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RESEARCH ARTICLE

Boldness predicts plasticity in flight responses to winds

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Abstract

1. Behavioural plasticity can allow populations to adjust to environmental change when genetic evolution is too slow to keep pace. However, its constraints are not well understood. Personality is known to shape individual behaviour, but its relationship to behavioural plasticity is unclear.
2. We studied the relationship between boldness and behavioural plasticity in response to wind conditions in wandering albatrosses (*Diomedea exulans*).
3. We fitted multivariate hidden Markov models to an 11-year GPS dataset collected from 294 birds to examine whether the probability of transitioning between behavioural states (rest, prey search and travel) varied in response to wind, boldness and their interaction.
4. We found that movement decisions varied with boldness, with bolder birds showing preferences for travel, and shyer birds showing preferences for search. For females, these effects depended on wind speed. In strong winds, which are optimal for movement, females increased time spent in travel, while in weaker winds, shyer individuals showed a slight preference for search, while bolder individuals maintained preference for travel.
5. Our findings suggest that individual variation in behavioural plasticity may limit the capacity of bolder females to adjust to variable conditions and highlight the important role of behavioural plasticity in population responses to climate change.

KEYWORDS
behavioural plasticity, foraging behaviour, hidden Markov models, personality, seabirds

1 | INTRODUCTION

Behavioural plasticity, the ability of animals to adjust behaviour in response to changing environmental conditions, is crucial for animal adaptability and survival. By expressing behaviour that is targeted to their environment, individuals can increase survival and fitness by ensuring their behaviour is appropriately matched to its context (Dall et al., 2004; DeWitt et al., 1998). In the long term, plasticity

allows species to adjust to rapid environmental change beyond that possible through genetic evolution, ultimately helping populations reduce their vulnerability to extinction (Chevin et al., 2010; Ducatez et al., 2020; Mery & Burns, 2010). Despite these apparent benefits of plasticity, not all individuals respond to changes in conditions in the same way, for reasons that are not fully understood (Dubois, 2019). Understanding the extent and nature of this variation is important, because inter-individual differences in plasticity may result in some members of populations being disproportionally impacted by environmental change (Dingemanse & Wolf, 2013; Nussey et al., 2007).

If no evolutionary constraints acted upon plasticity, all animals would exhibit limitless flexibility that allowed them to perfectly tailor their behaviour to the environment (DeWitt et al., 1998). Clearly, this is not the case, and plasticity is believed to impose a number of costs and limitations: for example, by leading individuals into 'ecological traps' in which responses to an environmental cue lead to expression of maladaptive behaviour (Wong & Candolin, 2015), through energetic costs (Van Buskirk & Steiner, 2009; Vinton et al., 2022), or because the detection of the environmental cues shaping behaviour can be unreliable (DeWitt et al., 1998). Consequently, individuals differ in the degree to which they express plasticity (Dingemanse et al., 2012; Stamps, 2016).

Personality, broadly defined as consistent among-individual differences in a behavioural trait, places limitations on individual behaviour (Dall et al., 2004), and may therefore be associated with individual variation in plasticity (Dingemanse & Wolf, 2013; Mathot et al., 2012). Boldness, a personality trait measuring the responses of animals in novel contexts (Sih et al., 2004; Wilson et al., 1994), correlates with many aspects of behaviour: bolder animals take more risks (Montiglio et al., 2018; Réale et al., 2010), are more competitive (Patrick et al., 2014; Webster et al., 2009) and forage superficially (Eccard et al., 2020; Patrick et al., 2017), compared to their shyer counterparts. Boldness may also covary with behavioural plasticity (Dingemanse et al., 2010; Mathot & Dingemanse, 2012; Sih & Del Giudice, 2012): while bolder animals exhibit relatively inflexible behaviour (Coppens et al., 2010; Verbeek et al., 1994), shyer animals have been reported to exhibit greater plasticity (Adriaenssens & Johnsson, 2011; Dubois, 2019; Gibelli & Dubois, 2017; Groothuis & Carere, 2005).

Personality-dependent plasticity differences may reflect the approaches individuals take to manage uncertainty about their environment (Mathot et al., 2012). Animals can either invest time and energy in gathering information to make informed decisions about behaviour, or alternatively, superficially sample their environment. These alternative options are captured in the 'speed-accuracy' trade-off, whereby fast individuals gain quick, but variable, rewards, while slow individuals pay the cost of time investment to make accurate and 'safe' decisions about their behaviour (Dubois, 2019; Mathot et al., 2012; Sih & Del Giudice, 2012). These choices manifest as higher and lower behavioural plasticity, respectively, but should ultimately yield equivalent fitness outcomes (DeWitt et al., 1998; Dubois, 2019; Sih & Del Giudice, 2012). These differences should be most apparent in changeable environments, where mismatches between behaviour and the environment have greater consequences.

Marine ecosystems are highly variable environments where resources are distributed ephemerally in space and time, and which are changing at a particularly rapid rate due to climate change (Henson et al., 2017; Hoegh-Guldberg & Bruno, 2010; Schreiber & Burger, 2001; Steele et al., 2019; Weber et al., 2021; Weimerskirch, 2007). The extent to which individuals exhibit plasticity in such environments depends on their perception of this resultant uncertainty and associated 'risk', which, in turn, may be linked to their personality. Seabirds are apex marine predators whose behaviour is strongly shaped by environment, which dictates both the location of feeding sites and the energetic costs of moving towards them. Many seabird species exhibit repeatable individual differences in behaviour that may represent differences in the perception of environmental uncertainty. Foraging specialisation has been documented in 80% of species tested, representing 12% of species overall and spanning diverse taxa including the procellarids, alcids, larids and phalacrocoracids (Ceia & Ramos, 2015). In seabirds, personality covaries with reproductive investment, foraging behaviour, and distribution (Harris, Descamps, Sneddon, Bertrand, et al., 2020; Krüger et al., 2019; Patrick & Weimerskirch, 2014; Wolf et al., 2007), but there has been little explicit investigation into whether personality may also affect behavioural plasticity.

Existing variation in personality in seabirds suggests that, over evolutionary time, alternative foraging strategies have given rise to equivalent fitness outcomes allowing such variation to persist. However, this may change in the future. As climate change leads to extreme and rapid changes in environmental conditions, some foraging strategies might become inadequate. Shifts in behaviour associated with environmental change have already been observed in wandering albatrosses (*Diomedea exulans*), for which climate change-induced wind alterations have affected foraging range distributions and fitness (Somveille et al., 2020; Weimerskirch et al., 2012). This probably reflects the energetic demands of flight in this species, which make wandering albatrosses heavily dependent on strong winds for movement (Clay et al., 2019; Richardson et al., 2018; Shaffer et al., 2001; Weimerskirch et al., 2000). While wandering albatrosses are responsive to changes in wind (Clay et al., 2020), it is not known whether differences in plasticity mean individuals vary in this response.

We hypothesised that boldness predicts behavioural plasticity in wandering albatrosses in response to changing wind conditions. Wandering albatrosses exhibit consistent, measurable boldness that correlates with foraging behaviour (Patrick et al., 2013, 2017). Specifically, bolder birds invest more in current reproduction, forage more exploratively (feeding superficially at multiple patches) and are more competitive in securing food at foraging sites (Harris, Descamps, Sneddon, Cairo, et al., 2020; Krüger et al., 2019; Patrick et al., 2017). Conversely, shyer birds prioritise survival, and forage exploitatively, by investing more time and effort in sampling patches of known reward. We measured the propensity of birds to switch between three behavioural states at sea (searching for prey, travelling between patches and resting), as a function of boldness score. We predicted that shyer birds would show greater behavioural adjustment, indicated by a steeper gradient between wind conditions and the propensity to remain in or switch behavioural states. Conversely, we predicted that

bolder birds would show more consistent expression of behaviour across all wind conditions encountered. Using high-resolution GPS tracks collected from 294 birds over 11 years, individual boldness estimates and hidden Markov models (HMMs), we tested whether boldness covaried with the propensity to switch between behaviours. High propensities to switch behaviour in response to wind conditions should indicate greater plasticity. We aimed to determine whether behavioural plasticity covaries with boldness, and whether individuals vary in their ability to adjust to environmental change.

2 | MATERIALS AND METHODS

2.1 | Study population and data collection

We tracked the movements of 294 wandering albatrosses breeding on Possession Island, Crozet Islands archipelago, south-western Indian Ocean (46°24′ S, 51°46′ E) from 2010 to 2021. Each year, all adults and chicks on the colony were captured by hand to be fitted with a metal ring with a unique identification number, and individuals within breeding pairs were sexed based on size and plumage dimorphism (Weimerskirch et al., 2005).

Incubating albatrosses were fitted with GPS loggers (IgotU 120/600, Mobile Action Technology, weighing up to 32 g, up to 0.5% body mass; XGPS and Centurion, Sextant Technology, NZ weighing 60–75 g, up to 1.21% body mass; see details in Weimerskirch et al., 2018, 2020) recording fixes at frequencies from 1 to 15 min. All data were resampled to have fixes at 15-min intervals. Loggers were deployed dorsally using thin strips of marine Tesa tape (Weimerskirch et al., 2014), and removed after the birds had completed at least one foraging trip.

2.2 | Ethics statement

Animal care was performed humanely following rules issued by the Réserve Nationale des Terres Australes. The field procedures and manipulations on Crozet, after approval from Comité National de la Protection de la Nature, were given permission by the 'Préfet of Terres Australes et Antarctiques Françaises' to Program IPEV N°109 (PI H Weimerskirch).

2.3 | Boldness

We measured individual boldness annually for incubating birds breeding in the Crozet Islands population, from which the birds in this study were sampled. Boldness is commonly assayed by measuring the behavioural responses of individuals to a novel object or approach of an observer (Patrick et al., 2013; Sih et al., 2004; Stamps & Biro, 2016). In this study, a human observer approached each bird from 5 m up to the nest and recorded all behaviours exhibited. Observers were trained to estimate 5 m during rigorous training, as measuring an exact distance would cause disturbance that would prevent robust personality testing. The response of birds was measured on a 6-point ordinal scale of increasing responsiveness from 0 to 5, where 0 = no response; 1 = bird lifts head; 2 = bird rises onto tarsi; 3 = bird vocalises; 4 = bird stands up and 5 = bird vacates nest. As so few birds responded by leaving the nest ($n = 10$), category 5 was collapsed into category 4. Under this scale, high scores indicate bolder birds. A mean of 2.91 ± 1.70 (1 SD) assays were taken per bird. We estimated boldness by extracting individual-level best linear unbiased predictors from a generalised linear mixed model (GLMM) that controlled for other known influences while accounting for the categorical nature of the response variable (Patrick et al., 2013). Full details can be found in the Supporting Information; in brief, a GLMM with an ordinal error structure was fitted to boldness score using the R package MCMCglmm (Hadfield, 2010) which included the fixed effects of observation ID and observer ID, a random intercept for individual ID, and a random effect for the additive genetic variance, which was incorporated as the matrix of pairwise relatedness among all individuals. Boldness was repeatable and heritable (Supporting Information), and the boldness of the study population did not differ significantly from that of the wider Crozet Islands population (study mean = −0.11 ± 1.23, Figure 1; Crozet mean = 0.001 ± 1.26). To ensure that behavioural differences associated with personality could not be explained by systematic morphological differences that might influence flight performance, we examined whether individuals of differing boldness scores also differed in their wing chord length or body mass (Supporting Information). We found no correlation between morphology and boldness score (Table S2; Figure S1).

2.4 | Statistical analysis

All data processing and statistical analyses were carried out in R version 4.1.0. Full details on initial GPS data processing steps and the collection of environmental data can be found in Clay et al. (2020) and so to avoid repetition are briefly summarised here. Individual foraging trips were extracted from GPS data by defining the start and end of each trip as the last fix at departure and the first after return to the colony. We applied a conservative filter to remove GPS fixes with an estimated flight speed greater than 90 km h^{-1}, which exceeds normal flight speeds (Phalan et al., 2007; Richardson et al., 2018). Hourly wind data were obtained for 10 m above sea level, which is as close as possible to the average observed height for wandering albatrosses (Pennycuick, 1982), from the European Centre for Medium Range Weather Forecasts ERA5 reanalysis dataset (Copernicus Climate Change Service (CS3) 2021). Wind data are estimated on a 0.25° lat-lon grid, and so reflect the localised wind conditions of birds at any given time point.

2.4.1 | Behavioural classification and transition probabilities

We used the momentuHMM R package (McClintock & Michelot, 2018) to fit three-state generalised HMMs to foraging

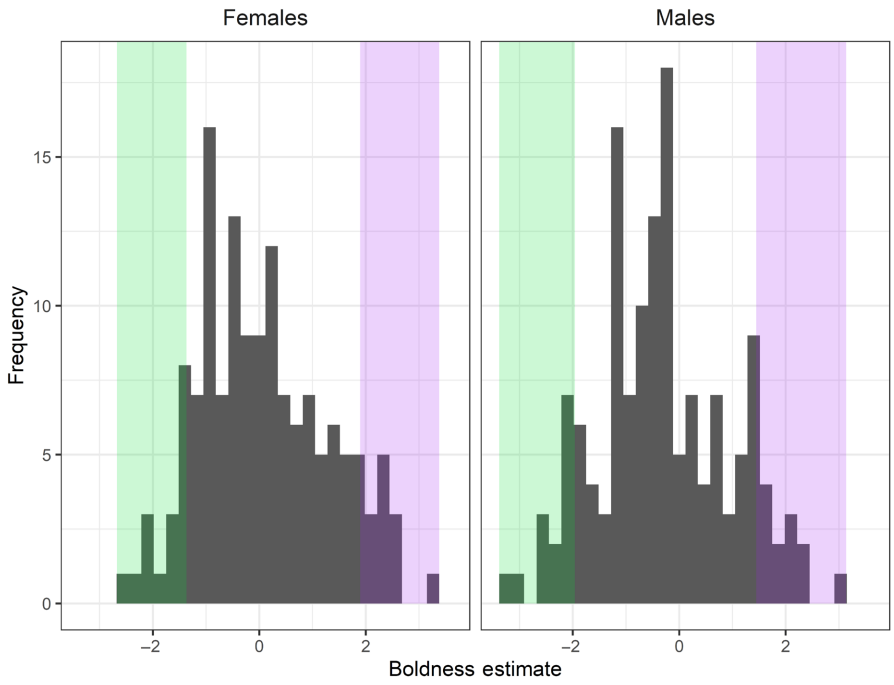

FIGURE 1 Frequency histogram of boldness estimates observed in the study population (left = females; right = males). Boldness estimates represent the best-linear unbiased predictors for individuals as estimated from an 'animal' model. Shaded areas represent lower (green) and upper (purple) 10% quantiles of boldness estimates, used to illustrate results throughout the text.

tracks. We fitted HMMs both to categorise 15-min fixes into states representing discrete behaviours (rest, travel and search) and to model for each sex the effect of boldness and wind covariates on the probability of transitioning between each state. We fitted HMMs using the input variables of step length and turning angle, which categorised rest as fixes with low speeds and low (concentrated) to moderate turning angles, search as fixes with moderate speeds and moderate to wide turning angles, and travel as fixes with high speeds and concentrated turning angles. Initial values for the parameters of the observed model were obtained by randomly iterating parameters 100 times within a biologically realistic range and extracting those values that were most frequently estimated. The step lengths and turning angles were modelled using a gamma distribution and a von Mises distribution, respectively. While the precision of our data (in minutes) may not reflect the actual scale that decisions are made (in seconds), in a previous study using very similar methods (Clay et al., 2020), behavioural states assigned using HMMs were found to broadly reflect activity patterns (time on water and in flight) as identified using higher-resolution (every 6 s) immersion data (i.e. wet or dry). To determine the validity of our model for characterising behavioural states on foraging trips, we compared the behavioural outputs of our best fitting HMM to expert-assigned classification, obtaining an accuracy of 75% (Supporting Information).

Multivariate HMMs can be used to analyse the effect of covariates on step lengths, turning angles and state transitions. As we were specifically interested in what causes individuals to transition between different behavioural states, we examined the relationship between boldness and transition estimates. Building on previous methods (Clay et al., 2020), which identified the importance of wind speed and direction on foraging behaviour, we tested whether boldness by wind interactions influenced the probability of transitioning between rest, search and flight states. Behavioural responses in wandering albatrosses have previously been reported to vary according to the three-way interaction of wind speed, relative wind direction (the angular difference in direction between bird heading and wind direction, standardised to between 0° and 180°) and sex (Clay et al., 2020). We therefore built for each sex a candidate model set around a global model that included the two-way interaction of wind speed and direction, as well as every possible interaction between personality and each of the wind variables individually. We additionally included the 2-factor variable of 'LoD', indicating daylight or darkness, to control for diel rhythms in behaviour, as wandering albatross do not usually search at night (Phalan et al., 2007). From this global model, we ran separate models including every possible combination of boldness and boldness by wind interactions (Table S1) and compared relative support for each using Akaike information criterion.

As sex was previously reported to influence foraging behaviour and space usage (Clay et al., 2020), and to improve interpretability and reduce the possibility of model overfitting, all combinations of covariates were fitted for males and females separately. To determine the effect of boldness on time-activity budgets (Patterson et al., 2017), we plotted stationary probability distributions as a function of wind speed, split by relative wind direction (tail-, cross- and headwind), for each sex and the two extremes of boldness score.

2.4.2 | Effect of personality on reproductive success

Annual reproductive success (the probability that a pair fledges their single chick) has been previously reported not to vary with boldness

in wandering albatrosses (Patrick & Weimerskirch, 2015). Given our larger and more recent dataset, we aimed to confirm this was still the case by fitting the effect of boldness and the quadratic effect of age, as well as their interaction, to annual reproductive success using a binomial GLMM. We included random effects terms representing individual and year to account for repeated measures and potential annual effects, respectively.

3 | RESULTS

We obtained 510 foraging trips from 294 wandering albatross (males: 148, females: 146) breeding on Crozet Island (46°24′ S; 51°46′ E), with an average of 1.7 ± 1.1 (1 SD) trips per individual, and a mean of 1066 ± 664 (1 SD) behavioural transitions per trip. Birds across the range of estimated boldness scores and across years foraged in similar locations and experienced similar wind conditions (Figure 2; Supporting Information).

Our best supported model for females retained the two-way interaction between wind speed and wind direction, as well as the two-way interaction between wind speed and boldness, while for males the best supported model retained the two-way interaction between wind speed and wind direction as well as the fixed effect of boldness (Table 1). These results suggest that while boldness influenced transition probabilities in both sexes, this was only mediated by wind conditions in females. Both wind direction and wind speed were important in movement decisions for both sexes, with travel dominating in strong crosswinds, search in strong headwinds and rest in strong tailwinds (Figure S3).

We first examined whether the decision to take off and commence flight depended on boldness. For females, the probability of take-off (i.e. transition from rest to search) increased with wind speed, and individuals across the boldness range showed similar responses (Table 2). On average, shyer males were marginally more likely to take off into flight than bolder males.

Overall, we found that the probability of transitioning between behaviours varied with boldness, with shyer birds of both sexes being more likely to remain in or switch to search states while bolder birds were more likely to remain in or switch to travel states (Figure 3; Table 2). For female birds, these transition probabilities additionally depended on wind speed. In low–mid wind speeds, shyer birds showed greater preference for search states compared to bolder birds. However, as wind speeds increased, both shyer and bolder females became increasingly likely to transition from search to travel states, with minimal differences between the boldness types at high wind speeds (Figure 3).

We used the stationary probability distributions (i.e. the equilibrium of the Markov process) of the best-supported models to illustrate time-activity budgets across the range of wind speeds experienced by foraging albatrosses (Figure 4; Table 3). In all wind speeds and directions, bolder males and females prioritised exploratative behaviour (i.e. travel over search; Figure 4). Shyer males and females conversely prioritised exploitative behaviour (i.e. search over travel), and further, for shyer females this depended on wind speed. While in low- to mid-wind speeds, shyer females showed a preference for search states, as wind speed increased this preference switched, such that they spent more time in travel states and ultimately converged on similar preferences to bolder females.

We found no effect of boldness on annual breeding success ($z = -0.64$, $p = 0.52$).

While our focus was on behaviour at the extremes of the distribution of boldness scores, the behavioural responses (transition estimates and stationary probabilities) for all individuals in the population are presented in Figures S4 and S5.

4 | DISCUSSION

Across species, the degree to which behavioural plasticity varies among individuals is unclear. We show that boldness influences

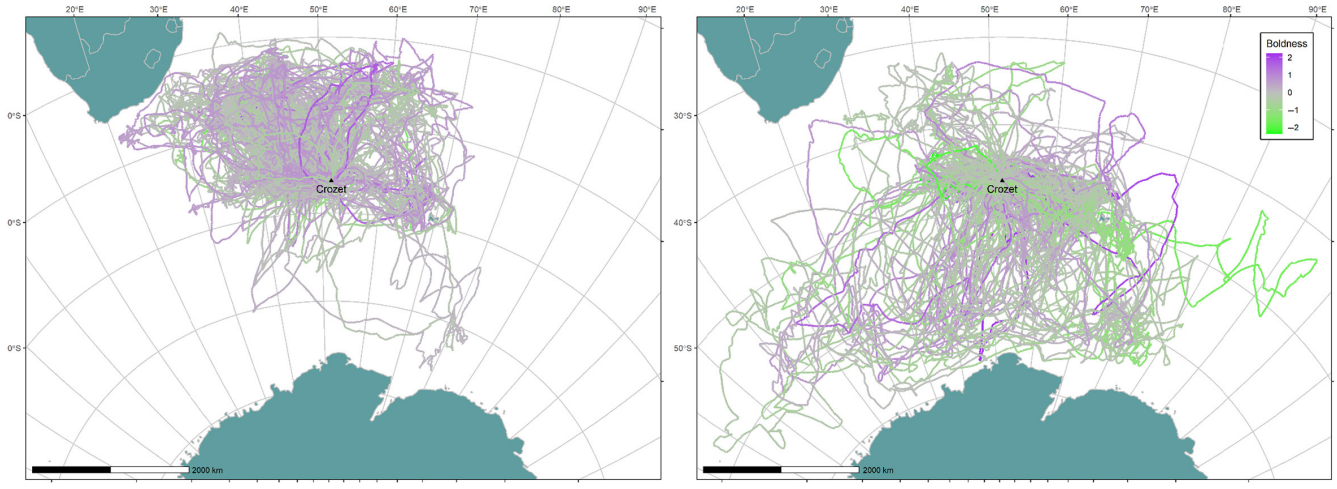

FIGURE 2 Foraging trips of incubating wandering albatross *Diomedea exulans* from Crozet Islands (black triangle). Left = female tracks; right = male tracks). Trips coloured according to individual boldness scores (purple = bolder; green = shyer). Map displayed in the Azimuthal Equal Area projection, centred on Crozet.

TABLE 1 Model selection tables showing the top 10 best-supported candidate hidden Markov models examining the effect of covariates on the transition probabilities of foraging albatross from Crozet Island of different boldness scores.

Sex	Formula	*N*	ΔAIC	AIC
Male	**LoD + WindSp + WindDir + bold + WindSp^{a}WindDir**	**5**	**0.00**	**904,792.76**
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindDir^{a}bold	6	7.79	904,800.55
	LoD + WindSp + WindDir + WindSp^{a}WindDir	4	40.18	904,832.93
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}bold	6	339.74	905,132.50
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}bold + WindDir^{a}bold	7	342.92	905,135.68
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindDir^{a}bold + WindSp^{a}WindDir^{a}bold	7	344.27	905,137.03
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}WindDir^{a}bold	6	344.58	905,137.33
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}bold + WindDir^{a}bold + WindSp^{a}WindDir^{a}bold	8	354.37	905,147.13
	LoD + WindSp + WindDir + bold	4	864.54	905,657.30
	LoD + WindSp + WindDir + bold + WindSp^{a}bold	5	865.09	904,792.76
Female	**LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}bold**	**6**	**0.00**	**1,133,250.08**
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}bold + WindSp^{a}WindDir^{a}bold	7	2.24	1,133,252.32
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}bold + WindDir^{a}bold	7	4.65	1,133,254.73
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindSp^{a}bold + WindDir^{a}bold + WindSp^{a}WindDir^{a}bold	8	8.46	1,133,258.54
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindDir^{a}bold	6	16.10	1,133,266.17
	LoD + WindSp + WindDir + bold + WindDir^{a}bold + WindSp^{a}bold	6	20.70	1,133,270.78
	LoD + WindSp + WindDir + bold + WindDir^{a}bold	5	21.40	1,133,271.47
	LoD + WindSp + WindDir + bold	4	33.84	1,133,283.92
	LoD + WindSp + WindDir + bold + WindSp^{a}bold	5	34.70	1,133,284.77
	LoD + WindSp + WindDir + bold + WindSp^{a}WindDir + WindDir^{a}bold + WindSp^{a}WindDir^{a}bold	7	38.52	1,133,288.60

Note: Best supported models in bold. *N* = number of model parameters. Bold = mean-centred boldness score for all birds.

Abbreviations: ΔAIC, change in Akaike information criterion from the best supported model; AIC, Akaike information criterion; LoD, factor indicating daylight or darkness; WindDir, wind direction relative to bird trajectory; WindSp, wind speed, taken at 10 m above sea level.

[a]Interaction between covariates.

TABLE 2 Predicted probabilities of transitioning from rest to search, search to travel or travel to search, for bolder and shyer wandering albatrosses, split by sex. Female estimates given for wind speed categories within crosswinds (90° to bird trajectory); male estimates given for crosswinds and mean wind speed experienced (9 ms^{-1}). 95% confidence intervals are given in square parentheses.

	Females					Males	
	Shyer			Bolder			
Transition	Low (<5 ms^{-1})	Mid (5–10 ms^{-1})	High (>10 ms^{-1})	Low (<5 ms^{-1})	Mid (5–10 ms^{-1})	High (>10 ms^{-1})	Shyer	Bolder
Rest–search	0.11 [0.10, 0.12]	0.16 [0.15, 0.16]	0.27 [0.24, 0.29]	0.11 [0.10, 0.12]	0.15 [0.15, 0.16]	0.25 [0.22, 0.27]	0.20 [0.19, 0.21]	0.19 [0.18, 0.20]
Search–travel	0.12 [0.11, 0.13]	0.13 [0.13, 0.14]	0.15 [0.14, 0.16]	0.17 [0.16, 0.18]	0.16 [0.15, 0.16]	0.18 [0.16, 0.19]	0.12 [0.11, 0.12]	0.14 [0.14, 0.15]
Travel–search	0.14 [0.13, 0.15]	0.13 [0.13, 0.14]	0.12 [0.11, 0.13]	0.13 [0.12, 0.14]	0.13 [0.13, 0.14]	0.13 [0.12, 0.14]	0.13 [0.12, 0.13]	0.11 [0.10, 0.11]

transitions between behavioural states in albatrosses and that for females, boldness additionally influences the plasticity of these transitions in response to wind speed. Bolder individuals were more likely to switch to or remain in travel states, an explorative behaviour, while shyer individuals showed the opposite trend, tending to invest in search, an exploitative behaviour. In weaker winds, bolder and shyer females diverged slightly in transition probabilities such that shyer females invested primarily in search. However, in strong winds, which are most favourable for soaring flight, both ends of the boldness spectrum converged on investment in travel, ultimately reducing individual differences in foraging behaviour. Our results add to a growing and taxonomically-diverse body of literature showing personality-related differences in plasticity, including birds (Beauchamp, 2001; Dingemanse et al., 2012; Verbeek et al., 1994), mammals (Hessing et al., 1994; Koolhaas et al., 1999), reptiles (Rodríguez-Prieto et al., 2011) and even gastropods (Salerno & Kamel, 2023), highlighting that among-individual differences can have significant consequences for how animals deal with environmental change.

We focused on transitions between search and travel, which are likely to represent trade-offs between exploitative and explorative behaviour (Dall et al., 2004; Mehlhorn et al., 2015; Patrick et al., 2017), and therefore should show consistent inter-individual variation associated with boldness (Mathot et al., 2012). Bolder females consistently prioritised travel (48% overall time budget), and spent more time in this state with increasing wind speed (low to high winds = 37% increase in travel). Conversely, shyer females prioritised search in weaker winds (42% overall time budget), but as wind speeds increased, were more likely to transition to travel, ultimately converging on similar probabilities as bolder females (shyer birds = 54% of time budget; bolder birds = 56% of time budget). Such differences may be underlain by differences in variance sensitivity, as per the speed-accuracy trade-off (Mathot et al., 2012; Sih & Del Giudice, 2012; Spiegel et al., 2017; Wolf et al., 2008). Shyer animals are expected to prioritise consistent gains by reducing uncertainty about their environment (Groothuis & Carere, 2005; Wolf et al., 2008). By investing time in sampling foraging patches, shyer birds may gain information about local conditions and prey distribution that allows them accurately match their behaviour to the environment, ensuring stable payoffs. Conversely, bolder birds appeared to take a faster approach to foraging, gaining variable rewards without paying the costs of information gathering and processing. By prioritising travel in all conditions, bolder individuals may minimise the opportunity costs of remaining at a single foraging patch by giving up some immediate patches to increase the probability of encountering new patches elsewhere (Charnov, 1976; Ventura et al., 2020; Viswanathan et al., 2008).

Despite this, all individuals were more likely to take-off into flight in strong winds, suggesting that bolder individuals still mediate their behaviour relative to wind in a cost-effective way. Trade-offs weaken when the perceived cost-to-benefit ratio of a behaviour decreases, for example due to favourable conditions (Gotthard, 2000; Välimäki & Kaitala, 2007) or increased resource availability (Boggs & Ross, 1993), leading to reduced individual perceptual differences.

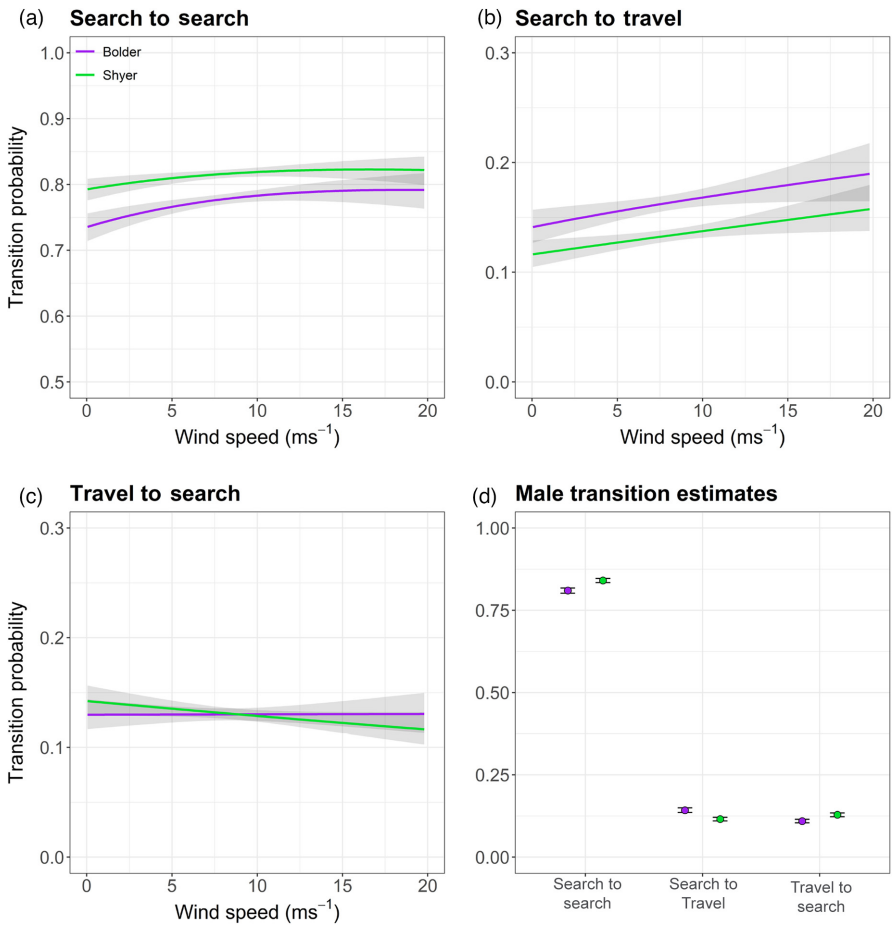

FIGURE 3 Model-estimated transition probabilities derived from hidden Markov models for foraging wandering albatrosses of different boldness estimates, separated by sex. (a–c) Female transition probabilities as a function of wind speed, calculated for crosswinds (90° to bird trajectory). (d) Male transition probabilities as a function of boldness, separated by transition type, calculated for a crosswind and mean wind speed (9 ms^{-1}) experienced. Estimates are shown as separate lines for the 10th and 90th percentiles of boldness scores (purple lines = bolder; green lines = shyer). Grey shaded areas (a–c) and error bars (d) indicate 95% confidence intervals.

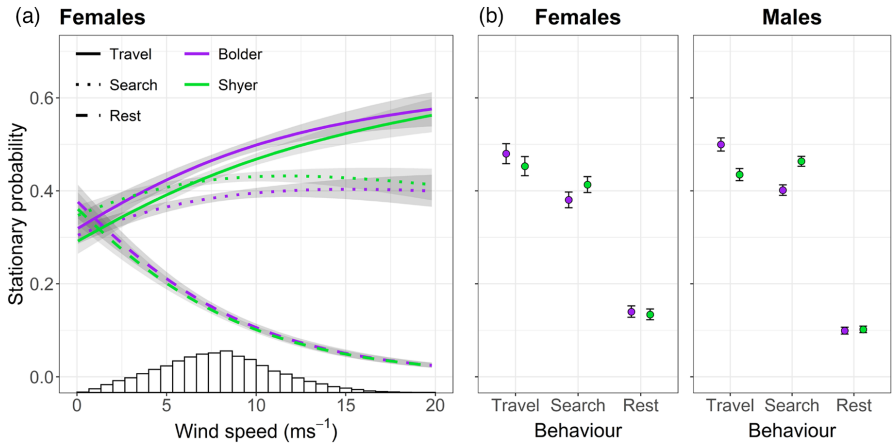

FIGURE 4 Model-estimated stationary probabilities of being in each of three behaviours for (a) given values of wind speed for female wandering albatross (solid = travel, dotted = search, dashed = rest) and (b) as a function of boldness alone. Predictions were generated for a crosswind (both panels; 90° to bird trajectory) and mean wind speed (panel b; 9 ms^{-1}) experienced across the dataset. Probability estimates are estimated separately for the 10th and 90th percentiles of boldness scores, which were retained in the best supporting HMM for both males and females (purple = shyer; green = bolder). Grey shaded areas (a) and error bars (b) indicate 95% confidence intervals. The stationary probability distribution remains unchanged as time progresses, and therefore can be used as a proxy of time-activity budgets.

Consequently, individual differences in behaviour should reduce when conditions overwhelmingly favour a particular strategy. Indeed, our findings suggest that for females, boldness-related behavioural differences were more pronounced in winds that are energetically inefficient for movement, that is weak winds.

Individuals in a stable environment may employ different plasticity strategies while maintaining long-term fitness outcomes, resulting in weak selection on personality (Sih & Del Giudice, 2012). However, this may not remain the case when environmental conditions change. When environments change, animals have three

TABLE 3 Predicted stationary probabilities for travel, search and rest states, for bolder and shyer wandering albatrosses, split by sex. Female estimates given for wind speed categories within crosswinds (90° to bird trajectory); male estimates given for crosswinds and mean wind speed experienced (9 ms^{-1}). 95% confidence intervals are given in square parentheses.

	Females						Males	
	Shyer			Bolder				
Behaviour	Low (<5 ms^{-1})	Mid (5–10 ms^{-1})	High (>10 ms^{-1})	Low (<5 ms^{-1})	Mid (5–10 ms^{-1})	High (>10 ms^{-1})	Shyer	Bolder
Travel	0.34 [0.31, 0.36]	0.43 [0.41, 0.44]	0.52 [0.40, 0.54]	0.38 [0.35, 0.41]	0.47 [0.45, 0.48]	0.55 [0.52, 0.58]	0.43 [0.41, 0.44]	0.51 [0.49, 0.53]
Search	0.38 [0.37, 0.40]	0.42 [0.42, 0.44]	0.43 [0.40, 0.45]	0.33 [0.31, 0.35]	0.38 [0.36, 0.39]	0.40 [0.37, 0.42]	0.47 [0.46, 0.49]	0.39 [0.38, 0.40]
Rest	0.28 [0.25, 0.31]	0.15 [0.14, 0.16]	0.05 [0.05, 0.06]	0.29 [0.27, 0.32]	0.16 [0.15, 0.17]	0.06 [0.05, 0.07]	0.10 [0.09, 0.11]	0.10 [0.10, 0.11]

options—disperse, adjust through plasticity or adapt through genetic change (Wong & Candolin, 2015). When change is rapid, behavioural adjustment is usually the first response, as genetic adaptation is limited by its long timescale and dispersal may also be limited by physical or geographical limitations (Caplat et al., 2016; Clobert et al., 2004; Moore et al., 2008). Behavioural plasticity may therefore provide an extinction escape route for populations experiencing rapid environmental change (Sih, 2013; Vinton et al., 2022), as observed in populations of great tits (Charmantier et al., 2008), collared flycatchers (Przybylo et al., 2000) and red squirrels (Réale et al., 2003). At an individual level, variation in plasticity might mean subsets of the population are unable to adjust to new conditions, ultimately leading to important demographic change (Sih, 2013; Tuomainen & Candolin, 2011; Wong & Candolin, 2015). Our findings lend tentative empirical support to this theory, showing that individual variation in plasticity may play a relatively unexplored role in determining population vulnerability to rapid environmental change.

Changes in wind patterns in the Southern Ocean have already been linked to alterations in foraging distribution ranges in wandering albatrosses, with individuals moving southwards to coincide with strengthening Westerly winds (Weimerskirch et al., 2012). Our findings suggest that these changes could affect individuals differently depending on their boldness. Females forage in more northerly locations where this southerly movement of wind may be more important (Weimerskirch et al., 2012). While shyer females adjusted responsively to wind conditions, bolder birds expressed comparatively fixed behaviour, and may therefore be exposed to suboptimal conditions—or alternatively are less affected by these. We did not observe a link between personality and breeding success in wandering albatrosses, which may indeed suggest that the impacts of suboptimal conditions are reduced for bolder birds. However, differences in responsiveness could have fitness consequences in poor environmental conditions if these exacerbate boldness-mediated trade-offs in foraging behaviour. Such a relationship between reproductive success, boldness and year quality has been observed in the closely related black-browed albatross (Patrick & Weimerskirch, 2014), and suggests that in poor environments, personality-related differences could lead to differential fitness outcomes.

We found no difference in wind responsiveness in male albatrosses, possibly due to sex differences in morphology. Males are 20% larger than females and have higher wing loading (mass per unit wing area) despite their longer wingspans (Shaffer et al., 2001). The resultant increased costs of flapping flight, particularly take-off, mean they are constrained to seek out areas with strong winds that minimise movement costs (Clay et al., 2020; Wakefield et al., 2009). This lack of variation in wind conditions may mean there is minimal residual variation in movement decisions for boldness to show an effect. Within the sexes, differences in behavioural responses between bolder and shyer birds cannot be explained by similar morphological differences, as comparisons of body mass and wing chord (a proxy for wing size) against boldness showed no relationship (Supporting Information).

Our results demonstrate that individual-level trade-offs in foraging may be both more pronounced and have greater consequences in

suboptimal environmental conditions. Shyer females showed somewhat greater responsiveness to changes in wind conditions, which may indicate greater plasticity for these individuals during foraging flight. However, both bolder and shyer females converged on travel behaviour in conditions that allow for efficient flight, that is, strong winds. While behavioural plasticity might allow species to compensate for rapid environmental change (Chevin et al., 2010; Draghi & Whitlock, 2012), we demonstrate that this may not be ubiquitous across individuals within populations. Incorporating consistent individual traits, such as boldness, into species vulnerability modelling may enable a more comprehensive prediction of population responses to climate change.

AUTHOR CONTRIBUTIONS

Natasha Gillies designed the study, performed the analyses and wrote the manuscript. Henri Weimerskirch and Samantha C. Patrick conducted the data collection and designed the study. Jack Thorley, Thomas A. Clay, Lucía Martina Martín López and Rocío Joo helped design the study and perform the analyses. Mathieu Basille helped to perform the analyses. All authors reviewed and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and scripts supporting the results and analyses can be accessed on Zenodo at https://doi.org/10.5281/zenodo.5753023 (Gillies, 2021).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Additional figures, analyses, and methodological information relating to the article.

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