

RESEARCH ARTICLE

Functional Ecology



Predator abundance drives the association between exploratory personality and foraging habitat risk in a wild marine meso-predator

Félicie Dhellemmes^{1,2,3} | Matthew J. Smukall^{3,4} | Tristan L. Guttridge^{3,5} |
Jens Krause^{1,2} | Nigel E. Hussey⁶

¹Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany; ²Faculty of Life Sciences, Albrecht Daniel Thaer-Institute of Agricultural and Horticultural Sciences, Humboldt-Universität zu Berlin, Berlin, Germany; ³Bimini Biological Field Station Foundation, South Bimini, Bahamas; ⁴College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA; ⁵Saving the blue, Cooper City, FL, USA and ⁶Integrative Biology, University of Windsor, Windsor, ON, Canada

Correspondence

Félicie Dhellemmes

Email: dhellemmes@igb-berlin.de

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Handling Editor: Zacchaeus Compson**Abstract**

1. In recent years, the incorporation of lower levels of organization to the understanding of population ecology, has led to an increase in interest for animal personality and individual foraging specialization. Despite these topics investigating comparable phenomena, that is, individual consistency in behaviour and in food resource use respectively, they have rarely been investigated together.
2. Food resource use is thought to be at the interface between personality and life history. More explorative individuals in a population, for example, are thought to increase encounter rates with food resources and consequently have faster growth than less explorative conspecifics.
3. Such hypotheses have so far only received partial support, and the link between personality and life history is increasingly speculated to be plastic and dependent on spatio-temporal variation in ecological conditions. Intraspecific competition and/or predation risk, for example are known to influence foraging specialization.
4. Here, we investigated the relationship between exploration personality of juvenile lemon sharks *Negaprion brevirostris* (measured in captivity) and foraging habitat use (high risk vs. low risk; measured via stable isotope analysis in the field) in relation to conspecific and predator abundance.
5. We identified predator abundance as the main driver for the association between foraging habitat and exploration personality. When predators were less abundant, increased exploration was associated with foraging in riskier habitats. When predator abundance increased, an inverse relationship occurred, with less explorative individuals using more dangerous habitat.

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6. We conclude that the relationship between personality and resource use is plastic and context dependent, which could explain the inconclusive results of previous studies investigating links between personality and life history.

KEYWORDS

ecological drivers, pace-of-life syndrome, shark, stable isotope analysis, trait covariance

1 | INTRODUCTION

Population ecology is often studied while identifying and incorporating sources of variation within populations. Age (Polis, 1984) and sex (Shine, 1989) have, for instance, long been recognized as significant sources of ecological variation. But variation can also be observed at the individual level (i.e. within sex and age groups), a phenomenon that is essential for understanding population and ecosystem dynamics (Toscano et al., 2016). In behavioural sciences, animal personality research has emerged as a means to investigate individual level differences in behaviour that are consistent across time and situation (i.e. set of conditions at one point in time; Réale et al., 2007). Such consistency in individual behaviour has been hypothesized to have multiple ecological and evolutionary consequences (Wolf & Weissing, 2012), which include implications for life history (Dammhahn et al., 2018). Individual bluegill sunfish *Lepomis macrochirus*, for example, that are consistently bolder (i.e. faster at emerging from a refuge) have been shown to have greater maximum metabolic rates than shyer individuals (Binder et al., 2016), while more explorative female wild cavies *Cavia aperea* grow faster than their less explorative conspecifics (Guenther, 2018). The evolution and maintenance of animal personalities are hypothesized to be favoured by trade-offs that promote a range of behavioural phenotypes with similar fitness (Mangel & Stamps, 2011).

The field of food web ecology has concurrently intensified its focus on the concept of 'individual resource specialization', defined as consistent inter-individual differences in food resource use within populations (Bolnick et al., 2002). Resource acquisition is governed by the need for animals to maximize their rate of energy intake while minimizing other costs such as energy expenditure, predation risk and intraspecific competition (see optimal foraging theory, Pyke, 1984). Individual resource specialization arises when multiple specialists with different resource acquisition strategies coexist within a population (Powell & Taylor, 2017). These resource acquisition strategies can be observed on a geographical level, with individuals consistently foraging at different locations (Harris et al., 2020; Wakefield et al., 2015), at a prey level, with individuals specializing in particular prey types (Ratcliffe et al., 2018) or a combination of both. Such specializations can be mediated through morphological traits (e.g. bill length in hummingbirds, *Trochilidae*, Tinoco et al., 2017), physiological state (e.g. hunger, reproductive state, developmental stage, as reviewed in Bedoya-Perez et al., 2013) and behaviour

(e.g. boldness in black-legged kittiwakes, *Rissa tridactyla*, Harris et al., 2020). The emergence of individual foraging specialization is hypothesized to be dictated by factors that promote consistent variation in resource use among individuals (Carneiro et al., 2017). Intraspecific competition, for example, may limit the abundance of available prey leading to the emergence of foraging specialization (Araújo et al., 2008, 2011; Svanbäck & Bolnick, 2007). This is illustrated in gentoo penguins *Pygoscelis papua*, where an increase in intraspecific competition led to the specialization of individuals for one resource (krill), or another (fish) (Ratcliffe et al., 2018). Predation risk has also been hypothesized to promote the emergence of individual foraging specialization within populations if perceived risk varies among individuals (Araújo et al., 2011). For instance, increased predation from ants and birds led to a reduction in individual diet breadth in caterpillars, *Lepidoptera* (Singer et al., 2019).

Despite parallel growth of the 'animal personality' and the 'individual foraging specialization' research areas, and overlap in key features (e.g. individual consistency), these topics have developed in almost complete isolation (Kalinkat, 2014, Toscano et al., 2016, but see Harris et al. (2020), for personality driven foraging specialization in black-legged kittiwakes). This is surprising because studies suggest that resource acquisition is at the interface between personality and life history (Spiegel et al., 2017). For instance, risk-inclined behaviours are predicted to facilitate greater resource acquisition, leading to a subsequent increase in growth, but also to higher probabilities of predation mortality (Réale et al., 2010; Stamps, 2007). Understanding how personality, foraging specialization and life history are causally linked is likely crucial, as the association between personality and life history is still not well understood and empirical studies often have inconclusive results (Moirón et al., 2020; Royauté et al., 2018). Such ambiguity may be due to environmental conditions (e.g. predator or resource abundance) inconsistently favouring the covariance between observed personality and life-history traits across time (Royauté et al., 2018). In this situation, we argue that it is necessary to investigate how personality covaries with foraging behaviour under varying ecological conditions as an important step to bridge the gap between personality, resource specialization and life history.

The paucity of studies investigating animal personality in parallel with individual foraging specialization may in part be due to a methodological divide. Animal personality studies involve standardized designs that allow for repeated measures of behaviour (Dingemanse & Wright, 2020). For example, the novel open-field test, a popular

personality test, assesses the willingness of individuals to explore a novel arena (Perals et al., 2017). The need for standardized, repeatable tests has led to an abundance of studies on captive bred animals and/or studies conducted in captivity, as these tests would be impractical or impossible to achieve in the wild (Archard & Braithwaite, 2010). In contrast, individual foraging specialization typically relies on monitoring animals' foraging in the field (Toscano et al., 2016). Stable isotope analysis has become an increasingly popular tool to investigate animals' foraging habitat and trophic level (Carneiro et al., 2017). Carbon ($^{13}\text{C}/^{12}\text{C}$, measured as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$, measured as $\delta^{15}\text{N}$) stable isotopes are integrated into consumers' tissues (e.g. skin, blood) from assimilated resources, creating a record of their diet and foraging ecology (Boucher et al., 2020). Nitrogen stable isotopes are typically enriched in consumers relative to their food, serving as an indicator of trophic position (Cherel & Hobson, 2007). In contrast, carbon stable isotopes are relatively conserved across trophic levels, allowing the determination of consumer foraging habitat related to the primary carbon sources within a given trophic network (Cherel & Hobson, 2007).

In Bimini, The Bahamas (Figure 1), juvenile lemon sharks *Negaprion brevirostris* inhabit coastal shallow water lagoon habitats characterized by a mangrove-fringed shore (red mangrove: *Rhizophora mangle* and black mangrove: *Avicennia germinans*) and shallow seagrass beds (turtle grass: *Thalassia testudinum* and shoal grass: *Halodule wrightii*) interspersed by exposed sediment patches. Previous work demonstrated that carbon isotope ratios of individual lemon sharks were consistent over time (i.e. individual foraging specialization) representing sharks' foraging in habitats on a continuum between protected low-risk mangrove (low $\delta^{13}\text{C}$) and presumably riskier exposed seagrass (high $\delta^{13}\text{C}$) (Hussey et al., 2017). In addition, exploration personality (measured in a novel open-field test) was found to predict distance from the mangrove shore (measured via acoustic telemetry), growth and mortality in one of two subpopulations (Dhellemmes, Finger, Smukall, et al., 2020). Previous work on this system found that predator and conspecific abundance were crucial drivers for trait associations involving personality and life history (Dhellemmes, Finger, Laskowski, et al., 2020; Dhellemmes, Finger, Smukall, et al., 2020). Here we combined captive personality tests and stable isotope analysis to test how the correlation between foraging habitat and exploration personality varies with predation and intraspecific competition in two subpopulations of juvenile lemon sharks (North Sound and Sharkland, Figure 1) across 4 years. Because foraging specialization has been documented to be stronger in the context of high intraspecific competition (Ratcliffe et al., 2018; Sheppard et al., 2018), we predicted a stronger trait correlation when competition was high. Similarly, with specializations being stronger in high predation contexts (Singer et al., 2019) one could also expect stronger trait correlations when predator abundance was high. Juvenile lemon shark exploration score was, however, previously found to predict distance from the shore in the subpopulation with the lowest predator abundance (North Sound), but not in the neighbouring subpopulation with high predation risk (Sharkland; Dhellemmes, Finger, Smukall, et al., 2020). Given these

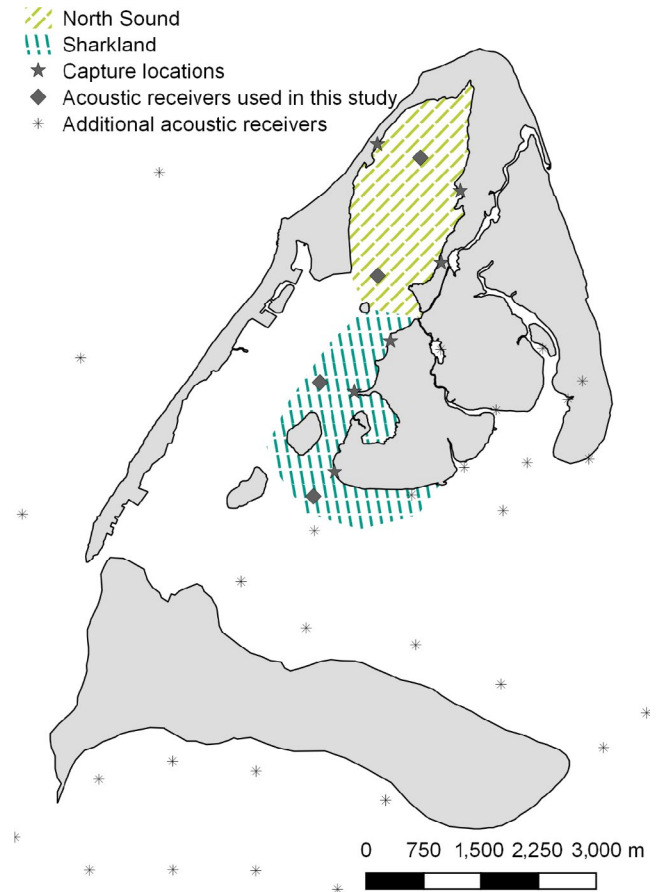


FIGURE 1 Map of the Bimini Islands, The Bahamas (25.736232°N, -79.267353°W) showing the two principal juvenile lemon shark subpopulations, the six capture locations and the locations of fixed acoustic telemetry receivers

results, we predicted a stronger association between personality and foraging habitat (as indicated by stable isotope values) when predator abundance was low, with more exploratory individuals foraging in riskier seagrass habitat.

1.1 | Study site and sampling

The current study was conducted in Bimini, The Bahamas (Figure 1), a mangrove-fringed chain of islands located approximately 80 km off the coast of Florida (U.S.A.). Juvenile lemon sharks are known to use nursery habitats consisting of nearshore protected mangrove habitats and offshore exposed seagrass beds, until they disperse around 3–5 years of age (Chapman et al., 2009; DiBattista et al., 2007). Inhabiting small home ranges (<600 m² for sharks under 56 cm pre-caudal length, PCL, Morrissey & Gruber, 1993), recapture probabilities of individuals from 1 year to the next are high (0.67–0.85; DiBattista et al., 2007). Here, we focus on juvenile lemon shark subpopulations inhabiting two adjacent nursery areas (North Sound and Sharkland, see Figure 1) which are known to differ in their predator abundance (Sharkland has higher predator abundance; Dhellemmes, Finger, Laskowski, et al., 2020), and that are

almost completely isolated in regard to emigration and immigration of juvenile sharks <2 years of age due to their small home ranges (Chapman et al., 2009; 1.5% of the sharks in the current study emigrated between 0 and 2 years of age, unpublished data).

Between 2014 and 2017, we captured juvenile lemon sharks using gillnets (180 m length, 10 cm stretch-mesh size) set perpendicular to the shore at six standard locations in the North Sound and Sharkland (see Figure 1). Sampling was undertaken for six nights (12 hr each) in each nursery, with the three nets sampled simultaneously in each area, resulting in a total of 12 nights of fishing effort. Upon capture, sharks were scanned for the presence of a uniquely coded passive integrated transponder (PIT, Destron Fearing) tag. Tag ID (if no PIT tag was found, one was implanted subcutaneous at the base of the dorsal fin), measurements (PCL, nearest mm), sex (the presence or absence of claspers) and the state of umbilical scar healing (for age determination; see below) were recorded. When possible (i.e. when sample collection was safe for the animal and the operator) we took a sample of the trailing edge of the first dorsal fin (<5 mm²) and immediately stored it on ice. Fin samples, used for subsequent stable isotope analysis, were stored at -18°C within 12 hr of their collection. Each shark was then housed in semi-captive arenas temporarily built within the nursery areas (see below section 1.2 for details on arena construction) until the end of the sampling campaign, that is, the 12 days of fishing, to avoid repeated captures.

Lemon sharks, a placental viviparous species, are born with an umbilical wound which heals during the first few weeks of life (Feldheim et al., 2002). This allowed assignment of age for each shark according to their umbilical state (opened to any extent: young-of-the-year (YOY); closed: unknown age from 1 to 5 years). Given that shark sampling has been systematically undertaken each year since the 90s as part of a capture-mark-recapture study (Gruber et al., 2001), most sharks could be precisely aged, as they had been captured as YOY in previous years. When the umbilical state of an individual could not be recorded (e.g. the shark was difficult to handle), or a shark had never been captured as a YOY, we determined age using a linear regression of age on PCL (accuracy: 91%, see Dhellemmes, Finger, Smukall, et al., 2020 for details).

At the two study sites, YOY and 1-year-old sharks are the most commonly captured age classes (Dhellemmes, Finger, Smukall, et al., 2020; DiBattista et al., 2007). Because stable isotope value of YOY sharks is initially confounded by the maternal isotopic signature (Olin et al., 2011), sampling targeted sharks of age 1 year, resulting in data for 131 individuals (see Table 1).

TABLE 1 Summary of age 1-year-old individuals sampled for stable isotopes and tested for personality for each year and each subpopulation

	2014	2015	2016	2017	Total
North Sound	18	14	15	14	61
Sharkland	15	11	32	16	74

1.2 | Assessment of exploration personality

At the conclusion of the gillnet survey in each nursery area, a randomly selected subset of captured lemon sharks was transferred to a nearby behavioural testing arena (Figure 2A), where they were acclimated for 4 days before commencing experiments. We inserted T-bar anchor tags (Floy Tag Inc.) in the first and/or second dorsal fin of each shark in a unique colour combination to allow individual visual recognition during tests. While in captivity, sharks were fed every 2 days with approx. 2% of their body weight of locally caught barracuda *Sphyræna barracuda* and *Sardinella* spp. (with the feeder ensuring every shark received food) to match their estimated daily ration in the wild (Cortés & Gruber, 1990).

The behavioural testing arena consisted of three parts: (a) an oblong enclosure (10 × 5 m) divided into three compartments used to house sharks, (b) a circular arena (diameter, 10 m) that was built close (4 m) to the housing enclosure to host a social behaviour test and (c) a rectangular arena (6 × 12 m) that was built 2 m from the sociability arena to host the novel open-field test, the focus of the current study. Each arena was connected to the adjoining one via a channel, allowing sharks to be ushered from one arena to the next without the need for handling (Figure 2A). The channel that separated the sociability arena and the novel open-field served as a start-box, where sharks spent 5 minutes after being ushered to recuperate from potential stress. All parts of the behavioural testing arena were constructed with orange construction mesh (6 cm mesh size, Tenax Sentry HD; Tenax Fence), steel rebars, cable ties and cinder blocks. We erected wooden towers (~4 m height) on the North side of the sociability arena and the novel open-field arena to allow for behavioural observations while limiting shadows from observers (Figure 2A).

One day prior to tests, we transferred six size-matched sharks into the sociability arena via the channel. Sharks were then fed to satiation and left to acclimate overnight. On the following day we observed sharks in the sociability arena for 20 min followed by immediate individual testing in the novel open-field. The results of the sociability test are not included in the current analyses, but see Finger et al. (2018) for repeatability of sociability.

The novel open-field test was conducted as follows. An individual shark was ushered from the sociability arena to the start-box (Figure 2B) connecting the sociability arena to the novel open-field arena. Sharks were ushered opportunistically, accepting that previous research found that the order of testing did not influence test results (Dhellemmes, Finger, Laskowski, et al., 2020). After 5 minutes in the start-box, a sliding door was remotely opened allowing entrance to the novel open-field (Figure 2B). Once a shark entered the novel open-field, the door was closed, and behavioural observation was conducted for 10 min. The novel open-field arena was divided into 16 sectors (2 × 2 m) by green concrete markers placed on the substrate (Figure 2B). An exploration personality score was derived as the mean number of sectors visited per minute of the test (including multiple visits to the same sectors). This exploration score was previously shown to measure a shark's reaction to a novel environment

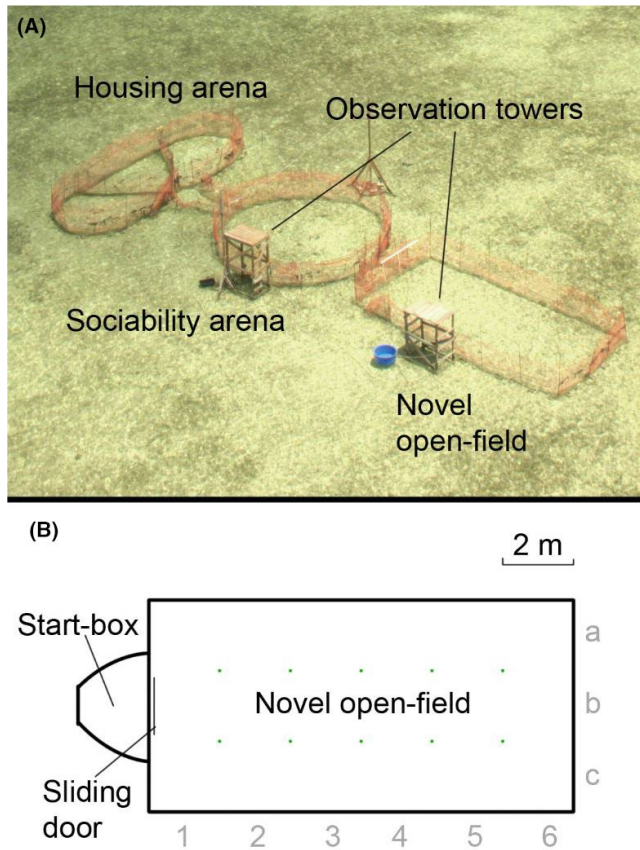


FIGURE 2 Behavioural testing arena: (A) aerial view of the complete set-up, (B) schematic representation of the novel open-field. The section markers are represented by green dots, each section is identified by a unique coordinate as represented by the numbers and letters on the side of the arena (e.g. the sliding door is in section b1)

rather than general activity (Finger et al., 2016). Furthermore, exploration of the novel open-field was found to be repeatable (R adjusted for $PCL = 0.33$, 95% confidence interval (CI) [0.13, 0.52]) in a sample that included all sharks between 1 and 3 years of age that were repeatedly tested in North Sound and Sharkland over the years of the current study ($n = 95$; 85% 1-year-old; Dhellemmes, Finger, Laskowski, et al., 2020) and to predict sharks' distance from the mangrove shore in North Sound but not in Sharkland (Dhellemmes, Finger, Smukall, et al., 2020). The density of sharks held in captivity prior to the test was found not to impact the exploration score in a separate population and a different year (see Appendix 1.1).

1.3 | Foraging habitat: Seagrass versus mangrove

Carbon stable isotope values ($\delta^{13}\text{C}$) have been previously shown to be consistent within individual juvenile lemon sharks over time (i.e. between two measurements a year apart) and to represent differences in individual foraging habitat on a continuum between low-risk protected mangrove (lower $\delta^{13}\text{C}$) and high-risk exposed seagrass (higher $\delta^{13}\text{C}$) (Hussey et al., 2017). Consequently, we inferred

foraging habitat of each shark through measuring the $\delta^{13}\text{C}$ values of fin tissue. In the current study, it was not possible to test for consistency in $\delta^{13}\text{C}$ values through repeat sampling, consequently our single $\delta^{13}\text{C}$ value for each individual (referred to as 'foraging habitat' throughout the manuscript) provides a proxy for foraging specialization (Hussey et al., 2017).

To avoid lipid and urea biases on stable isotope values, we lipid extracted and water washed fin samples following Kinney et al. (2011) and Li et al. (2016). Samples were then freeze dried, weighed (400–600 mg) and placed into small tin capsules. Carbon isotope values and the total carbon per cent were determined using a continuous flow isotope ratio mass spectrometer (Finnigan MAT Deltaplus; Thermo Fisher Scientific) equipped with an elemental analyser (Costech Analytical Technologies) at the Great Lakes Institute for Environmental Research (Windsor, Ontario, Canada).

The stable isotope ratio is expressed in δ value and represents the parts per thousand (‰) deviation from a standard according to the following formula:

$$\delta^{13}\text{C} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1,000,$$

where R is the ratio of ^{13}C on ^{12}C . An assessment of the standard deviation of replicate analyses of four standards (Standard bovine liver (NIST1577c), internal laboratory standard (tilapia muscle), USGS 40 and Urea ($N = 45$ for all)), revealed a precision $\leq 0.18\text{‰}$ for all standards. Accuracy showed a difference of -0.04‰ from the certified values of USGS 40 ($N = 45$) analysed throughout runs and not used to normalize samples.

1.4 | Measuring intraspecific competition

We used the annual population size of juvenile lemon sharks in each nursery area (i.e. North Sound and Sharkland) as a proxy for intraspecific competition. This acknowledges that intraspecific competition does not solely depend on population density, but also on resource abundance and distribution. Estimates of resource abundance were not available during the current study, but previous work has reported that mangrove fish communities are stable across seasons (Newman et al., 2007), therefore the changes in population size of juvenile lemon sharks were deemed to provide a reasonable proxy for changes in intraspecific competition. Shark subpopulation size was measured during the annual gillnet survey described above and accounts for every shark captured regardless of age. Since all sharks captured were held in an arena during the sampling campaign, a sharp decline in capture rate over the duration of the survey was observed, as would be expected. By the sixth night of sampling in each nursery area, we estimated that the full juvenile lemon shark population in that area had been captured (96% of the subpopulation captured by the fourth night of fishing as estimated by Gruber et al., 2001).

1.5 | Measuring predator abundance

We estimated predator abundance in each area using passive acoustic telemetry undertaken for a concurrent project quantifying shark movement and habitat use around Bimini. Large sharks were captured monthly using fisheries-independent longlines surveys (for more information see Hansell et al., 2018) or other shark fishing methods and acoustic transmitters (V16, 90–150 s delay, 10 year life, VEMCO, Bedford, Canada) were surgically implanted following standard procedures. Sharks' movements were monitored using an array of ~65 acoustic receivers (VR2W, VEMCO), deployed around the islands (including two in North Sound and two in Sharkland, Figure 1). The receivers recorded the date, time and unique transmitter identity of each shark that swam within their range (50% detection probability at 255 m, see Guttridge et al., 2017). Data on predator presence collected in 2015, 2016 and 2017 were considered here, as the receivers in North Sound and Sharkland were only deployed at the end of 2014. We calculated predator abundance in each nursery as the number of large sharks detected in a given nursery area during a calendar year divided by the total number of sharks detected around Bimini that same year. Predator abundance was calculated for all detected sub-adult/adult lemon sharks ($N = 34$, $PCL = 152$ mean ± 62 SD), bull sharks (*Carcharhinus leucas*, $N = 19$, $PCL = 183$ mean ± 13 SD) and blacktip sharks (*Carcharhinus limbatus*, $N = 13$, $PCL = 110$ mean ± 9 SD) that are known to feed on juvenile lemon sharks and other chondrichthyans (Guttridge et al., 2012; Hoffmayer & Parsons, 2006; Morrissey & Gruber, 1993; Tuma, 1976; Vorenberg, 1962; Wetherbee et al., 1990).

1.6 | Ethical note

The experimental procedures for this study were approved by the Department of Marine Resources, Bahamas (Permit no: MAF/LIA/22). Handling was kept under 5 min (e.g. for measuring and fin sampling) to limit stress. No sharks died in captivity and upon test completion, sharks were fed to satiation, all external tags removed, and sharks released at their site of capture.

1.7 | Statistical methods

Comparisons of mean between groups (i.e. the two subpopulations) were conducted using two-sample *t* tests when sample size was equal between groups. In cases of unequal sample sizes, we conducted a test of variance and used a two-sample *t* test with equal variance accordingly.

To test whether exploration score predicted foraging habitat in each subpopulation, we constructed a linear mixed model in the MCMCGLMM package (Hadfield, 2010). We used a lowly informative inverse gamma prior, with 240,000 iterations, a thinning interval of 200 and we discarded the first 40,000 iterations resulting in a Markov chain Monte Carlo with a sample size of 1,000 and low

autocorrelation. The model included foraging habitat ($\delta^{13}\text{C}$) as the response, and exploration score in an interaction with subpopulation as fixed effects. We accounted for yearly differences by including 'year' as a random effect.

To test whether predator abundance and/or population density drove the correlation between exploration and foraging in high- versus low-risk habitat, we used meta-analytic methods in the metafor package (Viechtbauer, 2010). Traditionally, meta-analytic approaches are used to compare results from different studies (e.g. correlation coefficients) by converting values into a common currency called 'effect size' which considers differences in precision (e.g. sample size) among studies (Lajeunesse & Forbes, 2003). These approaches also allow for the use of a 'test of heterogeneity' to assess whether the effect sizes are different across studies. If this is the case, we can assess whether the observed heterogeneity can be attributed to the different variables of interest (i.e. the moderators).

Here we implemented these methods to investigate if the correlation between foraging habitat and exploration varied among years and subpopulations (i.e. significant test of heterogeneity) and if predator abundance (i.e. proportion of predators present in each nursery) and intraspecific competition (i.e. total size of the juvenile lemon shark subpopulation in each nursery) could explain the heterogeneity. Accordingly, we first created a null model, that included no moderators to run a test of heterogeneity. For each year and each subpopulation, we calculated the Spearman's correlation coefficient and computed effect sizes using the 'escalc' function within the METAFOR package, using the 'ZCOR' argument to apply a Fisher *z*-transformation to the coefficients and to meet assumptions of normality. The obtained effect sizes and their corresponding sampling variances were used in the model.

If the test of heterogeneity was significant, we tested for the effect of predator abundance and intraspecific competition, mean centred at both the between subpopulation level (i.e. overall mean = 0) and the within subpopulation level (i.e. North Sound mean = 0 and Sharkland mean = 0). We did this to tease apart effects that were due to the subpopulations being different (e.g. *x* is always higher in Sharkland than North Sound and so is *y*, causing a positive *x*-*y* relationship) from the effects due to fluctuations in ecological conditions within subpopulation (e.g. when *x* goes up within Sharkland, *y* goes up as well, regardless of what happens in North Sound; see van de Pol & Wright, 2009 for similar methods). In effect, the variables centred between subpopulations represented a combination of between and within subpopulation effects, while the variables centred within the two subpopulations represented only the within-population effect.

Because predator abundance was not available for 2014, we always ran the test of moderators in separate models (containing all years for intraspecific competition, and missing 2014 for predator abundance) before testing them together in the same model (excluding intraspecific competition data from 2014).

We first tested the variables centred between subpopulations. We then tested the moderators centred at the within-population level while adding subpopulation as an interaction. We used

log-likelihood ratio tests to compare models with the moderators in an interaction with subpopulation (i.e. different slope and intercept for each subpopulation) and with subpopulation as an independent effect (i.e. different intercept but same slope for each subpopulation) to determine whether each subpopulation required modelling with a different slope.

All analysis were performed in R, version 3.6.2 (R Core Team, 2017). The data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.rr4xgxd8f> (Dhellemmes et al., 2021). A R markdown file documenting the step-by-step analytical process is uploaded as Supporting Information (Appendix 2).

2 | RESULTS

Exploration personality and foraging habitat was determined for a total of 131 individual lemon sharks age 1 year (female = 85, male = 91) captured in North Sound and Sharkland subpopulations. Sharkland had higher predator abundance than North Sound (paired t test: $t_3 = -4.26$, $p = 0.02$; Sharkland mean = 28.9 ± 11.1 SD, North Sound mean = 6.6 ± 4.2 SD; Figure 3A), but juvenile lemon shark population size, used here as a proxy for intraspecific competition, was similar (paired t test: $t_6 = -0.28151$, $p = 0.7$; Figure 3B). Sharks from North Sound and Sharkland did not differ in their captive exploration score (t test: $t_{129} = 1.72$, $p = 0.09$; Figure 3C), but sharks from Sharkland had higher $\delta^{13}\text{C}$ values than their North Sound

conspecifics suggesting Sharkland sharks used proportionally more higher risk seagrass habitat than North Sound individuals (t test: $t_{133} = -5.82$, $p < 0.0001$; Sharkland mean = -11.1 , North Sound mean = -12.3 ; Figure 3D).

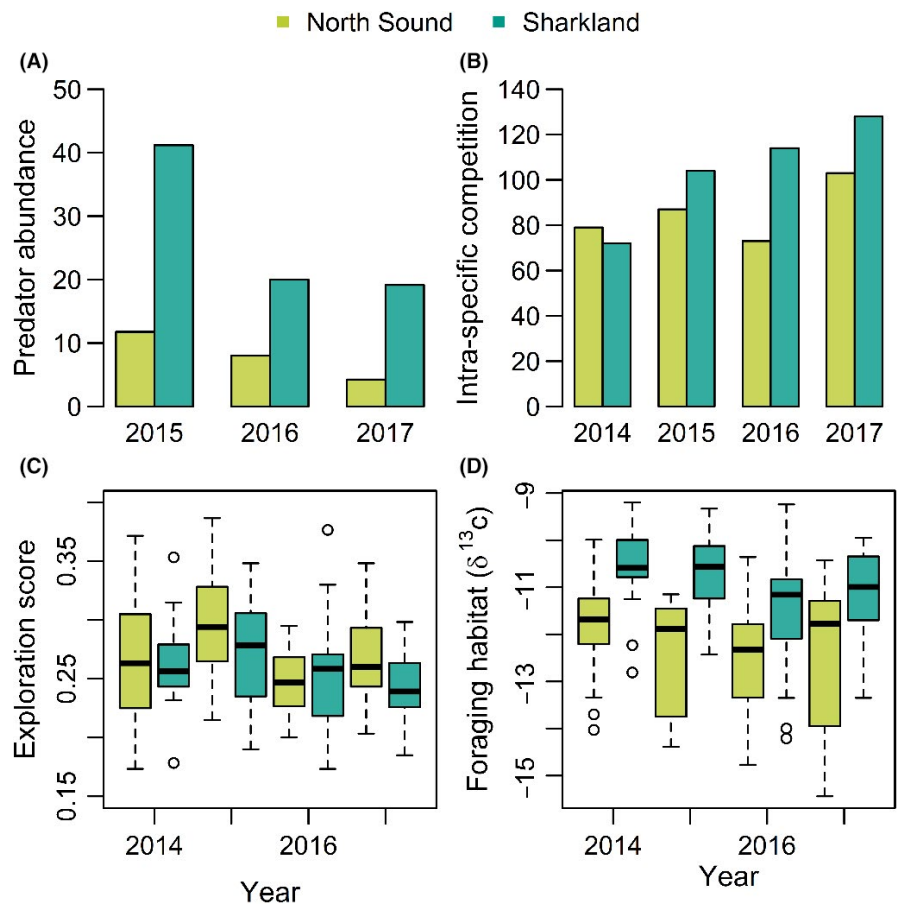
2.1 | Do subpopulations differ in their exploration-foraging habitat relationship?

When testing for a relationship between exploration personality and foraging habitat (high-risk seagrass vs. low-risk mangrove, as designated by $\delta^{13}\text{C}$), we found an effect of exploration personality score on foraging habitat in North Sound (Posterior mean = 13.36 [7.01, 19.83], Figure 4A), but not in Sharkland (Posterior mean = -2.57 [-17.85, 12.26], Figure 4B).

2.2 | What drives the association between foraging habitat and exploration?

When no moderators were included in the meta-analytic model, significant heterogeneity in effect sizes was observed ($Q_7 = 27.56$, $p = 0.0003$). Consequently, the correlation coefficients between exploration score and foraging habitat were different between year and subpopulation, allowing for a subsequent test of moderators (Figure 5).

FIGURE 3 Graphical visualization of each variable of interest across years and nurseries. Histograms of (A) the abundance of predators (predators detected in the nursery/predators detected in Bimini $\times 100$) and (B) the subpopulation size (number of juvenile lemon sharks in the area) as a proxy for intraspecific competition in each year and each subpopulation. Boxplots of (C) the exploration score of sharks and (D) the foraging habitat occupied (i.e. protected low-risk mangrove [low $\delta^{13}\text{C}$ value] versus exposed high-risk seagrass [high $\delta^{13}\text{C}$ value]) in each year and each nursery. Data are not available for predator abundance in 2014 given acoustic receivers were not deployed in the study area for most of that year



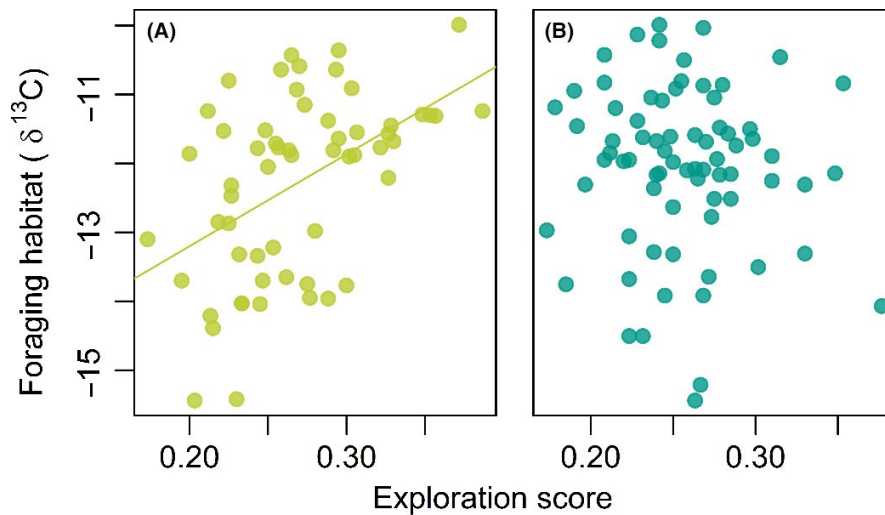


FIGURE 4 Foraging habitat (on a spectrum from high-risk exposed seagrass to low-risk protected mangrove as designated $\delta^{13}\text{C}$) as a function of captive exploration personality in (A) North Sound and (B) Sharkland. Solid lines represent significant linear regressions

We found the tests of moderators to be significant when we individually tested predator abundance and intraspecific competition centred at the between subpopulation level (i.e. overall mean = 0; predator abundance: $QM_1 = 19.35$, $p < 0.0001$; intraspecific competition: $QM_1 = 3.92$, $p = 0.047$). This identified that both moderators were important predictors of the correlation between exploration habitat and foraging habitat. In the final model including both moderators, predator abundance had a negative effect on the relationship between foraging habitat and exploration score (estimate = -0.05 [-0.07 , -0.02], Figure 6A), while intraspecific competition did not influence the relationship between traits (estimate = 0.0097 [-0.03 , 0.01], Figure 6B).

At the within subpopulation level, models were not improved by the addition of interactions between subpopulation and the moderator of interest (predator abundance: Log-likelihood ratio = 0.63 , $p = 0.42$; intra-specific competition log-likelihood ratio = 2.02 , $p = 0.15$). In the absence of interactions, predator abundance was the only significant moderator ($QM_1 = 5.28$, $p = 0.02$; intraspecific competition $QM_1 = 1.16$, $p = 0.28$), showing a negative effect on the relationship between foraging habitat and exploration score (estimate = -0.05 [-0.09 , -0.007], Figure 7).

Given we compared two distinct sampling sites, one within each subpopulation, rather than a continuum across the nursery regions, we repeated the above analyses on our data organized into three sampling groups. Sharks captured in the two northern most gillnets in North Sound, were assigned to a 'North North Sound' group, sharks captured in the south of North Sound and North of Sharkland in a 'Middle' group and sharks captured in the two southernmost gillnets of Sharkland in a 'South Sharkland' group (see Figure 1 for capture locations). The results of this alternative gradient analysis, in terms of the significance and direction of the relationships, supported those obtained using the original two subpopulations providing further confidence in our conclusions (Appendix 1.2). The results from this later analysis, however, were limited by low sample sizes within year and groups.

3 | DISCUSSION

In the current study, we aimed to bridge the gap between animal personality and individual foraging specialization by investigating under which ecological circumstances personality correlates with low- versus high-risk foraging habitat in two subpopulations of wild juvenile lemon sharks known to differ in predator abundance and with varying intraspecific competition. In North Sound, we found an overall positive relationship between exploration and $\delta^{13}\text{C}$ values, indicating that sharks which explored more in captivity also foraged predominantly in exposed seagrass habitats. In Sharkland, no link between exploration score and $\delta^{13}\text{C}$ values was observed. When we sub-divided the data by year and subpopulation, we found that the correlation coefficients between foraging habitat and exploration personality were significantly heterogeneous, indicating that the relationship between these traits fluctuated across years and subpopulations. Importantly, predator abundance was a significant predictor of both the strength and direction of correlations, with reduced predator abundance associated with more positive coefficients (i.e. more explorative sharks in captivity predominantly foraged in risky seagrass habitats). This result was retained when predator abundance was centred within subpopulations, indicating that it was not exclusively driven by the known difference in predator abundance between the areas. Intraspecific competition was also a significant moderator of the relationship, but only at the between subpopulation level, and its effect on the coefficients was not different from zero when it was included in a model along with predator abundance.

With all years pooled, the differences observed between North Sound and Sharkland were in accordance with previous findings. Dhellemmes, Finger, Smukall, et al. (2020) found exploration of the novel open-field to predict the distance sharks swam from shore and their growth rate in North Sound, with fast growth and offshore swimming selected against suggesting individuals favoured the use of protected mangrove habitat. In Sharkland, fast growth was also found to be associated with higher mortality probabilities, however, no association was found between exploration of the

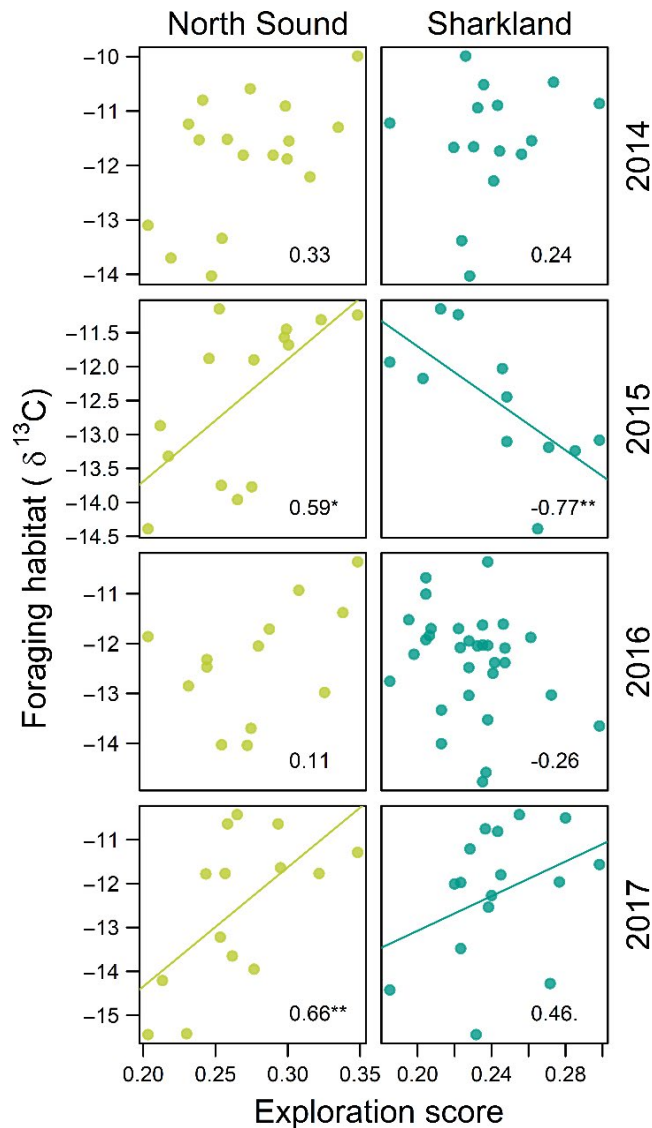


FIGURE 5 Foraging habitat (on a spectrum from high-risk exposed seagrass to low-risk protected mangrove as designated by $\delta^{13}\text{C}$) as a function of exploration score for each year and each subpopulation. The Spearman's rho for each subsample is given at the bottom right of the plots. Where correlations were significant, we present the linear regression of foraging habitat on exploration score as a solid line. (Significance: $.p = 0.05$, $*p < 0.05$, $**p < 0.01$)

novel open-field, distance swam from shore and growth rate. It was proposed that a personality driven growth mortality trade-off may arise because foraging in open habitats (e.g. seagrass) can be more productive, but also more dangerous (Dhellemmes, Finger, Smukall, et al., 2020). This suggestion is substantiated by our results here and further corroborated by Hussey et al. (2017) whereby high $\delta^{13}\text{C}$ values (i.e. seagrass foraging) predicted high growth rate in Bimini's juvenile lemon sharks. Dhellemmes, Finger, Smukall, et al. (2020) offered two potential explanations for the absence of a link between personality and life history in Sharkland: (a) The trade-off between growth and mortality was mediated via a different personality trait in this subpopulation or (b) the environmental conditions did not always favour the association between personality and life history.

Here, we found that the link between personality and foraging behaviour was unstable among years and subpopulations, and that predator abundance was a main driver of the trait association. This suggests that the observed lack of relationship between traits in Sharkland when all years were pooled together is due to yearly fluctuations in predator abundance. Predation has often been hypothesized as a driver of the association between personality traits (i.e. behavioural syndromes) with high predation leading to stronger associations (e.g. Bell, 2004; Dingemanse et al., 2007). Here, predation not only influenced the strength of the trait association, but also its direction. In North Sound, where predator abundance was lower, more explorative sharks had $\delta^{13}\text{C}$ values representative of offshore seagrass foraging, according to our expectations. This indicates that lower predator abundance reduced the cost of offshore foraging, leading individuals to behave in accordance with their personality score measured in captivity. When predator abundance was high, however, sharks did not forage according to expectations from their captive test (i.e. explorative individuals foraged more in safer mangrove habitat, see Figure 5, Sharkland, 2015). One explanation for this observation could relate to the fact that a captive personality test such as the novel open-field assay provides a safe environment where food is provided ad libitum (to avoid hunger biases, Biro & Booth, 2009). In the absence of ecological pressures present in the natural environment, animals may behave in accordance with their personality phenotype. Behaviour, however, is plastic and expected to fluctuate according to various external factors (Rodríguez-Prieto et al., 2011). For instance, low sociability was linked to high dispersal in mosquitofish *Gambusia affinis*, but this trait correlation was negated under high predator abundance (Cote et al., 2013). For Sharkland lemon sharks, predator abundance, could be expected to dampen sharks' risky foraging behaviour, given a reduction in foraging effort in response to perceived predation risk has been shown in numerous studies (Ferrari et al., 2009). The amount of food consumed by reef fishes, for example, was shown to drastically reduce when presented with predator decoys (Catano et al., 2016). This argument is contradicted by our finding that $\delta^{13}\text{C}$ values in Sharkland indicate a comparatively higher use of seagrass habitats than in North Sound. However, this result could be influenced by variability in the distribution and density of mangrove and seagrass habitats between North Sound and Sharkland.

In contrast, the behaviour of less explorative sharks (in captive trials) was influenced by predator abundance in Sharkland in an unexpected way: when predator abundance was high, less explorative individuals in captivity foraged predominantly in more dangerous exposed seagrass habitat. This result could suggest that food resource and/or space availability in the mangrove habitat in Sharkland alone is insufficient to support the requirements of the whole subpopulation. Forced high density of juvenile lemon sharks in the mangrove habitat due to predator presence could increase intraspecific competition, with more explorative personality types potentially dominating and expelling lower risk-taking sharks forcing them to adopt a new foraging specialization (i.e. switching from a mangrove to seagrass dominated diet).

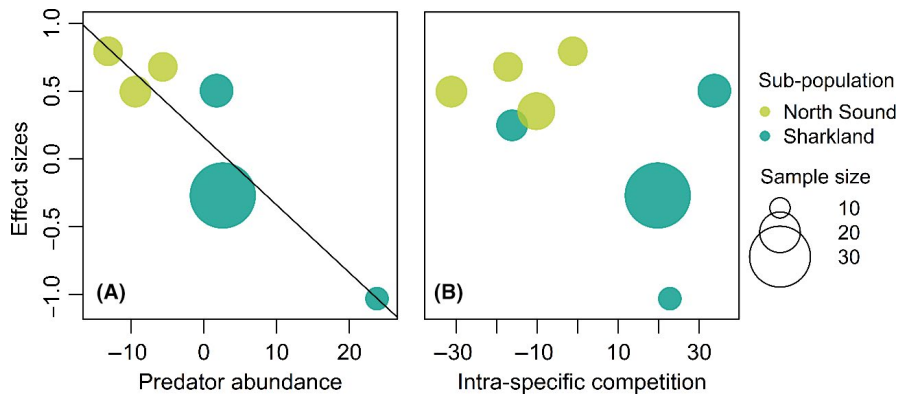


FIGURE 6 Effect sizes as a function of (A) predator abundance and (B) intraspecific competition (both centred at the between subpopulation level). Solid lines represent significant effects in the final model. The colours represent the different subpopulations, and each point is a different year. The points are scaled according to sample size (a larger point indicates a larger sample size)

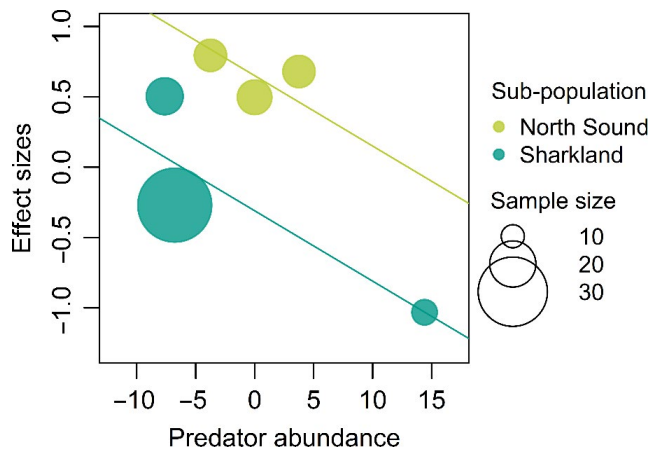


FIGURE 7 Effect sizes as a function of predator abundance (centred at the within subpopulation level). Solid lines represent significant effects in the final model. The colours represent the different subpopulations, and the points are scaled according to sample size (a larger point indicates larger sample size)

The fact that less exploratory individuals foraged in more dangerous seagrass habitats might also partly be due to state-dependent processes (i.e. driven by the internal state of individuals). Green sea turtles *Chelonia mydas* in Shark Bay were found to shift foraging habitat according to their body condition in the presence of their main predator, tiger sharks *Galeocerdo cuvier* (Heithaus et al., 2007). When predation risk was high (i.e. tiger sharks were abundant), turtles in poor body condition foraged in high risk, but profitable habitats, while turtles in good body condition preferred safer, but less productive habitats. For juvenile lemon sharks in Bimini, high exploration score and seagrass foraging have both been linked to higher growth rates (Dhellemmes, Finger, Smukall, et al., 2020; Hussey et al., 2017) suggesting that explorative individuals may have better body condition than less explorative sharks. This state-dependent explanation seems highly plausible given turtles with good body condition preferred high-risk habitat under low predator abundance, identical to the behaviour of lemon sharks in this study (Heithaus et al., 2007).

An increasing body of literature suggests that observed behavioural correlations among individuals might not be representative of what is happening at the within individual level ('individual gambit' Brommer, 2013; Niemelä & Dingemanse, 2018). To avoid making

the assumption that among-individual correlations are representative of within individual correlations the use of multivariate models is advised which allow for the decomposition of variances within and between individuals (Niemelä & Dingemanse, 2018). Such statistical tools require large sample sizes and multiple measurements, which was not possible due to logistical constraints (e.g. population size, difficulty of captures, duration of the captive tests) inherent to studying long-lived and naturally low abundance large species. While we took the 'individual gambit' we argue that our study provides an important step in understanding how natural conditions (e.g. competition and predation) shape the covariance between personality and ecologically relevant behaviours and their associated impact on life history. Furthermore, we acknowledge that foraging habitat might be highly plastic and therefore our single measurement of $\delta^{13}\text{C}$ may not accurately represent foraging specialization. Previous work based on multiple measurements per individual at the same study site, however, would suggest our data provides a reasonable proxy (Hussey et al., 2017). We also accept that recent evidence suggests that certain tissues may retain maternal isotopic influence for periods >1 year, which could bias interpretation of juvenile shark foraging habitat (Niella et al., 2021). We state that the issue of isotopic turnover rate is species dependent (i.e. related to growth rate and physiology) and we remain confident that isotope values in fin tissue of juvenile lemon sharks are reliable (Hussey et al., 2017; Rangel et al., 2020). While we were only able to record our measures of foraging specialization and personality annually, future studies should, when possible, repeatedly test the relationship between foraging specialization and personality in fast changing environmental conditions to overcome this caveat. One potential solution to address this challenge is to use tissues with faster isotopic turnover rates than fin: for instance the isotopic turnover rate of plasma occurs over a few weeks, allowing for more frequent sampling (as opposed to ~ 1 year, Matich et al., 2015). However, the downfall to this approach would be the increased number of captures, and therefore stress, needed for repeated samples. Therefore, animal welfare may preclude this approach for some species.

To conclude, we found that the association between personality measured in captivity and use of high- versus low-risk foraging habitats was principally regulated by one main environmental factor: predator abundance. This result provides a potential explanation

regarding why disentangling the association between life-history traits and personality has been complex in terms of conflicting results reported to date: the association between captive personality and wild traits is plastic and is regulated by relevant ecological pressures. We argue in this case that the study of consistent individual differences in behaviour and their ecological consequences would benefit from approaches that account for variability in relevant ecological pressures. Multi-population, multi-year studies in wild animals where ecological conditions can be monitored will in this case be an important addition to the field, along with highly controlled studies in captivity where conditions can be manipulated experimentally.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

F.D., T.L.G., J.K. and N.E.H. conceived the ideas and designed methodology; F.D., M.J.S. and T.L.G. collected the data; F.D. and N.E.H. analysed the samples; F.D. and M.J.S. analysed the data; F.D., M.J.S. and N.E.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.rr4xgxd8f> (Dhellemmes et al., 2021).

ORCID

Félicie Dhellemmes  <https://orcid.org/0000-0002-2043-4653>
 Matthew J. Smukall  <https://orcid.org/0000-0003-3790-3644>
 Tristan L. Guttridge  <https://orcid.org/0000-0002-6706-1452>
 Jens Krause  <https://orcid.org/0000-0002-1289-2857>
 Nigel E. Hussey  <https://orcid.org/0000-0002-9050-6077>

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SUPPORTING INFORMATION

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

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