

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

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## Abstract

Investigating the causes and consequences of differential migration may help us understand possible variability in resilience to environmental change within species and populations. Inter-individual variation in temperament 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 over 100 individuals overwinter using GLS devices and assessed whether exploratory behaviour and reaction to extraction from the nest corresponded to migratory strategy over a period of two years. While exploratory behaviour was unrelated to migratory strategy, birds that were more reactive towards extraction from the nest were more likely to migrate. This, together with previous findings that migrants display higher physiological stress over winter, suggests that migrants and residents may be distinguishable by their stress threshold.

## Introduction

Differential migration, whereby members of the same species differ in migratory behaviour, be it in timings, migratory routes, stop-over sites or non-breeding areas, has been increasingly reported with the widening applicability of tracking technologies (McKinnon & Love 2018). This diversity in migratory strategy within species and populations could impact animal population survivability under the environmental changes and unpredictability brought about by the climate crisis. Species with wider non-breeding ranges and/or partially migratory populations appear to be less susceptible to the effects of environmental change due to the capacity for faster adaptability and/or less acute risks experienced by a portion of the population (Gilroy *et al.* 2016; Briedis & Bauer 2018). As a result, investigating the causes of differential migration may help us understand implications to population survivability in a changing world.

Over the past few decades, inter-individual variation in temperament 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 & Réale 2005; Réale *et al.* 2007; Nilsson *et al.* 2010; Chapman *et al.* 2011; Wolf & Weissing 2012). Despite the ubiquity of partial migration in the animal kingdom 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.* 2011; Found & St. Clair 2017; Odermatt *et al.* 2017).

The Cory's Shearwater (*Calonectris borealis*) is a long-lived, monogamous, migratory seabird in which males are partial migrants. 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 (M. Gatt, unpublished). 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 (M. Gatt, unpublished), or to an intrinsic difference in stress responses between migrants and residents (Nilsson *et al.* 2014).

To date, there has been some research relating temperament to foraging movements in seabirds (Black-browed Albatross *Thalassarche melanophrys* : Patrick & Weimerskirch 2014; Kittiwake *Rissa tridactyla* : Harris *et al.* 2019; Cory's Shearwater *Calonectris borealis* : Krüger *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 predictability. Similar behavioural traits have been seen in migratory individuals of Roach (*Rutilus rutilus*) and Blue Tits (*Cyanistes caeruleus*) (Nilsson *et al.* 2010; Chapman *et al.* 2011). It is not yet known whether this trend persists in partially migratory seabirds.

Here we explored whether migratory strategy is linked to behavioural traits in the Cory's Shearwater. We assessed exploration of a novel environment and response to extraction from the nest in males, the partially migratory sex, during the pre-laying and incubation periods, and tracked their overwinter movements 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 migrants and residents to differ in their temperament, reflecting evolutionary correlates between migratory strategy and the behavioural adaptations required in the different environmental and biotic pressures experienced. In support of this hypothesis, we found that migrant and resident Cory's Shearwaters differed in their response to extraction from the nest. Together with previous findings that migrants display higher physiological stress over winter, this suggests that migrants and residents may be distinguishable by their stress threshold.

## Methods

### Field work

Selvagem Grande (Lat 30.140556, Long -015.868889) 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 February and March to undertake a long period of nest defence and mating (the pre-laying period) 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 (Granadeiro *et al.* 2006). In 2016 and 2017 we deployed a large number of geolocation loggers (GLS, Migrate Technology model C330; 122 in 2016, 104 in 2017) to track individuals' migratory movements over winter, 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, which, given the attachment method, can be assumed to bear minimal or no 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.* 2008).

### Behavioural tests

We carried out behavioural tests over three breeding seasons between 2016 and 2018.

We assessed exploration in an emergence/novel environment test. Birds were extracted from their nest, transported in a closed box to a small room which served as the novel environment, and transferred into a

box with a removable flap door situated in a corner of the room. Over a 10 minute time bracket, birds could leave the open box into the empty room while being filmed. The whole process lasted 20 minutes and had no implication on the breeding success of the individuals tested. Thirty two birds were tested during the incubation period of 2016, 69 during the pre-laying period of 2017, and 43 during the incubation period of 2017. Twenty seven individuals were tested twice over the two years. 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 on first encounter, either when retrieving GLS in the pre-laying period or as part of annual nest monitoring during incubation. A binary “extraction score” was assigned depending on the birds’ reaction to an approaching hand, reaction on being caught, and resistance to being pulled out of the nest (Table 1), classifying birds as either “reactive” (1) or “unreactive” (0). Behaviours that could not be classified into either of the two classes according to this classification were not considered. Around 60% of all assessments 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 (2017: 56 individuals; 2018: 147 individuals) and incubation (2017: 168 individuals; 2018: 107 individuals). 17 individuals were assessed twice during pre-laying in 2018 to determine short-term repeatability. In total, 153 males were scored; 43 males twice, 17 three times, and 11 more than three times.

## Statistical analysis

Statistical analyses were performed on R Statistical Package, version 3.5.1 (R Core Team 2018).

In order to identify whether age and annual cycle stage (pre-laying vs incubation) could influence the results of the behavioural traits, we ran generalised linear (mixed-effect) models (function `glm`, package `stats` or function `glmer`, package `lme4`). Age was treated a factor of six 5-year age classes. The latency to leave the box was fitted with a quasi-poisson error structure, while the emergence and extraction scores were fitted with a binomial error structure. Individual ID was added as a random intercept in models of emergence and extraction due to repeated assessments on the same individuals. To control for the effect of migratory strategy on extraction score (see Results), we fitted this model only on migratory individuals. Previous breeding success does not influence extraction score (see Appendix 1, Supporting Information).

We estimated individual repeatability in temperament over the entire period of study to ensure that individuals were consistent in their behaviour in the short term, and that therefore temperament could be related to migratory strategy at least over this time period. Repeatability was calculated as the intraclass correlation coefficient with a binomial error distribution (package `rptR`, Nakagawa & Schielzeth 2010) using bootstrapping without randomisation (1,000 iterations) to estimate confidence intervals. For assessing exploration behaviour, this was calculated on the emergence score using a binomial error distribution.

To investigate links between individual temperament and migratory strategy (migratory/resident) we ran generalised linear mixed effect models for the binary emergence and extraction scores as dependent variables in separate models, with individual as a random intercept. Age and annual cycle stage were added as fixed effects in the model explaining emergence.

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 while 89 migrated to the South Atlantic.

## Exploration

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. The latency to leave the box was also determined by age, with a decrease in exploration in older birds (Table 2, Fig. 1).

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 ( $R = 0.08$ ,  $CI = 0 - 0.229$ ,  $p = 0.304$ ). Mixed effect model results also suggest that individual emergence is not related to its migratory strategy (Table 3,  $n = 85$  observations of 69 individuals).

## Extraction score

Annual cycle stage and age had no influence on extraction score after controlling for migratory strategy (Table 2). 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 ( $R = 0.646$ ,  $CI = 0.253 - 0.711$ ,  $p < 0.0001$ ). However, repeatability values are inflated due to the omission of behaviours that did not classify under the two extremes.

Migratory males were far more likely to have been reactive towards extraction from the nest than were resident males (Est =  $4.03 \pm 1.55$ ,  $z = 2.61$ ,  $p = 0.009$ ,  $n = 175$  observations of 85 individuals) (Fig. 2).

## Discussion

Our results demonstrate a link between Cory's Shearwater migratory strategy and response on extraction from the nest. Links between migratory strategy and behavioural traits have 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.* 2011; Wild Elk *Cervus canadensis* : Found & St. Clair 2017; Hoverfly *Episyrphus* sps.: Odermatt *et al.* 2017). This study provides valuable insights into the causes and consequences of partial migration from a perspective that is not very well explored, making within-population comparisons made possible by our large sample size of simultaneously tracked individuals.

In Cory's Shearwaters, migrants and residents have also been found to differ in their physiological stress responses over the non-breeding period, with migrants showing higher feather corticosterone concentrations and greater tail feather fault bar intensity (Pérez *et al.*, 2016, M. Gatt, unpublished data). Tail feather fault bar intensity reported in Gatt *et al.* (unpublished) reflected experienced acute stress, such as antagonistic interindividual interactions and inclement weather (Jovani & Rohwer 2016), over the period of tail feather growth between 2017 and 2018, which coincides with the period of behavioural assessments presented here. Our current findings, that migrant and resident males differ in their behavioural reaction to a standardised stressor at the breeding colony, suggest that the differences in feather corticosterone and fault bar intensity within the population may be, at least partly, a result of variation in an endogenous threshold to a stress response between males of different migratory strategies rather than variation in exogenous triggers over winter.

The covariation in behavioural and physiological responses to a stressor has been well explored in animal behaviour studies and described as individual coping style (Koolhaas *et al.* 1999). Most studies report a correlation between low corticosterone responses to stressors and bold, aggressive, and/or fast exploring personalities (“proactive” personalities), while high corticosterone responses are associated with cautious, fearful, and slow exploring personalities (“reactive” personalities) (Cockrem 2007). Our observations appear to contradict these if the greater reactivity on extraction from the nest is interpreted as aggressiveness forming part of a “proactive” personality. However, we 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, and the correlation with higher activity of the parasympathetic system recorded over winter would be in agreement with previous literature. The authors have also repeatedly observed that the more reactive individuals are also more likely to attempt to escape the nest after handling, supporting this interpretation.

Coping style appears to determine individual prevalence and distribution under different scenarios (Koolhaas *et al.* 1999; Dingemanse *et al.* 2004; Cockrem 2012). “Reactive” personalities with high corticosterone responses are more successful in unpredictable conditions due to their higher plasticity in behaviour and more thorough exploration. “Proactive” personalities with low corticosterone responses 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 & 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. Unlike their response to extraction, 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 & 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 (pers. obs.). Entering unfamiliar environments may increase the risks of unnecessary fights resulting in energy loss 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 & 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 may be a simple, straightforward and informative measure of stress response for burrow nesting seabirds, particularly in regularly monitored populations in which individuals need to be handled for other purposes.

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.

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## Supporting information

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## Tables

**Table 1** 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 2** Results of generalised linear mixed models testing the effects of age and annual cycle stage (pre-laying vs incubation) 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. The latter model was run on migratory individuals to control for the confounding effect of migratory strategy. Reference for stage is incubation. Significant results are in *italic*.



	Emergence score (n = 108 obser- vations of 87 individuals)	Emergence score (n = 108 obser- vations of 87 individuals)	Emergence score (n = 108 obser- vations of 87 individuals)	Latency (n = 47 obser- vations of 40 individuals)	Latency (n = 47 obser- vations of 40 individuals)	Latency (n = 47 obser- vations of 40 individuals)	Extraction score (n = 119 obser- vations of 57 individuals)	Extraction score (n = 119 obser- vations of 57 individuals)	Extraction score (n = 119 obser- vations of 57 individuals)
	<b>Est (<math>\pm</math> SE)</b>	<b>z</b>	<b>p</b>	<b>Est (<math>\pm</math> SE)</b>	<b>t</b>	<b>p</b>	<b>Est (<math>\pm</math> SE)</b>	<b>z</b>	<b>p</b>
Age 10-15	-0.14 $\pm$ 0.58	-0.23	0.816	2.74 $\pm$ 1.02	2.70	0.010	3.36 $\pm$ 1.68	2.00	0.04
16-20	0.73 $\pm$ 0.87	0.85	0.397	1.96 $\pm$ 1.15	1.71	0.095	-4.78 $\pm$ 2.85	-1.68	0.09
21-25	0.94 $\pm$ 0.78	1.20	0.229	2.38 $\pm$ 1.6	2.25	0.030	-3.87 $\pm$ 2.29	-1.69	0.09
26-30	3.34 $\pm$ 1.85	1.81	0.071	2.80 $\pm$ 1.10	2.56	0.015	-3.04 $\pm$ 2.63	-1.16	0.25
31-35	0.25 $\pm$ 0.97	0.25	0.801	2.40 $\pm$ 1.11	2.16	0.037	-3.12 $\pm$ 2.48	-1.26	0.21
36-40	1.11 $\pm$ 1.95	0.57	0.571	3.54 $\pm$ 1.60	2.21	0.033	-	-	-
Stage	-1.79 $\pm$ 0.86	-2.07	0.039	-1.51 $\pm$ 0.55	-2.75	0.009	-0.44 $\pm$ 0.70	-0.63	0.52

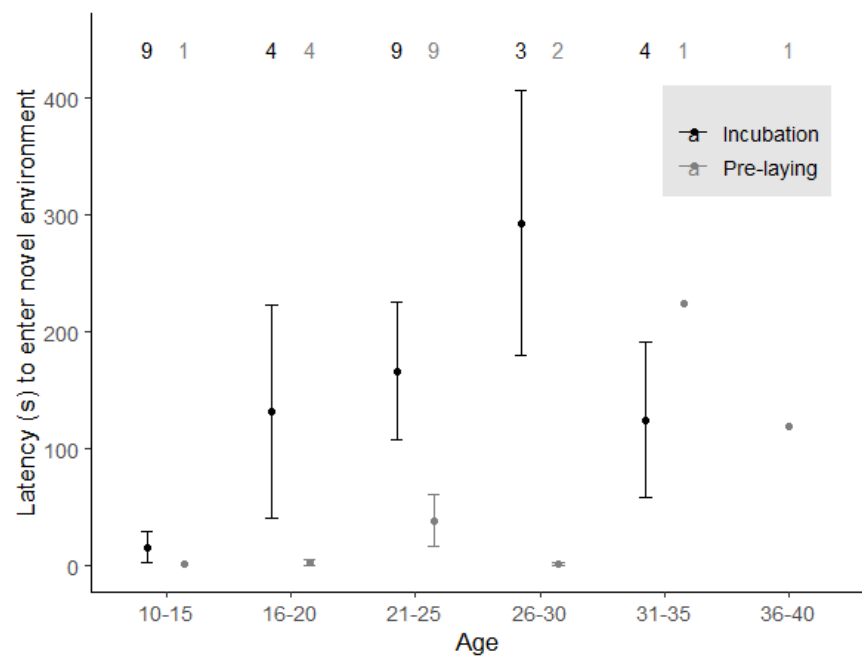
**Table 3** Results of generalised linear mixed models testing the effects of migratory strategy on individual emergence into a novel environment, with age and annual cycle stage (pre-laying vs incubation) as additional fixed effects. Reference for migratory strategy is “resident”, and that for stage is “incubation”.

	<b>Est (<math>\pm</math> SE)</b>	<b>z</b>	<b>p</b>
Migratory strategy	-0.64 $\pm$ 1.07	-0.60	0.548
Age	0.05 $\pm$ 0.05	1.00	0.320
Stage	-1.09 $\pm$ 0.68	-1.61	0.108

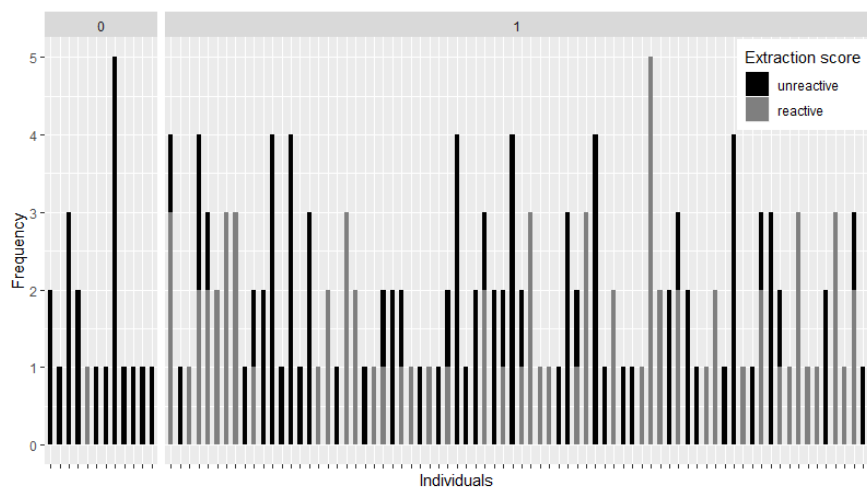
## Figures

**Figure 1** The latency (s) for individuals to enter a novel environment increased with age, suggesting a decrease in exploration with age. The plot only contains data of individuals that left the box and entered the novel environment during the 10 minute test period. This corresponds to 29 of 50 individuals tested during incubation (black), but only 18 of 58 individuals tested during the pre-laying period (grey). Points represent mean latency and whiskers represent the standard error. Sample sizes for each age-class and annual cycle stage are presented in the plot.

**Figure 2** Barplot showing the frequency of unreactive (black) and/or reactive (grey) responses for each individual on extraction from the nest. A higher proportion of reactive extraction scores were recorded from migratory males compared to residents.



**Figure 1**



**Figure 2**