

Research article

Relative brain size is associated with natal dispersal rate and species' vulnerability to climate change in seabirds

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The cognitive buffer hypothesis proposes that species with larger brains (relative to their body size) exhibit greater behavioural flexibility, conferring an advantage in unpredictable or novel environments. Therefore, behavioural flexibility – and relative brain size – are likely to be important predictors of a species' vulnerability to anthropogenic pressures and, ultimately, extinction risk. However, current evidence linking brain size to species' vulnerability and extinction risk is inconclusive. Furthermore, studies examining the relationship between relative brain size and behavioural flexibility have mainly focused on foraging innovations, whilst other forms of behavioural flexibility remain unexplored. In this study, we collate species-specific information and examine links between relative brain size, rates of natal and adult dispersal (a measure of flexibility in breeding site fidelity), vulnerability to six anthropogenic threats and extinction risk for 131 species of seabird. We focused our study on seabirds, a highly threatened group that displays large variation in both relative brain size and dispersal behaviour. We found a significant positive relationship between relative brain size and natal dispersal rate, suggesting that relative brain size could enhance flexibility in breeding site choice in seabirds, consistent with the cognitive buffer hypothesis. However, this relationship does not persist when we consider adult dispersal, possibly reflecting constraints imposed by mate selection and knowledge transfer in seabirds. We also show that relative brain size is negatively associated with vulnerability to climate change. These findings have immediate application for predicting interspecific variation in species' vulnerability to climate change and identifying priority species for conservation.

Keywords: climate change, cognitive buffer hypothesis, dispersal rate, extinction risk, relative brain size, seabirds

Introduction

The 'cognitive buffer hypothesis' proposes that species with larger relative brain sizes (i.e. brain size relative to body size) display greater behavioural flexibility and enhanced survival in variable or novel environments (Allman et al. 1993, Sol 2009). Although



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the exact neural mechanism is yet to be fully elucidated, a larger relative brain size appears to confer an improved ability both to alter existing, and generate new behaviours, as well as increase the accuracy of decision-making (Lefebvre et al. 1997, Sol et al. 2005, Lefebvre and Sol 2008). Across both primates and birds, a larger relative brain size has been associated with expressions of behavioural flexibility, such as increased frequency of feeding innovations and an enhanced capacity for social learning (Lefebvre et al. 1997, Timmermans et al. 2000, Reader and Laland 2002, Lefebvre et al. 2004). It has also been associated with a species' ability to inhabit and thrive within variable environments (Sayol et al. 2016a, Vincze 2016, Fristoe et al. 2017).

Evidence that a larger relative brain size and greater behavioural flexibility enhances survival probability in novel or variable environments (Sol and Lefebvre 2000, Sol et al. 2002, 2008, Sayol et al. 2016a, Vincze 2016, Fristoe et al. 2017) suggests that species with larger brains may also show greater adaptive capacity to anthropogenic threats, including land use change and climate change (Sih et al. 2011). The association between behavioural flexibility and a species' vulnerability to anthropogenic threats has recently been more formally examined across avian groups, showing that species displaying a greater number of feeding innovations (i.e. the use of novel foraging methods or the addition of novel foods into the diet) are less sensitive to the effects of habitat destruction (Ducatez et al. 2020). Similarly, long-term population trends of British farmland birds show that species with smaller relative brain sizes are more likely to experience declines in response to large-scale habitat alteration (Shultz et al. 2005). A relatively larger brain size is also one of the traits that explain tolerance to urban environments (Callaghan et al. 2019, Sayol et al. 2020). However, clear evidence of an association between relative brain size and species' extinction risk is lacking in birds (Nicolakakis et al. 2003), in part because behavioural flexibility might be able to help species to respond to some threats but not others (Ducatez et al. 2020).

Multiple forms of behavioural flexibility, including novel predator avoidance strategies and plastic foraging, are expected to minimise extinction risk by reducing vulnerability to anthropogenic threats (Ratcliffe et al. 2006, Lapiedra et al. 2018). Dispersal is also recognised as an important mechanism influencing a species' ability to adapt to environmental change (Clobert et al. 2012, Travis et al. 2013). Dispersal encompasses both natal, i.e. the movement of immature individuals from their natal site, as well as adult dispersal, i.e. the movement of breeding individuals to new breeding sites. In seabirds, juveniles spend multiple years prospecting alternative breeding sites and gathering information on site quality, including local reproductive success (Reed et al. 1999, Campioni et al. 2017), whilst adults must decide whether to remain faithful to their current breeding colony (Danchin et al. 1998, Fernández-Chacón et al. 2013, Ponchon et al. 2015a). Dispersal propensity, equivalent to a species' flexibility in breeding site location, and therefore a form of behavioural flexibility, is likely to be of

particular relevance to a species' ability to persist in variable and heterogeneous environments (Ganter and Cooke 1998, Clobert et al. 2012, Cristofari et al. 2019). Obligate site-fidelity suggests limited behavioural flexibility in this trait and is likely to be maladaptive for species inhabiting areas exposed to anthropogenic disturbance or environmental degradation (Péron et al. 2010, Dolný et al. 2013). By contrast, species with greater flexibility in breeding site location are possibly better able to respond to environmental change by seeking alternative breeding sites and relocating to higher quality habitat.

As a measure of a species' flexibility in breeding location, dispersal rate may be expected to correlate with relative brain size. To date, the association between relative brain size and behavioural flexibility has primarily been explored in the context of feeding behaviours (Lefebvre et al. 1997, Timmermans et al. 2000, Reader and Laland 2002), as opposed to other types of behaviour, such as dispersal. However, empirically measuring natal and adult dispersal is challenging. Mark-recapture methods require data collection over a large spatial scale, with large samples needed at each site if rates of dispersal are low (MacDonald and Johnson 2001). An improved understanding of the intrinsic traits, such as brain size, that may influence interspecific variation in dispersal could therefore prove valuable for predicting species-specific variation and increasing the taxonomic representation of dispersal information (Horswill et al. 2019).

Seabirds – defined in this study as a group that rely on marine environments – are typically characterised as being highly philopatric. However, this group exhibits significant interspecific variation in both natal and adult rates of dispersal (Coulson 2016). Seabirds are also highly threatened and considered vulnerable to threats across marine and terrestrial environments, including bycatch in longline fisheries and predation by invasive species (Dias et al. 2019). Many species are also highly vulnerable to climate change (Reynolds et al. 2015, Dias et al. 2019), as well as other marine pressures, including offshore renewable energy developments (Furness et al. 2013). Lifespan, diet and habitat breadth have previously emerged as predictors of seabird species-specific vulnerability to anthropogenic threats (Richards et al. 2021). Relative brain size, as a proxy for behavioural flexibility (e.g. dispersal rate), thus represents an additional biological mechanism that may be influential in determining the vulnerability and future extinction risk of these species.

In this study, we collate species-specific information on relative brain size, natal and adult dispersal rate, vulnerability to six anthropogenic threats and global extinction risk for 131 species of seabird. We examine links between these variables whilst accounting for life-history factors that may also influence dispersal rates and relative brain size (i.e. time to prospect different colonies and maternal investment). In line with previous studies demonstrating that a larger relative brain size confers increased behavioural flexibility, we expect seabird species that have larger relative brain sizes to be more likely to switch breeding site if local conditions (e.g. habitat quality, food availability) deteriorate or if conditions

are superior at alternative breeding sites. Therefore, we also expect these species to exhibit higher dispersal rates and lower vulnerability to anthropogenic threats and extinction.

Material and methods

Data collection

Brain and body size characterisation

We collated published estimates of brain size (g) for 131 species of seabird (Iwaniuk and Nelson 2003, Fristoe et al. 2017, Sayol et al. 2018, 2020). Here, we considered seabirds as a group of birds that rely on marine environments and include the Sphenisciformes, Procellariiformes, Phaethontiformes, Suliformes (excluding darters) and certain Charadriiformes (auks, skuas, gulls and terns). Brain size estimates were generated from the measurement of adult skulls in museum collections using the endocast method (Iwaniuk and Nelson 2002). This involves filling an empty skull with lead shot or glass microballons, which are then weighed to provide a value for skull volume and converted to an estimate of brain size (g). Seabirds exhibit delayed recruitment and select the site of their first breeding attempt at maturity (i.e. at full body size), therefore we consider adult brain size values to be applicable to the study of both natal and adult dispersal. For each species, multiple specimens were measured (mean = 7.9, SD = 3.4) and a mean value was calculated to provide a single, species-specific brain size estimate. We excluded species with brain size estimates for fewer than four specimens to minimise sampling biases. We also ensured that all species were represented by both male and female specimens, minimizing biases associated with sexual dimorphism. The sexes of the specimens used to calculate brain size estimates were provided in the datasets obtained from the literature and where they were not, we asked the authors of the datasets to provide this information. To account for the allometric relationship between brain and body size, we also obtained the body size values (g) associated with the museum specimens used to measure brain size, when available. For specimens where body size data was unavailable, we obtained species mean values from the Handbook of avian body masses (Dunning 2008) or from the Birds of the World (Billerman et al. 2020).

Natal and adult dispersal rates

For the 131 species of seabird with brain size estimates, we collated data on natal and adult dispersal rates by conducting a systematic literature search using the online database, Web of Science. We specified the species Latin binomial in the first topic search field and the terms 'prospecting OR natal dispersal OR breeding dispersal OR adult dispersal OR emigration OR immigration OR philopatry OR nest-site fidelity' in the second topic search field. Search fields were joined by the term 'AND'. A search using the same terms was also performed using Google Scholar to access grey literature, including PhD theses and reports, and selecting those that included the search terms in the title or abstract.

The literature search generated a total of 793 papers and reports and from these we extracted natal and adult dispersal rates. Here, natal dispersal is defined as the annual proportion of fledglings recruiting into a colony different from their natal colony, and adult dispersal is defined as the annual proportion of adults relocating to a new breeding colony. Where available, we also recorded the sex and age class of the group for which the estimate was made. The ability to estimate demographic parameters with mark–recapture data significantly increases with between five and ten years of data (Horswill et al. 2018). Therefore, to standardise the estimation of dispersal rates, we limited the final dataset to studies based on mark–recapture analysis with more than eight years of data. The final dataset included dispersal estimates from 47 studies and 29 species. For studies that provided multiple dispersal rate estimates, i.e. for different adult age classes or for males and females ($n = 9$), we calculated a species' mean value.

Additional life-history traits

To examine other possible drivers of dispersal, we collated information on relevant life-history traits. As many life-history traits are highly correlated (Stearns 1992), we focused this analysis on age at first breeding and fledging time. We selected age at first breeding to reflect the species-specific time that is available to prospect different colonies, and fledging time to reflect maternal investment. We extracted values for these traits from Birds of the World (Billerman et al. 2020). Where multiple species-specific values were provided for age at first breeding, we calculated the mean weighted by the percentage of individuals that had bred by each age. Where a range was provided for fledging time, we took the midpoint. For three species, *Larus ridibundus*, *Spheniscus humboldti* and *Sterna paradisaea*, information on one or both life-history traits was not included in Birds of the World and was obtained from the literature (Lemmetynen 1973, Prévot-Julliard et al. 2001, Valdés-Velasquez et al. 2013).

Although morphological traits associated with mobility, such as wingspan, are determinants of dispersal distance in other avian taxa (Dawideit et al. 2009), many seabird species migrate over large distances and make long foraging trips (Egevang et al. 2010, Clay et al. 2017). Consequently, such traits are less likely to influence natal and adult dispersal in seabirds and so were not included in analyses.

Species' extinction risk and threats

To test how relative brain size is related to extinction risk and species level vulnerability to different threat types, we extracted a species' threat status from the IUCN Red List database (www.iucnredlist.org, IUCN 2020) and their vulnerability to six relevant anthropogenic threats listed under the Threats Classification Scheme (ver. 3.3, IUCN 2020). The six anthropogenic threats we considered were: climate change, biological resource use (e.g. fishing), human intrusions and disturbance, invasive species, energy production and mining, and pollution. Threat vulnerability was classified as: 'vulnerable' or 'not vulnerable'. In addition, to assess

whether relative brain size could be a useful predictor of species' extinction risk, we obtained a species' global threat status from the IUCN Red List of Threatened Species (IUCN 2020). We used the IUCN classifications to group species into two broader categories of extinction risk. Here, species classified as Critically Endangered (CR), Endangered (E) and Vulnerable (V) were defined as 'threatened', and species listed as Near threatened (NT) and Least concern (LC) were defined as 'non-threatened'. We extracted vulnerability and threat status information for all 131 species of seabird with brain size data.

Data analysis

We conducted all data analysis in R ver. 4.0.3 (www.r-project.org).

Relative brain size and life-history values

To account for the allometric effect of adult body size on brain size, we calculated relative brain size as the residual from a log-log relationship between brain and body size. We used the same method to control for the effect of body size on the life history traits included in our analysis and obtain relative values for age at first breeding and fledging time. In birds, a larger relative brain size has been shown to reflect a disproportionate enlargement of pallial regions (Sayol et al. 2016b) and an increased proportion of pallial neurons (Sol et al. 2022), both of which are linked to enhanced behavioural plasticity (Overington et al. 2009, Sol et al. 2016, 2022). Although there are multiple methods to estimate relative brain size, the use of residuals from a log-log regression between brain and body size has emerged as one of the most commonly used, as one can account for the effect of body size on brain size (as a predictor) whilst including other predictors affecting the response variable. The alternative method of using both brain and body size as predictors could cause issues of collinearity and a failure to account for the effect of body size on the predictors (Sol et al. 2016, Smeele 2022). However, in models where brain size is modelled as a response, we test log-transformed brain size as a function of log-transformed body size and other predictors.

Relative brain size and age-specific dispersal rate

To examine phylogenetic non-independence between species, we constructed a PGLS model (R-package *caper*, Orme 2018). Here, the expectation was that closely related species are likely to have more similar rates of natal and adult dispersal. We used a maximum clade credibility tree for all avian species with the Ericson backbone (Jetz et al. 2012) pruned using the R-package *phytools* (Revell 2012) to include only the species of interest. Because species with estimates for natal dispersal ($n=21$) were different to those with estimates of adult dispersal ($n=21$), it was necessary to examine phylogenetic signal separately for each age class. We measured the effect of phylogenetic signal on the relationship between relative brain size and dispersal rate using the Pagel's lambda (λ) value provided by the PGLS models

(Pagel 1999). In both models, Pagel's lambda was calculated using a maximum likelihood method and was estimated to be zero, indicating no detectable phylogenetic signal, such that it was not necessary to account for phylogenetic non-independence (Revell and Harmon 2022). Therefore, to examine the relationship between relative brain size and age-specific dispersal rates we used a multiple linear regression. Here, mean dispersal rate was the response variable and relative brain size and dispersal type (natal or adult) were included as explanatory variables. We also included an interaction between relative brain size and dispersal type, and fixed effects for the two life-history traits that may also influence dispersal rates and relative brain size (i.e. relative age at first breeding and relative fledging time). To assess possible multicollinearity between the explanatory variables in our model, we calculated variance inflation factors (VIF) (R-package *car*, Fox and Weisberg 2019). All VIF values were < 2 , suggesting multicollinearity did not pose an issue. The assumptions of a linear model were also checked and supported using the R-package *car* (Fox and Weisberg 2019). To test the robustness of our results to the use of residual brain size, we also ran a PGLS model with log-transformed brain size as a response variable and both log-transformed body size and dispersal rate as predictors (Supporting information). We also performed a sensitivity analysis using the *infly_phylm* function from the *sensiPhy* (ver. 0.8.5) R-package (Paterno et al. 2020) to identify the data points with the greatest influence on the model. Removal of two potentially influential data points did not qualitatively alter the results (Supporting information).

Relative brain size and species' extinction risk

To determine whether relative brain size could be used to predict species' vulnerability to different anthropogenic threats, we examined the relationship between relative brain size and species-specific risk (i.e. vulnerable and not vulnerable) for all 131 seabird species with brain size data. To account for possible phylogenetic non-independence between species, we constructed a PGLS model to examine this relationship between brain size and species-specific risk, using log-transformed brain size as a function of log-transformed body size and extinction risk categories. We also repeated this analysis to examine the relationship between brain size (while accounting for body size) and our grouped extinction risk categories (i.e. threatened or non-threatened).

Results

Of the 131 seabird species with data on both brain and body size, we obtained dispersal estimates for 29 species. Specifically, we obtained natal dispersal rates for 21 species from five families: *Alcidae*, *Laridae*, *Phalacrocoracidae*, *Procellariidae* and *Spheniscidae*, and adult dispersal rates for a different subset of 21 species from seven families: *Alcidae*, *Laridae*, *Pelecanoididae*, *Phalacrocoracidae*, *Procellariidae*, *Spheniscidae* and *Stercorariidae* (Table 1).

Table 1. Summary of the number of species with published estimates of natal or adult dispersal by family. Seabird families listed alphabetically.

Dispersal type	Family	No. of species
Natal	<i>Alcidae</i>	5
	<i>Laridae</i>	11
	<i>Phalacrocoracidae</i>	1
	<i>Procellariidae</i>	3
	<i>Spheniscidae</i>	1
Adult	<i>Alcidae</i>	4
	<i>Laridae</i>	10
	<i>Pelecanoididae</i>	1
	<i>Phalacrocoracidae</i>	1
	<i>Procellariidae</i>	2
	<i>Spheniscidae</i>	2
	<i>Stercorariidae</i>	1

Relative brain size and age-specific dispersal rate

We found that the relationship between dispersal rate and relative brain size differed with age class, i.e. natal versus adult. Natal dispersal had a significant positive relationship with relative brain size (intercept = 0.55, slope = 1.38 ± 0.47 (SE), $t_{36} = 2.48$, $p < 0.01$) (Fig. 1), whilst adult dispersal was not significantly related to relative brain size (intercept = 0.15, slope = 0.21 ± 0.39 (SE), $t_{36} = 0.54$, $p = 0.59$) (Fig. 2).

We observed a large degree of variation in natal dispersal rates across species (SD = 23.12). For example, snow petrel *Pagodroma nivea* had the largest relative brain size and a

dispersal rate of 0.87, whilst Brünnich's guillemot *Uria lomvia* had the smallest relative brain size and exhibited almost total philopatry with an estimated dispersal rate of 0.0006. In contrast, we observed less interspecific variation in adult dispersal rates (SD = 12.11), with 90% of species exhibiting a dispersal rate between 0.03 and 0.30.

We did not identify a significant relationship between dispersal rate (natal and adult) and the two life history traits, relative age at first breeding (slope = -0.07 ± 0.08 (SE), $t_{36} = -0.85$, $p = 0.40$) and relative fledging time (slope = 0.06 ± 0.07 (SE), $t_{36} = 0.91$, $p = 0.37$). Furthermore, including these life-history factors in the PGLS regression model did not remove the significant relationship between relative brain size and natal dispersal rate.

Relative brain size and threat vulnerability

Using data for all 131 seabird species, we examined the relationship between relative brain size and a species' vulnerability status to six different anthropogenic threats. We identified that species vulnerable to climate change exhibited significantly smaller relative brain sizes (difference = -0.14 ± 0.06 (SE), $t_{129} = -2.22$, $p = 0.04$) (Table 2, Fig. 3A). However, we did not find a significant association between relative brain size and the five remaining threats, i.e. biological resource use, human intrusions and disturbance, invasive species, energy production and mining, and pollution (Table 2, Fig. 3B–F).

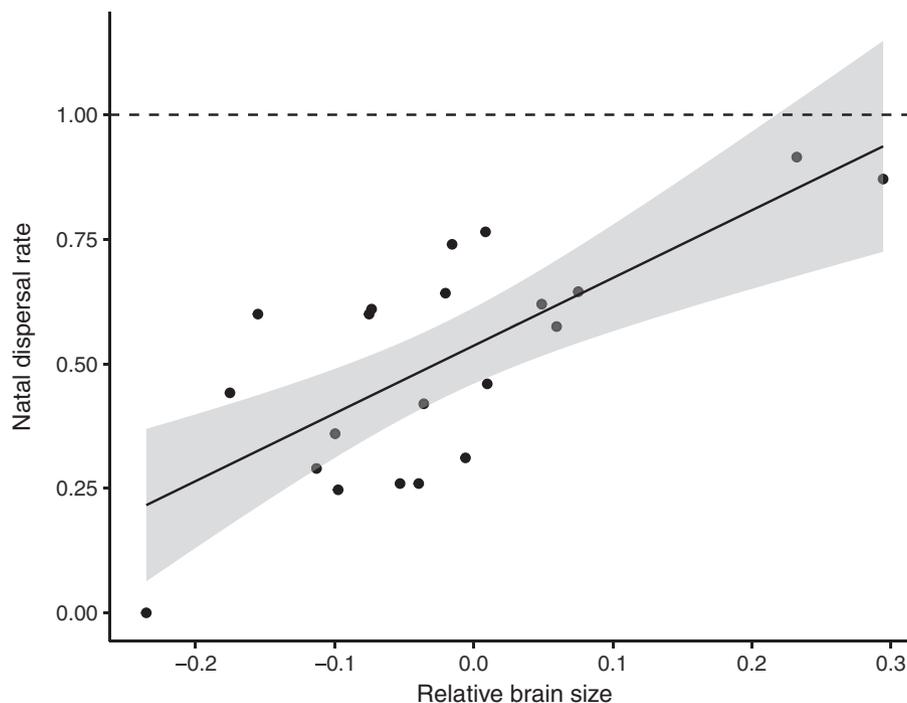


Figure 1. Relationship between relative brain size and natal dispersal rate. Species-specific natal dispersal in seabirds increases with relative brain size ($p < 0.01$, $R^2 = 0.68$). Fitted line from the phylogenetic generalised least squares (PGLS) regression shown as solid black line. Each data point represents the species-specific mean natal dispersal rate ($n = 21$). Relative brain size values greater than zero indicate a brain size greater than that expected for a species body size, and values less than zero indicate a brain size less than that expected based on a species body size. Horizontal dashed line at maximum dispersal rate.

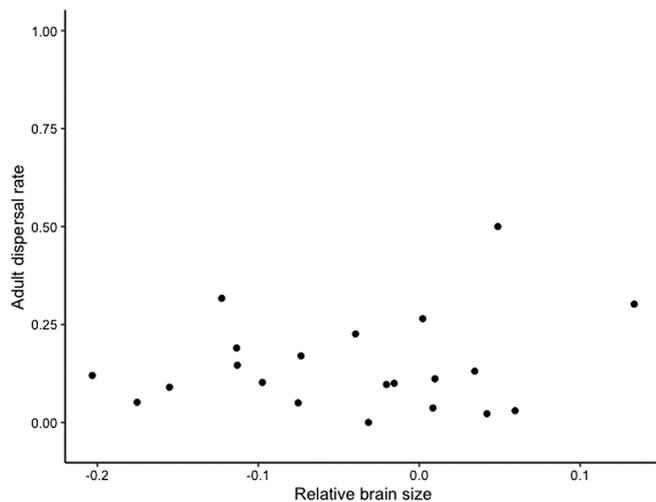


Figure 2. Relationship between relative brain size and adult dispersal rate. Species-specific adult dispersal in seabirds was not significantly related to relative brain size ($p=0.59$). Each data point represents the species-specific mean adult dispersal rate ($n=21$). Relative brain size values greater than zero indicate a brain size greater than that expected for a species body size, and values less than zero indicate a brain size less than that expected based on a species' body size.

Relative brain size and extinction risk

Of the 131 seabird species with estimates of relative brain size, 89.3% ($n=117$) were categorised as 'non-threatened' and 10.7% ($n=14$) were categorised as 'threatened'. However, we did not identify a significant relationship between relative brain size and global extinction risk (difference = -0.04 ± 0.08 , $\tau_{129} = -0.49$, $p=0.62$).

Discussion

In this study, we identify a positive relationship between relative brain size and natal dispersal rate, demonstrating that seabirds with larger relative brain sizes have greater flexibility in breeding site selection, i.e. lower philopatric site fidelity. Furthermore, we find that species of seabird with smaller relative brain sizes are more vulnerable to climate change, consistent with the predictions of the cognitive buffer hypothesis that a larger relative brain size confers increased survival in

changing environments. This study suggests that relative brain size could be a useful proxy to predict species' natal dispersal propensity, as well as an indicator of a species' vulnerability to future climate change.

Species with a larger relative brain size are assumed to possess a greater capacity for complex decision-making and information processing (Lefebvre and Sol 2008, Benson-Amram et al. 2016) and the findings presented here suggest that a larger relative brain size also supports elevated rates of natal dispersal. Selection of a breeding colony is a cognitively complex task, requiring an ability to assess local reproductive conditions (Forbes and Kaiser 1994, Reed et al. 1999), make use of public information (Boulinier et al. 2008) and compare alternative colonies. These links are further supported by an association between brain size and nest-site selection in common eider *Somateria mollissima* (Jaatinen and Öst 2016). The positive association between relative brain size and natal dispersal shown here indicates a potential mechanistic link underpinning a species' propensity for philopatry.

Even though dispersal is recognised as a determining factor in a species' adaptive capacity to environmental change (Clobert et al. 2012, Travis et al. 2013), the difficulties in empirically measuring this trait means that it is often oversimplified or omitted from models predicting global species' responses to environmental change (Ponchon et al. 2015b, Tobias and Pigot 2019). Consequently, there would be advantages to using a more easily obtainable proxy, and a predictable relationship between natal dispersal rate and relative brain size suggests relative brain size could be used to understand interspecific variation for this age class. Evaluating the relationship between brain size and dispersal in other taxa would help elucidate the wider taxonomic relevance of this finding, although studies will be limited by the availability of dispersal estimates. For example, although we performed an extensive literature review, we identified reliable estimates of natal dispersal rates for just 21 seabird species. Our dataset of natal dispersal is limited for groups with very large (e.g. *Diomedidae*) and very small (e.g. *Pelecanoididae*) mean relative brain sizes and further investigations would benefit from obtaining dispersal rate estimates in these species. Additionally, extrinsic factors can differentially influence groups of individuals within populations of seabirds (Wood et al. 2021) and evidence of sex-biased dispersal in seabirds (Hall et al. 2009) suggests future analyses may also

Table 2. Results from a phylogenetic generalised least squares (PGLS) regression model examining the relationship between brain size (while accounting for body size) and a species' vulnerability to various anthropogenic threats. $R^2=0.96$ and $\lambda=0$. Significantly influential threats are highlighted in bold.

Response	Predictor	Estimate (SE)	t-value	pvalue
Log (brain size)	Intercept	-2.16 (0.19)	-11.28	0.04
	Log (body size)	0.58 (0.03)	16.73	< 0.001
	Climate change	-0.14 (0.06)	-2.22	0.04
	Biological resource use	0.08 (0.09)	0.95	0.36
	Invasive species	0.04 (0.06)	0.61	0.55
	Pollution	0.04 (0.06)	0.68	0.50
	Human intrusions and disturbance	-0.01 (0.08)	-0.14	0.89
	Energy production and mining	0.06 (0.08)	0.75	0.47

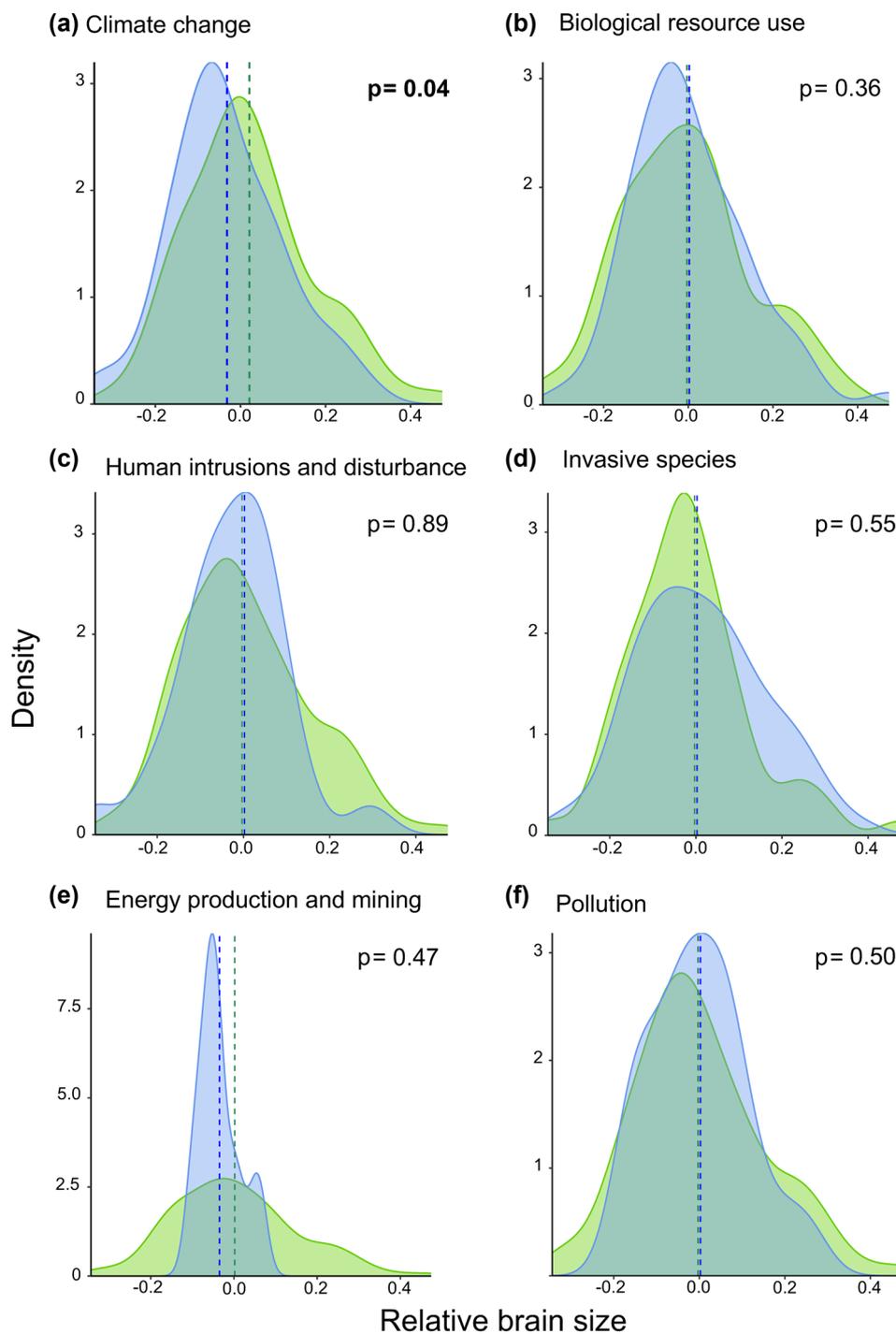


Figure 3. Density distributions of relative brain size where blue represents species 'vulnerable' to the threat and green represents species 'not vulnerable' to the threat for six different anthropogenic threats (A–F). Dotted lines represent the mean relative brain size for each group. Significant p-values are highlighted in bold.

benefit from considering sex-specific relationships between dispersal rates and brain size.

The positive relationship between relative brain size and natal dispersal was not replicated for adults. Published estimates of adult dispersal rates (range = 0.00–0.50) displayed considerably less interspecific variation compared to natal dispersal rates (range = 0.00–0.91). Limits to adult dispersal

may be imposed by the costs of losing familiarity when switching to a novel colony. For example, individuals breeding at the same site acquire local knowledge regarding predator behaviour and resource location (Greenwood and Harvey 1982, Pärt 1995). Therefore, adult dispersal incurs time and energy costs, possibly accompanied by missed breeding opportunities if individuals fail to obtain a nest-site or mate

(Danchin and Cam 2002). By contrast, local knowledge loss is unlikely to constrain natal dispersal as seabirds have an extended immature period to prospect different colonies and the ability to acquire breeding-relevant information in the days before fledging is limited (Steiner and Gaston 2005).

Seabirds typically display strong mate fidelity, such that high site fidelity is thought to ensure mate reunion at the beginning of the reproductive season (Cézilly et al. 2000, Bried et al. 2003). It is notable that, of the species considered here, those with the highest adult dispersal rates are also those with high divorce rates. For example, adult dispersal rates are comparatively higher in little penguin *Eudyptula minor* (0.26) (Rogers and Knight 2006) and Cassin's auklet *Ptychoramphus aleuticus* (0.32) (Pyle et al. 2001), which also display elevated divorce probabilities: 0.5 (Chiaradia 1999) and 0.45 (Pyle et al. 2001), respectively. The role of breeding site fidelity in enabling mate reunion may constrain adult dispersal rate even in species with a large relative brain size, thereby offering an additional explanation for the similarity in adult dispersal rates across seabirds with differing relative brain sizes.

Species' life-history traits could potentially confound an association between brain size and dispersal rate. Age at first breeding has a significant effect on dispersal distance in passerines (Paradis et al. 1998), although these species have considerably faster life-histories and earlier ages of first breeding than seabirds. Maternal investment, measured here using fledging time, has also been linked to brain size in avian groups, as well as chondrichthyans and primates (Iwaniuk and Nelson 2003, Barton and Capellini 2011, Mull et al. 2020). We did not identify a significant relationship between dispersal (natal or adult) and relative age at first breeding or fledging time in seabirds, and the identified relationships between dispersal and brain size remain unaltered when including these life-history traits in analyses. Therefore, rather than an indirect relationship mediated by life-history strategy, relative brain size itself appears to be one of the factors determining dispersal propensity in seabirds.

As posited by the cognitive buffer hypothesis, larger relative brain sizes should enhance behavioural flexibility, conferring a survival advantage in variable environments (Sol 2009, Sayol, Maspons et al. 2016). Although global studies indicate that behavioural flexibility is associated with reduced extinction risk (Ducatez et al. 2020), we did not identify a significant association between relative brain size and overall extinction risk in seabirds. This finding agrees with previous studies that have also failed to find a significant association between relative brain size and extinction risk in birds (Nicolakakis et al. 2003). However, it may also be necessary to consider possible dataset biases. Currently, 31% of seabird species are listed as threatened (Dias et al. 2019), but just 11% of the 131 species in our dataset have this status, such that threatened species were underrepresented in our analysis. Obtaining brain and body size estimates for threatened seabirds currently lacking published estimates is therefore a priority.

Global extinction risk is determined by a species' exposure to a diverse range of threats but the resilience conferred by behavioural flexibility, and therefore relative brain size, is likely

threat-specific (Ducatez et al. 2020). This may explain the lack of a significant association when considering overall extinction risk but the presence of a significant association when specific threats are considered. When extinction risk is partitioned into the different anthropogenic pressures that seabirds experience, we find a significant negative association between relative brain size and a species' vulnerability to climate change. This is consistent with the cognitive buffer hypothesis whereby species with a larger relative brain size are better able to cope in changing environments (Sol 2009) and respond to climate change (Baldwin et al. 2022). This finding also supports the relationship between relative brain size and natal dispersal; whereby species with smaller relative brain sizes and lower rates of natal dispersal experience increased vulnerability to climate change because they cannot easily respond as local environmental conditions become unsuitable. We acknowledge that we cannot confirm that individuals switch colonies solely due to a change in the condition of their natal or current breeding site. However, we assume this to be the case as previous studies have identified this as a key driver of seabird dispersal (Danchin et al. 1998, Fernández-Chacón et al. 2013).

Links between relative brain size and flexibility in feeding behaviours have been repeatedly identified (Lefebvre et al. 1997, 2004, Overington et al. 2009), such that the association between climate change vulnerability and brain size identified here cannot conclusively be attributed to flexibility in natal site fidelity alone. Flexibility in foraging strategies (i.e. location and prey type) are also likely to be beneficial for mitigating climate driven alterations in prey availability. For example, short- and long-term dietary changes have been identified in seabirds in response to changing availability of key prey species (Waluda et al. 2012, Howells et al. 2017). Plasticity in seabird foraging range, trip duration and breeding investment have also been shown in response to changes in local prey availability (Horswill et al. 2017, Campbell et al. 2019). Understanding the links between flexibility in seabird foraging strategies and relative brain size may therefore also prove valuable for further determining the utility of brain size as a proxy for species' vulnerability.

The absence of a relationship between relative brain size and threats such as 'human intrusion and disturbance' or 'invasive species' is consistent with previous work demonstrating that behavioural flexibility in feeding does not mitigate these threats (Ducatez et al. 2020). Visualisation of mean relative brain sizes suggests a possible difference for species threatened by 'energy production and mining' (Fig. 3E). Offshore renewable energy developments threaten seabirds through collision mortality and displacement from foraging habitats. A proposed link between variability in behavioural responses and vulnerability to such threats (Furness et al. 2013, Bradbury et al. 2014) suggests brain size may play a role. However, it may be that the treatment of species' vulnerability as a binary variable is too simplistic. The proportion of the population affected (i.e. scope) and overall declines caused (i.e. severity of the threat) may provide a more nuanced assessment in future analyses.

Several limitations have been suggested regarding the use of species-level relative brain size as a proxy for behavioural flexibility, which may challenge our conclusions. For instance, brain size estimates may differ across datasets due to intraspecific variation (Hooper et al. 2022), such that measurement of additional specimens would provide more robust species-average values, even for species with available brain size estimates. In this study, we tried to minimize this potential bias by focusing on species with larger sample sizes and for which male and female specimens were measured. Additionally, some studies suggest that the use of whole brain size data may overlook variation across individual regions of the brain specialized to certain cognitive functions (Healy and Rowe 2007, Logan et al. 2018). However, there is increasing evidence in birds that larger brains (relative to body size) result from a disproportionate increase in the size of pallial regions linked to domain-general cognition and behavioural flexibility (Sayol et al. 2016b, Sol et al. 2022). Nevertheless, future studies could still benefit from including more specific measures of cognitive capacity, for example the number of neurons in different regions of the brain (Sol et al. 2022). Although this data is currently limited to just a few species, the majority of which are terrestrial birds (Olkowicz et al. 2016, Sol et al. 2022), future research could further explore the cognitive basis of dispersal flexibility in seabirds when more information is available. Where possible, future analyses would also be strengthened by considering the role of spatial and temporal variation in brain size (Hooper et al. 2022) and its link with dispersal (Horswill et al. 2022) and threat severity (Genovart et al. 2018).

Conclusions

In this study, we demonstrate a positive association between seabird relative brain size and natal dispersal rate, a form of behavioural flexibility that has not previously been considered in this context. However, this relationship was not replicated for adult dispersal, possibly reflecting constraints imposed by mate selection and knowledge transfer in seabirds. Our findings could position relative brain size as a useful proxy for natal dispersal rate, a trait that is challenging to estimate empirically. We also provide initial evidence that seabird species with larger relative brain sizes are less vulnerable to climate change, indicative of an enhanced ability to respond to environmental change and consistent with predictions based on the cognitive buffer hypothesis. Understanding the intrinsic traits that underlie species' vulnerability is important in developing future evidence-based management policies and identifying species, such as small-brained seabirds, for conservation prioritisation.

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Author contributions

Laurel Constanti Crosby: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Writing – original draft (lead); Writing – review and editing (lead). **Ferran Sayol:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Writing - original draft- Supporting; Writing – review and editing-Supporting. **Catharine Horswill:** Conceptualization (equal); Data curation-Supporting; Writing - original draft-Supporting; Writing – review and editing-Supporting.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpvnv9g> (Constanti Crosby et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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