age to the closest integer. We considered this linear estimation relevant as the relationship between body length and age (estimated via growth-band counts on vertebral centrum) shows a strong linear relationship in sexually immature lemon sharks (<180 cm PCL; mean PCL of sharks included in this study: 50.2 cm $\pm$ 3.34 SD; Gruber & Stout, 1983). Eight unaged sharks did not have a measure of PCL, we therefore used a similar model with the total length of the sharks instead. This method proved to be 90.1% accurate when used to predict the age of sharks for which umbilical opening data were available.

2.3 | Growth and apparent survival estimations

Juvenile lemon sharks are likely to disperse from their natal nursery between age 3 and age 5 (Chapman et al., 2009; DiBattista et al., 2007). In addition, most sharks captured via the mark–recapture program described above were 0 or 1 year old, therefore, we only considered in this study animals that were under 2 years old ($n = 2,627$). We calculated growth as the body length (PCL) gained from one year to the next (in cm). The sharks' small home-ranges (<400 m² for sharks under 54 cm PCL, Morrissey & Gruber, 1993), coupled with the efficiency of the capture methods and the negligible emigration at age 0 and 1 (DiBattista et al., 2007), enabled us to estimate apparent survival based on whether sharks were recaptured (apparent survival = 1) or not (shark assumed to have died: apparent survival = 0). To avoid underestimating survival, we assumed every shark that was never recaptured but was over 2 years old to have dispersed and survived.

2.4 | Personality assay

From 2012 to 2017, a subset of the sharks captured ($n = 286$ individuals, $M = 54$ tests per year, see Table 1) was subjected to a novel open-field test each year in June. A behavioural testing arena, in which sharks were transferred between 4 and 7 days after capture, was built <1 km away from the mangrove shore. It consisted of three interconnected pens constructed of mesh: a housing pen divided in three compartments (10 × 5 m), a circular pen for a sociability assay (10 m diameter; Finger, Guttridge, Wilson, Gruber, & Krause, 2018) and the novel open field (6 × 12 m; Figure 2a). We used two different testing sites: one in North Sound from 2012 to 2015 and the other in south Sharkland in 2016 and 2017 (see Figure 1). This was due

TABLE 1 Overview of sample sizes. A count of each data point is given, followed by the number of individuals for which multiple measurements are available

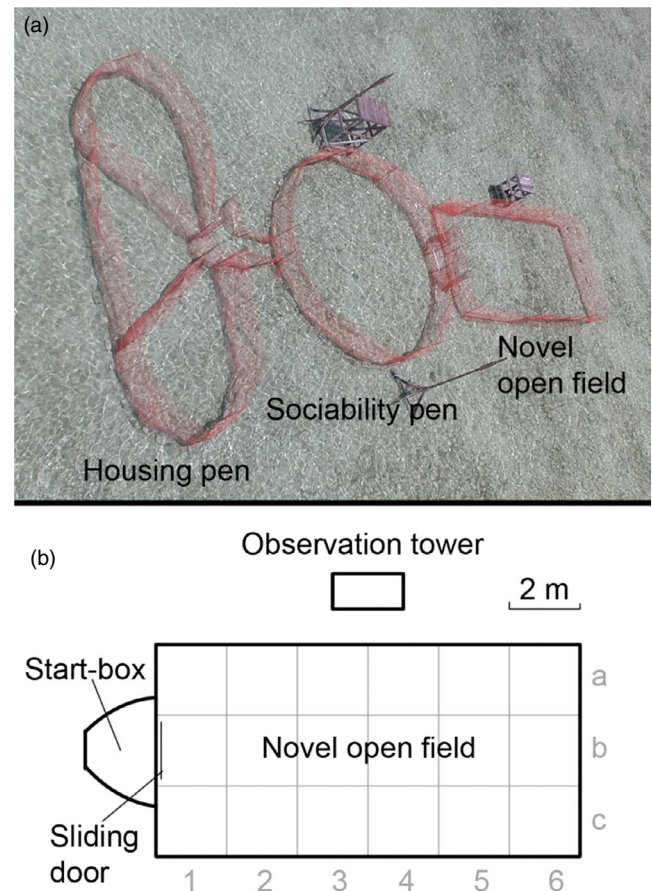|	PCL	Growth	Exploration	Distance
North Sound	1,629 (343)	702 (125)	173 (15)	624 (22)
Sharkland	1,789 (313)	702 (148)	151 (10)	407 (24)

FIGURE 2 (a) Aerial view of the behavioural testing arena. (b) Schematic representation of the novel open field

to concerns regarding a dredging project on the west side of North Sound, which could have compromised visibility and made the tests impossible. In every model presented in this study, we account for the potential effect of the testing location by adding the year as a random effect.

Between 12 and 18 hr prior to the assays, sharks were fed to satiation with locally caught *Sphyraena barracuda* filets to avoid hunger biases in behaviour (Biro & Booth, 2009). Each trial day, six sharks were observed in a sociability assay with a 25-min duration. Sharks were then individually subjected to the novel open-field assay. Data on sociability is not presented here as the sample size was significantly lower than on the novel open-field assay due to difficulties with the observations (but see Finger et al. (2018) for repeatability of Sociability). The sociability and exploration tests could not be conducted on separate

days without reducing our sample size. This compelled us to consider the potential impact of the social interactions experienced during the sociability test on the novel open field's results. We performed pilot tests to study the influence of the size of the group with which tested sharks are kept in captivity on the novel open field score and found no significant effect (Chi-square = 0.07, p = 0.77). In addition, we always mixed the groups for the sociability test, so sharks would not be tested twice with the same group (see Finger et al., 2018). For these reasons we are confident that the novel open field's results are not biased by the previous sociability assay.

For the novel open-field assay, sharks were ushered individually into the start-box which separated the sociability pen from the novel open field. Once a shark was in the start-box, it was left to acclimate for 5 min. An observer standing outside the pen then opened a sliding door to the novel open field. Once the shark entered the novel open field, the start-box was closed, and 10 min of behavioural observations initiated. We recorded the shark's position in the pen using small markers on the seafloor that divided the pen into a grid of eighteen 2×2 m areas (Figure 2b). The number of areas visited per second (including revisits; 'exploration score') was previously found to represent juvenile lemon sharks' reaction to novelty and to be repeatable (repeatability adjusted for body size and year: 0.37, (Dhellemmes, Finger, Laskowski, et al., 2020). Further, the order at which the sharks were tested in the open field was shown to not influence the exploration score (Dhellemmes, Finger, Laskowski, et al., 2020).

We included in this study only the first exploration score per year per individual, as lemon sharks are known to show short-term habituation to the novel open-field test (Finger et al., 2016). As a result, some sharks have two measures of explorations (see Table 1), but never in the same year (mean number of measurements per individual = 1.13, min = 1, max = 2).

2.5 | Risk-taking measurement in the wild

The novel open-field assay offered a quick, standardized way to obtain behavioural measurements on many individuals, but it is unclear whether it is relevant to natural behaviours. We measured individual risk-taking behaviour in the wild using acoustic telemetry on a subset of the sharks tested in the novel open field. For juvenile lemon sharks, the mangrove shore in Bimini constitutes an important protection from predators (Guttridge et al., 2012; Hussey et al., 2017). However, the main prey of lemon sharks (e.g. mojarras *Gerreidae*, grunts *Haemulidae*, Newman, Handy, & Gruber, 2009) also benefit from the refuge within the complex structure of this habitat. As a result, sharks have higher foraging success in open habitats such as seagrass patches as opposed to mangrove edges (R. Bullock, 2013, unpubl. data) and consequently have higher growth rates (Hussey et al., 2017). The decreased potential for sharks foraging away from the shore to escape predators within mangrove roots suggests the existence of a trade-off between efficient foraging and refuging (Hussey et al., 2017). In this context, we assume the distance juvenile sharks swim away from the shore to be a good proxy for their willingness to take risks, which is likely to be associated with a growth-mortality trade-off.

We randomly chose sharks within a size-matched group of individuals that had received the novel open-field assay to minimize size differences (PCL: M = 53.3 cm ± 1.8 SD). We surgically implanted acoustic transmitters (CT-82-2-I, battery life 14 months, Sonotronics) into the body cavity of sharks via a 2–3 cm incision made a few centimetres anteriorly to the pelvic fins using sterilized instruments. We closed the incision with two or three sterile monofilament resorbable sutures (75 cm × 24 mm; CP Medical®; see Kessel et al. (2014) for detailed methodology). Sharks were placed into a state of tonic immobility (a state of lethargy, comparable to hypnosis, Watsky & Gruber, 1990) for the entire procedure. This was preferred to the use of anaesthetic since sharks are still able to strongly ventilate their gills under tonic immobility and recovery is immediate after the surgical procedure (Kessel & Hussey, 2015). The implanted electronic transmitters weighted 9.5 g which did not exceed 2% of the sharks' body weight (as recommended by Kilfoyle & Baggeroer, 2000). After the procedure, sharks were kept in captivity for 7 days and were monitored for their healing daily. We then released them at their site of capture.

We tracked sharks in the North Sound during two consecutive summers (2014, n = 17; 2015, n = 12), and sharks from Sharkland the two following summers (2016, n = 14; 2017, n = 19). Logistical constraints of equipment and personnel limited our monitoring to one subpopulation at a time. Despite needing to spread the study over two consecutive years for each subpopulation, we expect conditions to be similar within sites and across years. In two separate studies looking at faunal communities of Bimini, no seasonal changes in abundance of teleost fishes were observed suggesting that within a habitat, resource abundance is stable (Grimmel, Bullock, Dedman, Guttridge, & Bond, 2020; Newman, Handy, & Gruber, 2007). In terms of predator abundance, no significant yearly fluctuations in capture rates were documented for tiger shark *Galeocerdo cuvier*, lemon sharks and blacktip sharks *Carcharhinus limbatus* which are potential predators for juvenile lemon sharks (Hansell et al., 2018).

From September to the end of April, we proceeded to the area where the tagged sharks lived using a 16 ft flat bottomed skiff powered by a 40-horsepower outboard engine. This was done twice a week, as long as the weather allowed it. To avoid observer biases in the search procedure, we followed a standardized transect to locate the sharks (see Appendix S1 for transect and exact methodology) with speed maintained below 2.5 m/s and usually completed the transect in 7 hr.

Once a shark was found, we recorded its identity, the GPS (Global Positioning System) coordinates of the boat (decimal degrees), the water depth (cm), the bearing to the shark (degrees) and estimated distance (m) from the boat to the shark. The position of the shark was then extrapolated from the position of the boat using the Haversine formula (Sinott, 1984). We then calculated the distance from the shark to the nearest shore using the 'gDistance' function provided in the RGEOS package in R (version 3.5.2; Bivand & Rundel, 2017; R Core Team, 2017). Only sharks that had been encountered on more

than five tracking events were included in the dataset. Therefore, if a tag was malfunctioning or a shark died or was predated upon early in the study, it was removed from the dataset. Consequently, following data filtering, the number of individuals for which distance from shore data was available in North sound was $n = 19$ (2014: $n = 10$, 2015: $n = 9$) and in Sharkland was $n = 27$ (2016: $n = 12$, 2017: $n = 15$; see Table 1). On average each shark was measured 22 times for distance from shore (min = 5, max = 65).

2.6 | Statistical analysis

All statistical analyses were performed in the R environment (R Core Team, 2017) version 3.5.2. When relevant, we visually checked normality of the data.

We acknowledge that multivariate analysis and structural equation modelling are becoming increasingly prominent to investigate questions related to POLS hypothesis (see e.g. Moiron, Araya-Ajoy, Mathot, Mouchet, & Dingemanse, 2019; Polverino, Santostefano, Díaz-Gil, & Mehner, 2018; Santostefano, Wilson, Niemelä, & Dingemanse, 2017). However, these methods call for a high amount of repeated measures within individuals and our dataset was not sufficient to employ them (see Table 1). We therefore present below univariate methods that are more suitable to the data used for this study.

We used two sample t tests to compare growth, distance from shore and exploration score in the two subpopulations. To verify whether both subpopulations presented the same diversity of phenotypes, we compared the variance of growth, distance from shore and exploration using F tests. The difference in apparent survival between the subpopulations was tested using a chi-square test.

All generalized linear mixed models described below were performed in the MCMCGLMM package (Hadfield, 2010). For all models, we set the number of iterations to 330,000 with a thinning interval of 100 and discarded the first 30,000 iterations. We obtained Monte Carlo Markov Chains with a sample size of 3,000 and with low autocorrelation. Each model was fit using a weakly informative inverse gamma prior. We used a gaussian error distribution for every model, except for the logistic regressions which were fit using the 'categorical' family. Growth, exploration and PCL were mean centred and standardized to units of one standard deviation within each year and subpopulation to set them on a similar scale and meet normality assumptions. Distance from shore was square root transformed to meet normality assumptions.

To test whether each individual's exploration score obtained in the novel open-field assay was a relevant indicator of the distance travelled from the shore (i.e. assumed to represent risk-taking) we modelled distance from shore (square root transformed) as a function of exploration score (standardized) with an interaction with subpopulation (factor). We included the interaction to allow for the detection of differences in the relationship between distance from shore and exploration between the subpopulations. Because we had on average 22 measures of distance from shore and 1.13 measures of exploration per individual, we used the value of exploration

measured before acoustic tracking for each individual and their mean distance from shore throughout the study.

To test whether the exploration score predicted growth in both subpopulations we modelled growth (standardized) as a function of exploration (standardized) with an interaction with subpopulation (factor). We accounted for yearly differences and repeated measures within individuals by including year (factor) and PIT Tag number (factor) as random effects. We tested whether distance from shore predicted growth using a similar model but without random effects: the mean distance from shore of each individual that received an acoustic transmitter was used as a fixed effect, with an interaction with subpopulation.

We then determined natural selection on the traits of interest according to the method developed by Lande and Arnold (1983). Because only sharks that had survived a year had a growth estimate, we also used PCL (which has a much larger sample size, see Table 1) in the selection analysis, as DiBattista et al., (2007) previously found by selection on growth and on body length (i.e. PCL) to act in the same direction in our system. This is likely because sharks' growth at the end of an interval is correlated to their pre-caudal length at the beginning of the interval (Pearson's $\rho = 0.16$, $p < 0.0001$). In addition, obtaining fast growth and maintaining a large body likely requires high resource acquisition (Blanckenhorn, 2000), resulting in both of those traits being selected against through risk-taking and exploration. We contend in this case that selection on PCL can be expected to be informative of a growth-mortality trade-off when sample size on growth does not allow for its detection.

To determine selection on growth, body size and exploration score we calculated standardized linear selection gradients (β') and standardized linear selection differentials (S'_i) in each subpopulation. Gradients estimate selection on a trait of interest while holding the effects of all other traits constant, while differentials estimate the total selection on a trait, including indirect selection via other correlated traits (Lande & Arnold, 1983; Réale & Festa-Bianchet, 2003). Accordingly, selection differentials are calculated by regressing fitness on the standardized value of each trait independently while selection gradients are calculated with every trait included in the model. Here, we regressed relative fitness [apparent survival divided by the mean apparent survival of the cohort (year and subpopulation)] on the standardized values of growth, PCL and exploration. In our case, the available sample size for PCL was much higher than for growth, which was much higher than for exploration (see Table 1). Therefore, we calculated selection for multiple sub-samples of the data: (a) selection differentials on PCL, (b) selection gradients on PCL and growth, (c) selection gradients on PCL and exploration, and (d) selection gradients on all traits. Because data on growth were only available if the shark had survived from one year to the next, apparent survival would always be '1' for sharks that had an available growth measurement. Therefore, any model including growth was made using apparent survival to year $n + 2$ rather than to year $n + 1$. To control for potential survival and growth benefits of elongated stay in captivity due to testing in the open field we also ran selection models on subsets of the data containing only sharks that were never tested in captivity.

Because survival is binomially distributed, we used logistic regressions for significance testing (Réale & Festa-Bianchet, 2003). All selection models were computed for each subpopulation separately given difficulties of model convergence. Therefore, we checked whether the selection gradients and differentials were different between populations using post-hoc t tests on the posterior distributions of each model. We accounted for yearly differences and repeated measures within individuals by including year (factor) and PIT Tag number (factor) as random effects in all selection models.

Selection gradients and differentials could not be computed on distance from shore due to low number of individuals (see Table 1). However, we computed a logistic regression of survival on distance from shore with an interaction with subpopulation to estimate the direction of selection on this trait and its significance. Similar to the models including distance from shore above, we used the mean distance from shore of an individual and its survival at the end of the tracking season.

The data used for this analysis are available on the Dryad Digital Repository https://doi.org/10.5061/dryad.ksn02v71r (Dhellemmes, Finger, Smukall, et al., 2020) and an R markdown file is available as Supporting Information (Appendix S2).

2.7 | Ethical note

All procedures were approved by the Department of Marine Resources of the Bahamas (permit no: MAF/LIA/22). When in captivity, sharks were fed on a diet of locally caught fish (*S. barracuda* and *Sardinella* spp.) to keep the daily ration to 2% of the sharks' body weight (estimated ration in the field, Cortés & Gruber, 1990). Handling was kept under 5 min to limit stress. Surgical procedures all lasted <8 min ($M = 351$ s $\pm$ 99 SD), with no mortality. On completion of the experiments, we removed all external tags and fed the sharks to satiation prior to release at their site of capture.

3 | RESULTS

3.1 | Do fast explorers in captivity swim further from shore in the wild?

Sharks from both subpopulations did not score differently in the novel open-field test (mean North Sound = 0.26 $\pm$ 0.05 SD, mean Sharkland = 0.26 $\pm$ 0.04 SD, $t_{321.6} = 1.15$, $p > 0.05$), but there was a difference in variance between the subpopulations, with North Sound having a higher variance than Sharkland ($F_{26,174} = 1.48$, $p = 0.01$, Figure 3a). Sharks from North Sound were found significantly further away from shore (mean square root distance = 8.74 $\pm$ 4.48 SD) than sharks from Sharkland (mean square root distance = 5.12 $\pm$ 3.13 SD), $t_{1,027.5} = 15.26$, $p < 0.001$ (Figure 3b). Additionally, the variance in distance from shore of the two subpopulations was different with North Sound presenting the most variance ($F_{163,596} = 2.05$, $p < 0.0001$, Figure 3b).

Exploration score predicted distance from shore in North Sound sharks (posterior mean = 0.87 [95% confidence intervals: 0.35, 1.50] $p < 0.005$), but not Sharkland sharks (posterior mean = 0.16 [−1.30, 1.40], Figure 4).

3.2 | Do fast explorers grow faster?

Growth rate was significantly different between subpopulations, sharks from Sharkland grew faster than North Sound sharks ($t_{1,403} = -5.00$, $p < 0.0001$, mean North Sound = 5.04 $\pm$ 2.59 SD, mean Sharkland = 5.72 $\pm$ 2.56 SD). However, variance was not significantly different between the subpopulations ($F_{5,704} = 1.02$, $p = 0.8$) meaning that both subpopulations maintained the same diversity in growth rates. Regarding exploration score in captivity, we found
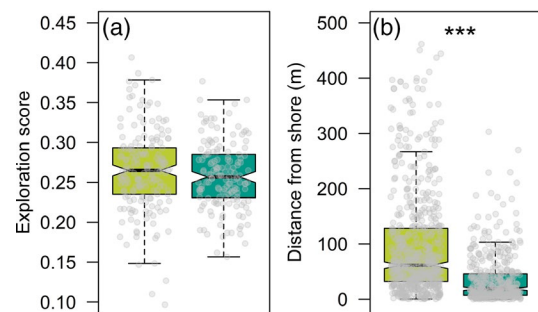

FIGURE 3 (a) Exploration scores and (b) distance from shore of sharks from North Sound ● and Sharkland ●. The original data points are shown in grey (***$p < 0.001$)
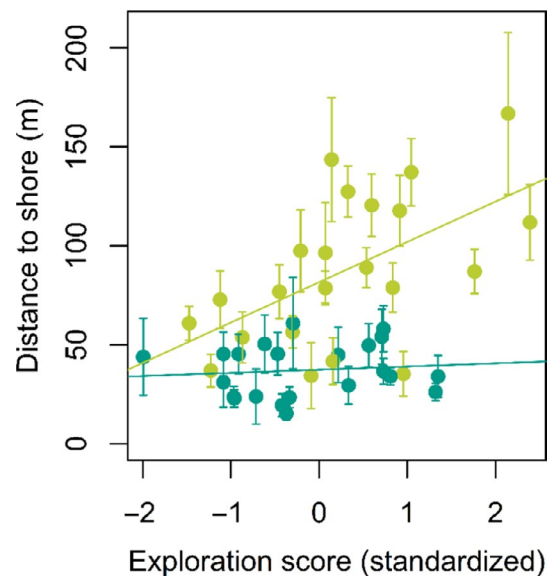

FIGURE 4 Mean (+SD) distance from shore for juvenile lemon sharks in relation to exploration score for two subpopulations, North Sound ● and Sharkland ●. Each point represents an individual's mean distance from shore. The linear relationship between standardized exploration and distance is represented by the solid lines

in North Sound that the exploration score in the novel open field was positively related to growth (posterior mean = 0.27 [0.05, 0.51], $p = 0.01$, Figure 5a). In Sharkland, the effect of exploration in captivity on growth was not different from zero (posterior mean = 0.09 [−0.45, 0.62], Figure 5b). Regarding risk-taking in the wild, we found no effect of distance from shore on growth in North Sound (posterior mean = −0.34 [−0.85, 0.12], $p = 0.09$) or in Sharkland (posterior mean = −0.26 [−1.43, 0.85]).

3.3 | Are fast explorers, fast growers and larger sharks selected against?

Apparent survival was significantly higher in North Sound (mean proportion of surviving sharks per year = 0.43 ± 0.09 SD) than in Sharkland (mean proportion of surviving sharks per year = 0.41 ± 0.11 SD, Chi-squared = 5.23, $p = 0.02$). We found significant negative selection differentials and gradients on PCL and growth in North Sound for all sub-samples of the data apart from those containing only sharks tested for personality (Table 2; Figure 6a–c). In Sharkland, we also found significant selection on growth and PCL in every sub-sample apart from the ones containing only the sharks tested for personality (Table 2). Additionally, selection on PCL was also significant in Sharkland when only sharks tested for personality that had a growth measurement were included in the model. This means that smaller sharks and slow growers survived better in both subpopulations (Figure 6a,b). The gradients and differentials were always significantly different in the subpopulations with selection differentials on PCL being stronger in North Sound than Sharkland and with selection gradients being generally stronger in Sharkland than North Sound (see Table 2). We found no selection on exploration in either of the subpopulations (Table 2; Figure 6c). Since DiBattista et al. (2007) made their selection analysis on relative growth (proportion of the body length gained from one year to the next) rather than absolute growth, we provide in Appendix S3, Table S1 the results of the models presented here using relative growth. Distance from shore negatively influenced apparent survival in North Sound (Posterior mean = −118.36 [−211.85, −40.05], $p < 0.0001$) and did not influence apparent survival in Sharkland (Posterior mean = −0.16 [−241.2, 206.14], Figure 6d).

4 | DISCUSSION

Here we used two wild subpopulations of juvenile lemon sharks to test predictions made under the POLS hypothesis: (a) that explorative sharks in a novel open field would be greater risk-takers in the wild (i.e. swim further from a protected habitat) and consequently would have higher growth rates and (b) that fast growers, and more
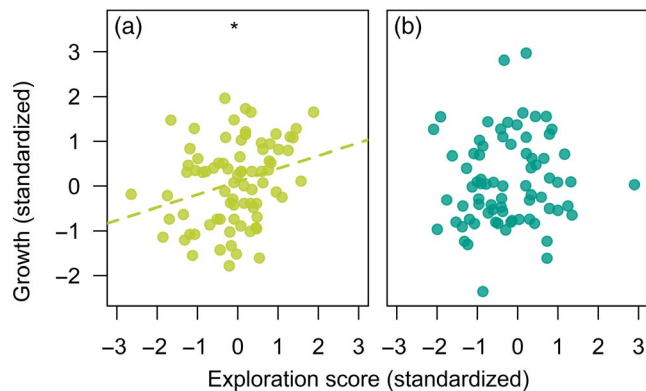

FIGURE 5 The relationship between standardized growth and standardized exploration scores of juvenile lemon sharks from (a). North Sound ● and (b) Sharkland ●. The dashed lines represent the regression lines fitted to the data (*$p < 0.05$)

TABLE 2 Linear (directional) selection differentials ($S'i$) and gradients (β') on precaudal length, growth and exploration of sharks from North Sound and Sharkland

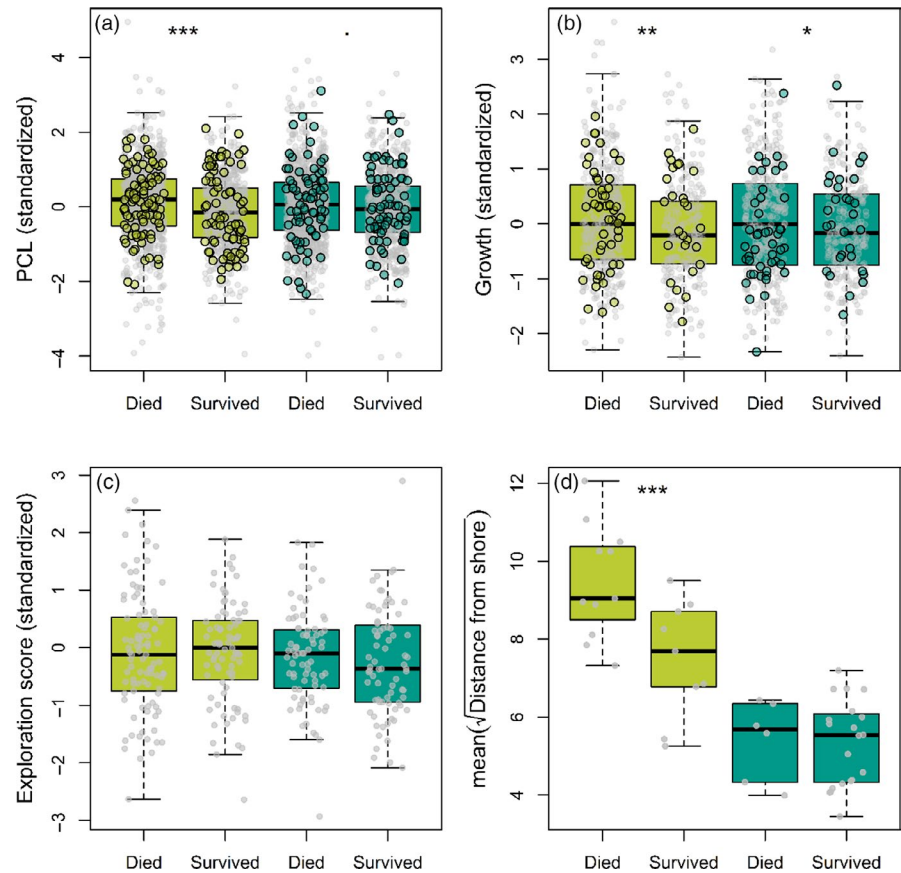| Variable	Measure of selection	Subpopulation		Post-hoc t
		North Sound	Sharkland	
PCL	$S'i$	**−0.15*** (1,618)	**−0.07.** (1,800)	**−90.7***
PCL[a]	$S'i$	**−0.15*** (1,448)	**−0.08*** (1,646)	**−74.4***
PCL[b]	β'	**−0.32*** (697)	**−0.49** (708)	**44.01***
Growth[b]	β'	**−0.25** (697)	**−0.31*** (708)	**15.44***
PCL[a,b]	β'	**−0.44*** (621)	**−0.46*** (629)	**−4.89***
Growth[a,b]	β'	**−0.25** (621)	**−0.36*** (629)	**29.93***
PCL	β'	−0.19 (173)	−0.008 (151)	
Exploration	β'	0.10 (173)	−0.03 (151)	
PCL[b]	β'	0.39 (76)	**−0.52*** (78)	**67.40***
Growth[b]	β'	−0.32 (76)	0.22 (78)	
Exploration[b]	β'	0.19 (76)	−0.41 (78)	

Note: Sample sizes are given in parenthesis. Significant results are shown in bold (.$p = 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

[a]Sample only includes sharks that were never tested for personality.

[b]Selection measured using survival at year $n + 2$ due to the inclusion of the growth variable.

FIGURE 6 (a) Pre-caudal length, (b) growth rate, (c) exploration and (d) mean distance from shore as a function of apparent survival in North Sound ● and Sharkland ●. The original data points are shown in light grey. For pre-caudal length and growth, we highlight in colour the data points of sharks tested for personality. Significance was determined by logistic regressions at the maximum sample size available (.$p = 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, see Table 2)

explorative sharks would be selected against as part of a growth-mortality trade-off. In both subpopulations, we found that selection acted against large body size and faster growth, confirming the presence of a trade-off between growth and mortality. But we found that sharks that were more active in the novel open-field assay, took higher risks in the wild and had higher subsequent growth rates only in North Sound (which has lower predator abundance). Neither subpopulation showed selection directly on personality. Therefore, our results provide strong support for trade-offs between growth and mortality but suggest that behaviour's role in mediating this trade-off is less clear.

In North Sound, our results are in accordance with predictions we made from the POLS hypothesis: faster explorers take more risks, grow faster and are more likely to die. The maintenance of inter-individual differences in risk-taking behaviour and growth rates in this subpopulation can be explained via the presence of a growth-mortality trade-off. In goldfish *C. auratus* risk-prone individuals, grew faster and in cavies *C. aperea* exploration of a known environment predicted growth (Balaban-Feld et al., 2019; Guenther, 2018). Similarly, juvenile lemon sharks who explore more, take more risks and profit from higher growth rates. This has the potential to make them reach a size at which they are less susceptible to predation faster (size-selective mortality, Sogard, 1997) and to make them reach sexual maturity earlier than slower-growing conspecifics. These advantages are mitigated by higher exposition to predation before they reach a less dangerous size class. In our case, the trade-off is likely favoured because open habitat foraging areas such as seagrass patches are

more productive but also more dangerous (DiBattista et al., 2007; Hussey et al., 2017) which is supported by our finding that sharks that swim further from shore have lower apparent survival. Bigger risk-takers in the wild were not found to grow faster, but we contend that this could be due to a lot of risk-takers dying and therefore not having a growth measurement at the end of the tracking year. It is worth noting however that we observed a loss of significance of the selection on growth and PCL when only sharks tested for exploration were included in the model and that exploration was never selected against in our models. Previous work on selection has shown high probability of making type II errors (i.e. failure to reject the null hypothesis) when selection is weak and sample size is low. For instance, 700 data points were necessary to have a 0.8 probability of detecting a selection of 0.12 (Hersch & Phillips, 2004). In this case, we contend that the absence of significance for selection in smaller sample sizes could be due to a lack of power. This seems especially reasonable for growth and PCL because inspection of survival rates (Figure 6a,b) reveals that the sharks tested in the novel open field were not driving the significance found in the larger samples.

In Sharkland, a growth-mortality trade-off was also detected but exploration in captivity did not predict growth or risk-taking and survival was not predicted by distance from shore. Failure to support the POLS hypothesis can be for several reasons. First, several different behaviours could covary with life history trade-offs (Montiglio et al., 2018). The constraints placed on predator avoidance and resource acquisition affect which behaviours covary with life history and which do not. In our study, we measured animals' exploration in

semi-captivity and their distance from a refuge in the wild. Exploration and risk-taking behaviours can be expected to covary with life history when an animal's vulnerability to predators depends on its ability to avoid predator encounters and/or when resources are clumped or ephemeral (Montiglio et al., 2018). In North Sound, sharks that had higher captive exploration, were found further from shore and were less likely to survive, which is likely due to increased predator encounters. Fast explorers also grew faster, suggesting increased resource encounters, which points to potentially low resource abundance or clumped resources. But in Sharkland, distance from shore did not predict survival, and sharks were mostly found close to the shore, where they are less vulnerable to predators. Furthermore, their growth was not predicted by exploration, suggesting that exploration does not impact resource acquisition. It seems possible in this case that in Sharkland, the life history trade-off is mediated through different behaviours than the one we investigated.

The association (or not) of traits could also be driven by feedbacks between behaviour and state (Dingemanse & Wolf, 2013). State-dependent feedbacks on behaviour predict that animals behave according to their state (e.g. energy reserves), and such feedback mechanisms also depend on environmental conditions such as predation risks and resource availability (see Luttbeg & Sih, 2010). Here, the subpopulations did not differ in mean exploration scores in captivity, where resource availability and predation risk are the same for every individual. But exploration in the wild was different between the populations and we know them to differ in their predator abundance (with Sharkland having more predators) and in their growth rates (with sharks from Sharkland growing faster). Both high predator pressure and high resource availability can be hypothesized to promote cautious behaviour via negative feedbacks (Luttbeg & Sih, 2010). If resources are abundant and accessible, sharks may have higher energy reserves and be less likely to take risks while foraging (Biro & Booth, 2009). If predators are abundant and foraging is dangerous, sharks may take risks while foraging only when their energy reserves are low (Biro, Abrahams, Post, & Parkinson, 2004). Even if sharks in Sharkland were rarely found far away from the mangrove edge, and thus displayed more risk-averse behaviours, their growth rates were still on average higher than in North Sound. This suggests that these individuals did not need to exhibit typically risky behaviours to gain the resources needed to maintain their faster growth rates. This seems especially likely as we occasionally observed juvenile lemon sharks foraging close the mangrove edge while tracking in Sharkland, but never made such an observation in North Sound. A recent description of the faunal community in Sharkland found that a larger abundance of fish is found within 50 m of the mangrove edge than offshore, further supporting this (Grimmel et al., 2020). In this case, in Sharkland, low distance from shore could be maintained via a negative feedback due to their higher state (illustrated here by faster growth). In other words, sharks from Sharkland might not display their full range of behaviour because the environment they live in negatively impacts risk-taking behaviours. This issue is especially interesting because Sharkland sharks did not exhibit lower exploration in captivity, despite being found closer to shore, which

suggests that the diversity in exploration and in distance from shore in Sharkland is highly plastic (i.e. adjusted on the short term to the current conditions) or is promoted through different mechanisms.

The fact that our exploration measure in captivity did not predict risk-taking in the wild in one population is of further interest. Previous studies have stressed that novel open-field assays are often hard to interpret, as an animal's behaviour in a novel environment might represent its willingness to explore and/or its reaction to a stress and/or its general activity (Carter et al., 2013). Here, we expected it to predict risk-taking in the field, and our prediction was confirmed in one subpopulation only. Our study emphasizes the need for researchers to carefully validate their personality assays, as the ecological relevance of the assay here was different between two geographically adjacent habitats.

It is important to note that despite providing important new insights into the understanding of a topic that has recently received much research interest (Dammhahn et al., 2018), our study has several limitations. Our dataset was only collected in two subpopulations, making firm conclusions on differences between populations impossible. We studied the exploration personality of 28 juvenile lemon sharks in a third Bimini subpopulation with high predator abundance at the beginning of the project. Unfortunately, the main refuge for this nursery was damaged in 2014, leading to a depletion of the lemon shark population and the impossibility to conduct further testing. Continued work on lemon sharks could benefit from including more subpopulations from neighbouring areas. In addition, the lack of repeated measures within individuals in our dataset prevented the use of multivariate analysis and structural equation modelling which are highly suitable for studies on trait association and POLS hypothesis (see Moiron et al., 2019; Polverino et al., 2018; Santostefano et al., 2017). Therefore, we could not further investigate the causal relationship between traits. Finally, the POLS hypothesis usually encompasses phenotypic traits that are involved in a trade-off between current and future reproduction (Dammhahn et al., 2018). Lemon sharks reach sexual maturity at approximately 12 years of age (Chapman et al., 2009), and here, logistical constraints compelled us to use sharks of 0 and 1 year. It is important to keep in mind that our study only investigates a part of lemon sharks' life history and thus offers a partial test of the POLS hypothesis.

In conclusion we tested a part of the POLS hypothesis using a novel open-field assay, measuring risk-taking in the field, and testing a growth-mortality trade-off in wild juvenile sharks. We found that the prediction that personality-mediated growth-mortality trade-off via wild risk-taking behaviour was present in one subpopulation but not the other, suggesting that the emergence of personality driven life history trade-offs is context dependent. Importantly, the subpopulations of juvenile sharks are known to differ in their predator abundance. We discuss mechanisms driving the conditional association of behaviour and life history and suggest that they are driven by predator abundance but also likely by resource availability. Understanding the processes that promote personality driven life history will require scrutinizing behaviour and life history across ecological gradients. Long-term,

multi-population datasets from the wild and controlled captive experiments where conditions can be manipulated will be crucial to our future understanding of how behaviour can mediate life history.

AUTHORS' CONTRIBUTIONS

F.D., J.-S.F., J.K., S.H.G. and T.L.G. designed the study; F.D., S.H.G., J.-S.F., M.J.S. and T.L.G. collected the data; F.D. and K.L.L. analysed the data; All authors participated in the discussions regarding the results of this study and the scope of the manuscript; F.D. led the writing of the manuscript; All authors contributed critically to the drafts; All authors but S.H.G. gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.ksn02v71r (Dhellemmes, Finger, Smukall, et al., 2020).

ORCID

Félicie Dhellemmes https://orcid.org/0000-0002-2043-4653
Kate L. Laskowski https://orcid.org/0000-0003-1523-9340

REFERENCES

Archard, G. A., & Braithwaite, V. A. (2010). The importance of wild populations in studies of animal temperament. *Journal of Zoology*, *281*, 149–160. https://doi.org/10.1111/j.1469-7998.2010.00714.x

Arvidsson, L. K., Adriaensen, F., van Dongen, S., De Stobbeleere, N., & Matthysen, E. (2017). Exploration behaviour in a different light: Testing cross-context consistency of a common personality trait. *Animal Behaviour*, *123*, 151–158. https://doi.org/10.1016/j.anbehav.2016.09.005

Balaban-Feld, J., Mitchell, W. A., Kotler, B. P., Vijayan, S., Tov Elem, L. T., Rosenzweig, M. L., & Abramsky, Z. (2019). Individual willingness to leave a safe refuge and the trade-off between food and safety: A test with social fish. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1907). https://doi.org/10.1098/rspb.2019.0826

Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2004). Predators select against high growth rates and risk–taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1554), 2233–2237. https://doi.org/10.1098/rspb.2004.2861

Biro, P. A., & Booth, D. J. (2009). Extreme boldness precedes starvation mortality in six-lined trumpeter (*Pelates sexlineatus*). *Hydrobiologia*, *635*, 395–398. https://doi.org/10.1007/s10750-009-9902-x

Bivand, R. S., & Rundel, C. (2017). *rgeos: Interface to geometry engine – Open source ('GEOS')*. Retrieved from https://cran.r-project.org/package=rgeos

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The Quarterly Review of Biology*, *75*(4), 385–407. https://doi.org/10.1086/393620

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: What are behavioural ecologists measuring? *Biological Reviews*, *88*(2), 465–475. https://doi.org/10.1111/brv.12007

Chapman, D. D., Babcock, E. A., Gruber, S. H., Dibattista, J. D., Franks, B. R., Kessel, S. T., ... Feldheim, K. A. (2009). Long-term natal site-fidelity by immature lemon sharks (*Negaprion brevirostris*) at a subtropical island. *Molecular Ecology*, *18*, 3500–3507. https://doi.org/10.1111/j.1365-294X.2009.04289.x

Cortés, E., Gruber, S. H., & Cortes, E. (1990). Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). *Copeia*, *1990*(1), 204–218. https://doi.org/10.2307/1445836

Dammhahn, M., Dingemanse, N. J., Niemelä, P. T., & Réale, D. (2018). Pace-of-life syndromes: A framework for the adaptive integration of behaviour, physiology and life history. *Behavioral Ecology and Sociobiology*, *72*(3). https://doi.org/10.1007/s00265-018-2473-y

Dhellemmes, F., Finger, J.-S., Laskowski, K. L., Guttridge, T. L., & Krause, J. (2020). Comparing behavioural syndromes across time and ecological conditions in a free-ranging predator. *Animal Behaviour*, *162*. https://doi.org/10.1016/j.anbehav.2020.01.009

Dhellemmes, F., Finger, J.-S., Smukall, M. J., Gruber, S. H., Guttridge, T. L., Laskowski, K. L., & Krause, J. (2020). Data from: Personality driven life-history trade-offs differ in two sub-populations of free ranging predators. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.ksn02v71r

DiBattista, J. D., Feldheim, K. A., Gruber, S. H., & Hendry, A. P. (2007). When bigger is not better: Selection against large size, high condition and fast growth in juvenile lemon sharks. *Journal of Evolutionary Biology*, *20*(514), 201–212. https://doi.org/10.1111/j.1420-9101.2006.01210.x

Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Animal Behaviour*, *85*(5), 1031–1039. https://doi.org/10.1016/j.anbehav.2012.12.032

Finger, J. S., Dhellemmes, F., Guttridge, T. L., Kurvers, R. H. J. M., Gruber, S. H., & Krause, J. (2016). Rate of movement of juvenile lemon sharks, *Negaprion brevirostris* in a novel open field, are we measuring activity or reaction to novelty? *Animal Behaviour*, *116*, 75–82.

Finger, J. S., Guttridge, T. L., Wilson, A. D. M., Gruber, S. H., & Krause, J. (2018). Are some sharks more social than others? Short- and long-term consistencies in the social behavior of juvenile lemon

sharks. *Behavioral Ecology and Sociobiology*, *72*(1), 17. https://doi. org/10.1007/s00265-017-2431-0

Grimmel, H. M. V., Bullock, R. W., Dedman, S. L., Guttridge, T. L., & Bond, M. E. (2020). Assessment of faunal communities and habitat use within a shallow water system using non-invasive BRUVs methodology. *Aquaculture and Fisheries*. https://doi.org/10.1016/j. aaf.2019.12.005

Gruber, S. H., de Marignac, J. R. C., & Hoenig, J. M. (2001). Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark–depletion experiments. *Transactions of the American Fisheries Society*, *130*(3), 376–384. https://doi.org/10.1577/1548-8659(2001)130

Gruber, S. H., & Stout, R. G. (1983). Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). *NOAA Technical Report NMFS 8: Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks*, *8*, 193–205.

Guenther, A. (2018). Life-history trade-offs: Are they linked to personality in a precocial mammal (*Cavia aperea*)? *Biology Letters*, *14*(4). https://doi.org/10.1098/rsbl.2018.0086

Guttridge, T. L., Gruber, S. H., Franks, B. R., Kessel, S. T., Gledhill, K. S., Uphill, J., … Sims, D. W. (2012). Deep danger: Intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series*, *445*, 279–291. https://doi.org/10.3354/meps09423

Guttridge, T. L., Gruber, S. H., Gledhill, K. S., Croft, D. P., Sims, D. W., & Krause, J. (2009). Social preferences of juvenile lemon sharks, *Negaprion brevirostris*. *Animal Behaviour*, *78*(2), 543–548. https://doi. org/10.1016/j.anbehav.2009.06.009

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22.

Hansell, A. C., Kessel, S. T., Brewster, L. R., Cadrin, S. X., Gruber, S. H., Skomal, G. B., & Guttridge, T. L. (2018). Local indicators of abundance and demographics for the coastal shark assemblage of Bimini. *Bahamas. Fisheries Research*, *197*(October), 34–44. https://doi. org/10.1016/j.fishres.2017.09.016

Hersch, E. I., & Phillips, P. C. (2004). Power and potential bias in field studied of natural selection. *Evolution*, *58*(3), 479–485. https://doi. org/10.1111/j.0014-3820.2004.tb01671.x

Hussey, N. E., DiBattista, J. D., Moore, J. W., Ward, E. J., Fisk, A. T., Kessel, S., … Chapman, D. D. (2017). Risky business for a juvenile marine predator? Testing the influence of foraging strategies on size and growth rate under natural conditions. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1852). https://doi.org/10.1098/ rspb.2017.0166

Jablonszky, M., Szász, E., Krenhardt, K., Markó, G., Hegyi, G., Herényi, M., … Garamszegi, L. Z. (2018). Unravelling the relationships between life history, behaviour and condition under the pace-of-life syndromes hypothesis using long-term data from a wild bird. *Behavioral Ecology and Sociobiology*, *72*(3), 52. https://doi.org/10.1007/s00265-018-2461-2

Kessel, S. T., Chapman, D. D., Franks, B. R., Gedamke, T., Gruber, S. H., Newman, J. M., … Perkins, R. G. (2014). Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (*Negaprion brevirostris*). *Marine Ecology Progress Series*, *514*, 175–190. https://doi.org/10.3354/meps10966

Kessel, S. T., & Hussey, N. E. (2015). Tonic immobility as an anaesthetic for elasmobranchs during surgical implantation procedures. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*, 1–5. https:// doi.org/10.1139/cjfas-2015-0136

Kilfoyle, D. B., & Baggeroer, A. B. (2000). The state of the art in underwater acoustic telemetry. *IEEE Journal of Oceanic Engineering*, *25*(1), 4–27. 0364-9059/00$10.00

Krebs, R., Linnenbrink, M., & Guenther, A. (2019). Validating standardised personality tests under semi-natural conditions in wild house mice (*Mus musculus domesticus*). *Ethology*, *125*(11), 761–773. https://doi. org/10.1111/eth.12930

Lande, R., & Arnold, S. (1983). The measure of selection on correlated characters. *Evolution*, *37*, 1210–1226.

Lapiedra, O., Schoener, T. W., Leal, M., Losos, J. B., & Kolbe, J. J. (2018). Predator-driven natural selection on risk-taking behavior in anole lizards. *Science*, *360*(6392), 1017–1020. https://doi.org/10.1126/scien ce.aap9289

Luttbeg, B., & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 3977–3990. https://doi. org/10.1098/rstb.2010.0207

Mangel, M., & Stamps, J. A. (2011). Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, *3*(1), 583–593.

Moiron, M., Araya-Ajoy, Y. G., Mathot, K. J., Mouchet, A., & Dingemanse, N. J. (2019). Functional relations between body mass and risk-taking behavior in wild great tits. *Behavioral Ecology*, *30*(3), 617–623. https://doi.org/10.1093/beheco/ary199

Moiron, M., Laskowski, K. L., & Niemelä, P. T. (2020). Individual differences in behaviour explain variation in survival: A meta-analysis. *Ecology Letters*, *23*(2), 399–408. https://doi.org/10.1111/ele.13438

Montiglio, P.-O., Dammhahn, M., Dubuc Messier, G., & Réale, D. (2018). The pace-of-life syndrome revisited: The role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology*, *72*(7), 116. https://doi.org/10.1007/s0026 5-018-2526-2

Morrissey, J. F., & Gruber, S. H. (1993). Home range of juvenile lemon sharks, *Negaprion brevirostris*. *Copeia*, *1993*(2), 425–434. https://doi. org/10.2307/1447141

Newman, S. P., Handy, R. D., & Gruber, S. H. (2007). Spatial and temporal variations in mangrove and seagrass faunal communities at Bimini, Bahamas. *Bulletin of Marine Science*, *80*(3), 529–553.

Newman, S. P., Handy, R. D., & Gruber, S. H. (2009). Diet and prey preference of juvenile lemon sharks *Negaprion brevirostris*. *Marine Ecology Progress Series*, *398*, 221–234. https://doi.org/10.3354/meps 08334

Niemelä, P. T., Dingemanse, N. J., Alioravainen, N., Vainikka, A., & Kortet, R. (2013). Personality pace-of-life hypothesis: Testing genetic associations among personality and life history. *Behavioral Ecology*, *24*(4), 935–941. https://doi.org/10.1093/beheco/art014

Polverino, G., Santostefano, F., Díaz-Gil, C., & Mehner, T. (2018). Ecological conditions drive pace-of-life syndromes by shaping relationships between life history, physiology and behaviour in two populations of Eastern mosquitofish. *Scientific Reports*, *8*(1), 14673. https://doi.org/10.1038/s41598-018-33047-0

R Core Team. (2017). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/%0A

Réale, D., & Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, *65*(3), 463–470. https://doi.org/10.1006/anbe.2003.2100

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 4051–4063. https://doi.org/10.1098/rstb.2010.0208

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*, 291–318. https://doi. org/10.1111/j.1469-185X.2007.00010.x

Royauté, R., Berdal, M. A., Garrison, C. R., & Dochtermann, N. A. (2018). Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology*, *72*(3), 64. https://doi. org/10.1007/s00265-018-2472-z

Santicchia, F., Gagnaison, C., Bisi, F., Martinoli, A., Matthysen, E., Bertolino, S., & Wauters, L. A. (2018). Habitat-dependent effects of personality on survival and reproduction in red squirrels. *Behavioral Ecology and Sociobiology*, *72*(8). https://doi.org/10.1007/s00265-018-2546-y

Santostefano, F., Wilson, A. J., Niemelä, P. T., & Dingemanse, N. J. (2017). Behavioural mediators of genetic life-history trade-offs: A test of the pace-of-life syndrome hypothesis in field crickets. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1864). https://doi.org/10.1098/rspb.2017.1567

Sinott, R. W. (1984). The virtues of the Haversine. *Sky and Telescope*, *68*(2), 158.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: A review. *Bulletin of Marine Science*, *60*(3), 1129–1157.

Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, *20*(1), 3–18. https://doi.org/10.1111/ele.12708

Stamps, J. A. (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, *10*(5), 355–363. https://doi.org/10.1111/j.1461-0248.2007.01034.x

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*(3), 259. https://doi.org/10.2307/2389364

Watsky, M. A., & Gruber, S. H. (1990). Induction and duration of tonic immobility in the lemon shark, *Negaprion brevirostris*. *Fish Physiology and Biochemistry*, *8*(3), 207–210. https://doi.org/10.1007/BF00004459

Wolf, M., van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*(7144), 581–584. https://doi.org/10.1038/nature05835

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Dhellemmes F, Finger J-S, Smukall MJ, et al. Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators. *J Anim Ecol*. 2020;00:1–13. https://doi.org/10.1111/1365-2656.13283