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Article

Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor

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Inter-individual variation in behaviour has been recognised as a major driver of population ecology, but its relationship to migratory strategy has been ill-explored. Here, we investigated whether male migrant and resident Cory's shearwaters *Calonectris borealis*, a long-lived partially migratory seabird, are distinguishable by their temperament at the colony. We tracked a large number of individuals over two winters using GLS devices and assessed whether exploratory behaviour and reaction to extraction from the nest corresponded to migratory strategy over this period. While exploratory behaviour was unrelated to migratory strategy, birds that were resident were more likely to be unreactive towards extraction from the nest. This difference in behavioural stress response, together with previous findings that migrants display higher physiological stress over winter, suggests that migrants and residents may be distinguishable by their stress threshold.

Keywords: behaviour, *Calonectris borealis*, partial migration, personality, seabird, stress response

Introduction

Inter-individual variation in behaviour has been recognised as a major driver of population ecology; individual responses in exploratory behaviour, boldness and aggression, among others, have been related to each other, to survival and fitness, and explained in terms of evolutionary stability (Dingemanse and Réale 2005, Réale et al. 2007, Nilsson et al. 2010, Chapman et al. 2011a, Wolf and Weissing 2012). Studies of individual behavioural responses to stimuli, or temperament, have found long-lived individual consistencies constituting personality traits, and correlations of personality traits within populations, creating behavioural syndromes (Carter et al. 2013). Despite the ubiquity of partial migration in the animal kingdom (Chapman et al. 2011b) and our increasing ability to track animal movements, investigations into temperamental correlates of migratory tendency are few and the subject remains ill-explored (Nilsson et al. 2010, Chapman et al. 2011a, Found and St. Clair 2017, Odermatt et al. 2017).

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The Cory's shearwater *Calonectris borealis* is a long-lived, monogamous, migratory seabird in which males are partial migrants – in the population breeding on Selvagem Grande, Madeira, a small proportion of males remain resident in the upwelling Canary Current surrounding the breeding colony, while the rest of the population undertakes trans-equatorial migrations to non-breeding areas off southern Africa and in the south-west Atlantic (Perez et al. 2014). Despite an apparent flexibility in over-winter movements and destinations, individuals are largely faithful to a particular non-breeding area (Dias et al. 2011). Migratory males return to the colony showing signs of higher overwinter stress levels than residents, as assessed by feather corticosterone (Pérez et al. 2016) and tail feather fault bar intensity (Gatt et al. 2020a). This difference could either be attributed to harsher environmental conditions experienced at distant non-breeding areas, although evidence of carry-over effects from this is absent (Gatt et al. 2020a), or to an intrinsic difference in stress responses between migrants and residents (Nilsson et al. 2014).

To date, there has been some research relating personality to foraging movements in seabirds (black-browed albatross *Thalassarche melanophris*: Patrick and Weimerskirch 2014, Cory's shearwater *Calonectris borealis*: Krüger et al. 2019, kittiwake *Rissa tridactyla*: Harris et al. 2019). The general indication is that bold individuals are more superficial explorers, less flexible in their foraging movements and fare better in conditions with high competition and high environmental predictability. These 'proactive' personality types are often associated with low physiological stress responses, as opposed to 'reactive' personalities on the other end of the spectrum, which elicit high physiological stress responses and are associated with cautious, fearful and slow exploring personalities (Koolhaas et al. 1999, Cockrem 2007). While proactive personality traits have been seen in migratory individuals of roach *Rutilus rutilus* and blue tits *Cyanistes caeruleus* (Nilsson et al. 2010, Chapman et al. 2011a), it is not yet known whether this trend persists in partially migratory seabirds.

Here we explored whether migratory strategy in male Cory's shearwaters is linked to two behavioural traits assessed during the pre-laying and incubation periods: 1) exploration of a novel environment and 2) response to extraction from the nest. The same males were tracked overwinter using GLS loggers. Based on the current scientific knowledge, and given the predominant medium-term, individual persistence in migratory strategy (Dias et al. 2013, Perez et al. 2014), we expected migrant and resident males to differ in their behaviour, reflecting evolutionary correlates between migratory strategy and the behavioural adaptations required in the different environmental and biotic pressures experienced. We also investigated the potential confounding effect of age due to the effect prior experience or pace-of-life could have on behaviour (Hall et al. 2015, Nilsson et al. 2016).

Male Cory's shearwaters that remain resident return to the colony earlier the following breeding season compared to migrants, which increases the probability of securing a nest and successfully reproducing (Perez et al., 2014). In order to disentangle possible effects of previous reproductive success/effort from those of migratory strategy on temperament, we compared the behaviour of individuals in which reproductive failure was experimentally induced against that of control individuals that successfully reproduced.

Methods

Study system and GLS tracking

Selvagem Grande (30°, 09′N, 15°, 52′W) is an island nature reserve that forms part of the Madeiran Archipelago, Portugal. Around 30 000 pairs of Cory's shearwaters breed on the island, arriving at their nest burrows between mid-February and early April (hereafter, the pre-laying period) to undertake a long period of nest defence and mating before laying a single egg in early June, which they incubate for around two months. Over 450 regularly occupied nest cavities within rubble walls are the subject of long-term research, with annual monitoring of nest occupancy and breeding output resulting in hundreds of ringed individuals, many of known or approximated ages (Catry et al. 2011a, Dias et al. 2011).

Cory's shearwaters occupy distinct oceanic currents during the non-breeding period (Fig. 1). The majority migrate to the Benguela and Agulhas Currents, while smaller numbers migrate to currents in the southwest and northwest Atlantic. Resident males remain largely in the Canary Current. These movements have been extensively studied in this population and non-breeding destinations described in several publications (Catry et al. 2011b, Dias et al. 2011, 2012, Perez et al.

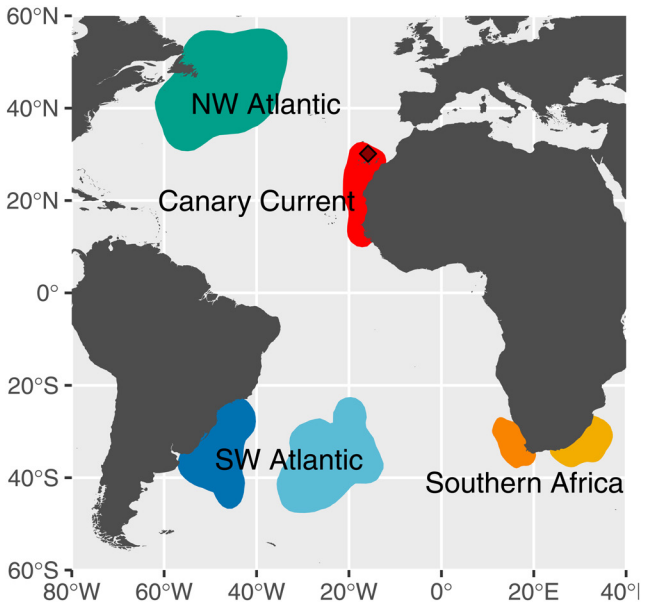

Figure 1. Schematic representation of the non-breeding destinations of Cory's shearwaters breeding on Selvagem Grande. The colony location is denoted by the red diamond. Resident males remain in the Canary Current over winter. Drawn from tracking data presented here and in Gatt et al. (2020).

2014). In 2016 and 2017 we deployed a large number of geolocation loggers (GLS, Migrate Technology model C330, 3.3 g, recording mode 9; 122 in 2016, 104 in 2017) to track individuals' migratory movements over winter. GLS light level data was analysed using IntiProc (ver. 1.03, Migrate Technology Ltd.). Sun elevation angle was calculated from device calibration data, setting a linear elevation angle when both pre- and post-calibration data was available, and averaged −6.5°. The (main) non-breeding area was assigned from the mapped tracking data, revealing the migratory strategy of 110 males (98 overwinter movements 2016–2017 and 83 overwinter movements 2017–2018). GLS were leg mounted and weighed less than 1% of the birds' body weight (male Cory's shearwaters typically weigh over 700 g, own data), which, given the attachment method, can be assumed to bear minimal effects on survival and fitness (Bodey et al. 2017). The resighting rate of birds fitted with GLS is consistent with the rate of return of breeding birds from one year to the next, at ca 85% (Mougin et al. 1997).

As part of a different study assessing carry-over effects of reproductive success, during the breeding season of 2017, 25 nests were selected for egg removal to experimentally reduce parental effort by inducing early breeding failure (Catry et al. 2013), with another 25 males selected as controls. Each group contained males of a variety of ages and previous migratory strategies. The eggs of these 'experimental birds' were removed between the end of June and early July, corresponding to around one month after laying.

Behavioural tests

We carried out behavioural tests over three breeding seasons between 2016 and 2018 during the daytime, prior to the start of the birds' activity at the colony – Cory's shearwaters only approach the colony/leave their nest from the late afternoon onwards at this colony (Granadeiro et al. 2009).

We assessed exploration in an emergence/novel environment test. Birds were extracted from their nest, placed into a small, black carrier box and transported to a small room (approximately 2 × 3 m) which served as the novel environment. The bird was then transferred into another black box with a removable flap door situated in a corner of the room (Fig. 2). Over a 10 min time period, birds could leave the open box into the empty room while being filmed. The whole process lasted approximately 20 min, keeping the time between capture at the nest and the start of the test constant. Behavioural tests were carried out during the incubation period of 2016 and during both pre-laying and incubation periods of 2017 (Table 1 for number of birds tested per field season). In total, 114 males were tested; of these, 27 were tested twice over the two years, and five were tested three times. From this test we extracted two scores; whether or not the bird left the box within the stipulated time (binary 'emergence' score) and, if it did, the latency (in seconds) for the bird to leave it.

In 2017 and 2018 we tested the reaction on extraction from the nest in male Cory's shearwaters when retrieving

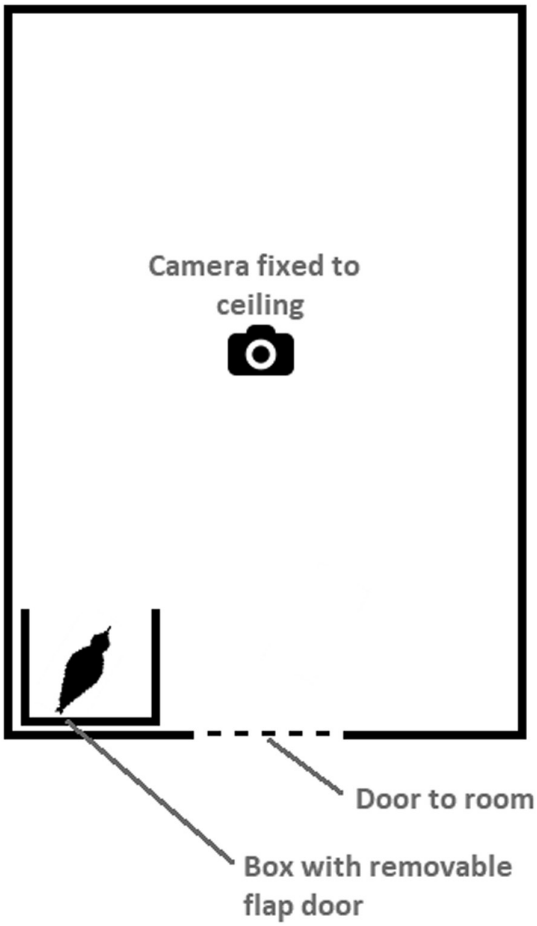

Figure 2. Diagram of the set-up of the novel environment test used to assess the emergence score and latency (s) to enter a novel environment in male Cory's shearwaters. Methods section for further details.

GLS in the pre-laying period and/or as part of annual nest monitoring during incubation in both years. A binary 'extraction score' was assigned to classify individuals as either 'reactive' (1) or 'unreactive' (0) depending on their behaviour throughout the process of extraction from the nest, namely their reaction to an approaching hand, reaction on being caught and resistance to being pulled out of the nest (Table 2). Combinations of behaviours that could not be classified into either of the two classes according to this classification were not considered. Between 55 and 60% of all assessments in each field season resulted in a classification of either 'reactive' or 'unreactive'. All assessments were performed by the same person to minimise subjectivity, and were only carried out at nests where the target individuals were the sole occupants of the nest at the time of testing, were facing towards the nest entrance, and could be reached easily without the use of a noose – this is the scenario for the vast majority of nests in the study site. Extraction scores were obtained during pre-laying and incubation periods of 2017 and 2018 (Table 1 for number of birds tested per field season). In total, scores were obtained from 153 males; of these, 43 males were

Table 1. The number of individual male Cory's shearwaters tested for exploration of a novel environment and reaction on extraction from the nest in each field season over the period of study. (Note: Two individuals were tested twice for exploration behaviour during the pre-laying period of 2017.)

	2016	2017		2018	
	Incubation	Pre-laying	Incubation	Pre-laying	Incubation
Exploration	32	69	43	–	–
Extraction score	–	38	78	91	58

scored twice over the two years, 17 three times and 11 more than three times. The minimum interval between repeated observations was around two months in individuals tested in successive pre-breeding and incubation seasons, with the exception of two individuals tested at 9 and 19 day intervals, respectively, during the pre-breeding season of 2017.

Statistical analysis

Statistical analyses were performed on R Statistical Package, ver. 3.5.1 (<www.r-project.org>).

In 2018, extraction scores were obtained from 20 males from the 'experimental' group and 20 control males which successfully reproduced in 2017. We assessed whether previous breeding success had any impact on extraction response the following year by comparing the extraction scores of experimental and control individuals by means of a Chi-squared test.

We estimated individual repeatability in exploration (emergence) and extraction over the entire period of study to ensure that individuals were consistent in their behaviour over this timeframe, and that therefore temperament could be related to migratory strategy over the two years. Repeatability was calculated as the intraclass correlation coefficient with a binomial error distribution (package rptR, Nakagawa and Schielzeth 2010) using bootstrapping without randomisation (1000 iterations) to estimate confidence intervals. The low number (n = 9) of individuals that left the box in repeated assessments precluded the ability to assess repeatability in latency.

To investigate links between individual temperament and migratory strategy (migratory/resident) we ran generalised linear (mixed-effect) models (function 'glm', package *stats* or function 'glmer', package *lme4*) (Bates et al. 2015) relating latency (quasi-Poisson error structure), emergence score and extraction score (both with a binomial error structure) as dependent variables in separate models to migratory strategy (migrant versus resident) in successfully tracked individuals, with individual as a random intercept in the last two models due to the many repeated assessments on the same individuals. Age and annual cycle stage (pre-laying versus incubation) were added as potentially confounding fixed effects. Testing for an effect of age on the extraction score also tests for habituation to handling, since individuals used in this study experienced being extracted from their nest annually or almost annually throughout their adult life, with older birds having been handled more often. Not all individuals whose behaviour was assessed were successfully tracked, and a small proportion were of unknown age (model sample sizes in Table 3).

Linear regression estimates ('Est') are presented with their standard error.

Results

Male Cory's shearwaters were consistent in their migratory strategy during the two tracked years – of the 75 males tracked in both years, none changed strategy. In total, 19 males remained predominantly in the Canary Current over the non-breeding season, 89 migrated to the south Atlantic, and another two overwintered in the north-west Atlantic.

Exploration

Emergence was not repeatable over the whole dataset (R = 0.103, CI = 0–0.282, p = 0.212), nor when analysing only data collected during incubation (R = 0.08, CI = 0–0.229, p = 0.304, n = 75 observations of 61 individuals).

Mixed effect model results suggest that annual cycle stage significantly influenced emergence into the novel environment – while 59% and 51% of individuals left the box when tested during incubation periods in 2016 and 2017 respectively, only 28% did during pre-laying 2017 (Table 3). Emergence was not related to age or migratory strategy.

Among those instances where individuals did emerge, their latency to leave the box was determined both by

Table 2. Scoring system used to classify Cory's shearwaters' reaction on extraction from the nest ('extraction score'). An individual had to satisfy all the conditions described in order to be classified as either reactive or unreactive.

Reactive (1)	The bird bites the approaching hand.
	The bird bites hard and/or attacks and releases continuously.
	The bird struggles on being pulled out and resists extraction.
Unreactive (0)	The bird does not react to the entering hand, does not try to escape.
	The head or beak of the bird can be grabbed with little to no reaction from the bird.
	The bird does not resist extraction.
NA	The bird cannot be scored since it does not satisfy the initial assumptions and/or the conditions for classification.

Table 3. Results of generalised linear (mixed) models testing the effects of Cory's shearwater migratory strategy on emergence into a novel environment, the latency for individuals to leave a box into a novel environment, and the behavioural score on extraction from the nest, with age and annual cycle stage (pre-laying versus incubation) as fixed effects. Reference for migratory strategy is resident and for stage is incubation. Significant results ($\alpha = 0.05$) are in italic. Sample sizes (n) refer to the number of observations from individuals in which behavioural scores were obtained, migratory strategy identified and ages known.

	Exploration								
	Emergence score (n = 102 observations of 81 individuals)			Latency (n = 43)			Extraction score (n = 140 observations of 67 individuals)		
	Est (± SE)	z	p	Est (± SE)	t	p	Est (± SE)	z	p
Migratory strategy	−0.32 ± 0.76	−0.42	0.676	0.18 ± 0.51	0.36	0.721	*2.67 ± 1.28*	*2.09*	*0.037*
Age	0.05 ± 0.04	1.18	0.240	*0.08* ± 0.03	*2.48*	*0.018*	−0.05 ± 0.07	−0.72	0.471
Stage	*−1.46 ± 0.70*	*−2.09*	*0.037*	*−1.30 ± 0.52*	*−2.49*	*0.017*	−0.23 ± 0.57	−0.40	0.692

age, with an increase in latency in older birds, and annual cycle stage (Fig. 3), but was unrelated to migratory strategy (Table 3).

Reaction on extraction from the nest

Previous breeding success, experimentally manipulated, had no impact on extraction score the following year ($\chi^2 = 1.64$, df = 1, p = 0.201, n = 40, Table 4). Therefore, we can exclude that differences in extraction score between migrants and residents are a result of possible differences in reproductive success between the two groups. Moreover, while none of the 75 repeatedly tracked males changed migratory strategy over the two years, 33 experienced a change in their reproductive outcome.

Repeatability estimates suggest that Cory's shearwaters are consistent in their response on extraction, rarely switching from 'reactive' to 'unreactive' responses over the course of the two years (R = 0.646, CI = 0.253–0.711, $p < 0.0001$; Table 5). While R is high compared to those reported in the literature (Bell et al. 2009), it may be inflated due to the omission of behaviours that did not classify under the two extremes. We did not test for a correlation between extraction score and exploratory behaviour since the latter was not repeatable in this population.

The GLMM results suggest that annual cycle stage and age had no influence on extraction score. The lack of an effect of age suggests that there is no indication that birds habituate to extraction from the nest. We found that individuals' response to extraction from the nest was correlated with their migratory strategy; Migratory males (n = 56) were more likely to have been reactive towards extraction from the nest than were resident males (n = 11) (Table 3, 5). The high individual repeatability supports the inclusion of single observations in the GLMM.

Discussion

Our results demonstrate a link between Cory's shearwater migratory strategy and reaction on extraction from the nest, and propose a new potential behavioural test that can be further investigated for wider use in similar biological systems. Links between migratory strategy and behavioural traits have

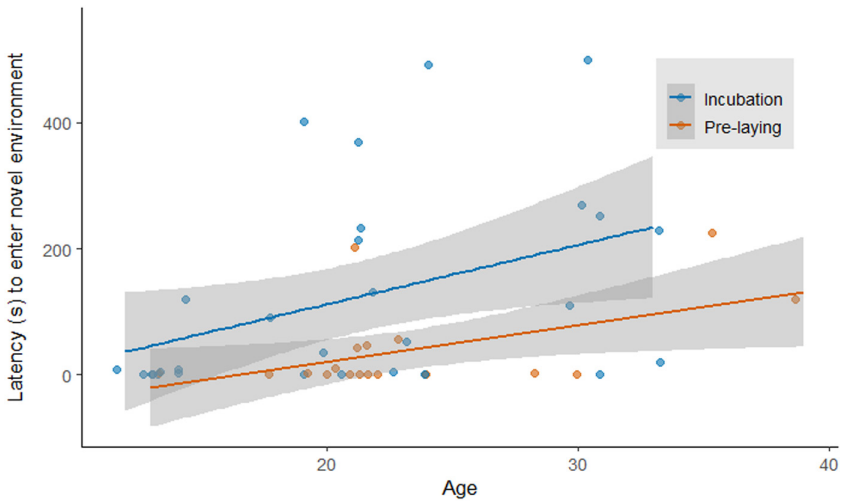

Figure 3. The latency (s) for Cory's shearwaters to enter a novel environment increased with age. The plot only contains data of individuals that left the box and entered the novel environment during the 10 min test period. This corresponds to 29 of 50 individuals tested during incubation (blue), but only 18 of 58 individuals tested during the pre-laying period (orange). Shaded areas represent the 95% confidence interval.

Table 4. The number of Cory's shearwaters from the experimental group (failed breeders) and control group (successful breeders) that fell within either of the two classifications of reaction from extraction from the nest (unreactive versus reactive).

	Extraction score	
	Unreactive	Reactive
Experimental group – failed breeders	14	6
Control group – successful breeders	9	11

so far only been explored in a handful of studies in very few taxa across the animal kingdom, and only one bird species (blue tit: Nilsson et al. 2010, roach *Rutilus rutilus*: Chapman et al. 2011a, hoverfly *Episyrphus* sp.: Odermatt et al. 2017, wild elk *Cervus canadensis*: Found and St. Clair 2017). This study provides valuable insights into the correlating behavioural features of partial migrants from a perspective that is not very well explored, making within-population comparisons with a large sample size of simultaneously tracked individuals.

Resident male Cory's shearwaters were found to be more likely to be unreactive to extraction from the nest than were migrants. Within the same population, migrants and residents have also been found to differ in their physiological stress responses over the non-breeding period, with residents showing lower feather corticosterone concentrations and fewer tail feather fault bars (Pérez et al. 2016, Gatt et al. 2020a). Tail feather fault bar intensity reported in Gatt et al. (2020a) reflected experienced acute stress, such as antagonistic inter-individual interactions and inclement weather (Jovani and Rohwer 2016), over the period of tail feather growth between 2017 and 2018, which coincides with the period of behavioural assessments presented here. While we do not exclude that extrinsic factors at the non-breeding areas may be acting, our current finding, that migrant and resident males differ in their behavioural reaction to a standardised stressor at their common breeding colony, suggests that the differences in stress responses reported within this population may be, at least partly, a result of a personality trait within the population with variation in an endogenous threshold to a stress response between males of different migratory strategies.

Table 5. The number (n) of migrant and resident male Cory's shearwaters with the different combinations of extraction scores recorded. Individuals were scored between one and five times during the pre-breeding and incubation periods of 2017 and 2018. Each time, birds were classified as either unreactive (0) or reactive (1) to extraction from the nest. The sample corresponds to all individuals in which behavioural scores were obtained and migratory strategy identified.

Combination of extraction scores	n	
	Migrants	Residents
0,0,0,0,0	0	1
0,0,0,0	4	2
0,0,0	3	1
0,0	7	5
0	17	3
1	13	2
1,0	6	1
1,0,0	0	1
1,1	8	0
1,1,0	5	0
1,1,0,0	1	0
1,1,1	7	0
1,1,1,0	1	0
1,1,1,1,1	1	0

Our observations appear to contradict the previously reported relationships between physiological stress responses and personality type if the greater reactivity on extraction from the nest is interpreted as aggressiveness forming part of a 'proactive' personality (Cockrem 2007). However, we have observed that the more reactive individuals are more likely to attempt to escape the nest after handling and show more visible stress responses, such as panting. We therefore argue that it is rather low reactivity to extraction from the nest that reflects greater boldness, similar to interpretations of kittiwakes at the nest presented with a novel object (Harris et al. 2019). Under this interpretation, higher reactivity towards extraction would be a sign of heightened stress response and self-defence, rather than nest defence, making the correlation with higher activity of the parasympathetic system recorded over winter in agreement with previous literature. The understanding of the physiological basis of these behaviours would benefit from the analysis of blood corticosterone alongside behavioural assessments in future studies.

Coping style appears to determine individual spatial distribution and survival under different scenarios (Koolhaas et al. 1999, Dingemanse et al. 2004, Cockrem 2012). 'Reactive' personalities are more successful in unpredictable conditions due to their higher plasticity in behaviour and more thorough exploration. 'Proactive' personalities are less neophobic but explore new environments more superficially and are more repetitive in their behaviour (Benus et al. 1991, Cockrem 2007). These correlated suites of characteristics have already been seen in the foraging behaviour of Cory's shearwaters (Krüger et al. 2019). Resilience to competition in bold individuals is also hypothesised to be an important factor determining foraging movements in seabirds, as suggested by their closer foraging distributions relative to the colony (Patrick and Weimerskirch 2014, Harris et al. 2019, Krüger et al. 2019). If these trends hold for the determination of migratory strategy in Cory's shearwater, we could expect that male Cory's shearwaters remaining resident at the Canary Current experience a more predictable environment, similar to that experienced during the breeding season, but perhaps also greater competition than migrants experience.

The novel environment test appears to be assessing different behavioural traits that are not strongly linked to the patterns discussed above and that it is not effective in measuring individuals' boldness in this system. The low individual repeatability across contexts suggests that the behaviours exhibited in the novel environment test do not reflect a personality trait. Cory's shearwater's exploratory behaviour shows phenotypic plasticity, particularly across annual cycle stages. The low likelihood to enter an unfamiliar environment during the pre-laying season may have fitness consequences in accordance with parental investment theory and nest defence

intensity hypotheses (Montgomerie and Weatherhead 1988). In the pre-laying period, Cory's shearwaters invest highly in nest defence and intense fights between individuals are often observed at dense colonies such as on Selvagem Grande. Such fights can result in injury, and occasionally even death (M. C. Gatt, pers. obs.). Entering unfamiliar environments may increase the risks of unnecessary fights resulting in high energy costs or physical damage. Additionally, during incubation birds may experience a perceived urgency to return to the nest due to increased motivation to provide parental care.

The novel environment test also exposed how young Cory's shearwaters, which recruited as breeding birds during or in the years directly before this study, emerged into the novel environment faster than older birds. One hypothesis in the literature that could explain this is that stress responses are suppressed in experienced breeders at ages at which the potential for current reproductive success are high, but are not suppressed in young, inexperienced birds which give greater value to their immediate survival than their reproductive attempt (Montgomerie and Weatherhead 1988, Elliott et al. 2014).

We acknowledge that the timeframe of the analysis presented here is not representative of the longevity of shearwaters and advise caution when interpreting the permanence of behavioural type, which may change over the long term, similar to individual quality (Catry et al. 1999) and migratory strategy (Perez et al. 2014). We encourage more long term individual observations of long-lived species to improve our understanding of the role of temperament in population ecology. The assessment of behaviour on extraction from the nest has potential to be a simple, straightforward and informative measure of stress response for burrow nesting seabirds. This may be a particularly useful tool in regularly monitored populations in which individuals need to be handled for other purposes, avoiding the need to expose the animals to an additional stressor. However, the interpretation of birds' responses requires further investigation in order to be able to extract more information. In particular, among the assessments which are not considered here, some birds retreated as a reaction to an approaching hand rather than staying put or attacking, which resulted in some confusion as to where such a response would lie in an ordinal list of categories of increasing reactivity (Patrick et al. 2013). An ability to classify more reactions could help describe a greater proportion of a population. Moreover, the extraction test can be further validated as a measurement of behavioural stress response by quantifying blood corticosterone levels in assessed birds.

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Author contributions

Marie Claire Gatt: Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **José Pedro Granadeiro**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (equal). **Paulo Catry**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.547d7wm4s> (Gatt et al. 2020b).

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