

## RESEARCH ARTICLE

# Does brain size matter? Linking cognitive and ecological traits to climate change vulnerability in seabirds

Junhyuk Keum<sup>1</sup>  | Ferran Sayol<sup>2</sup>  | Florian Orgeret<sup>3</sup>  | Catharine Horswill<sup>1,4</sup> 

<sup>1</sup>Centre for Biodiversity and Environmental Research, Department of Genetics, Evolution and Environment, University College London, London, UK

<sup>2</sup>Centre for Ecological Research and Forestry Applications (CREAF), Cerdanyola del Vallès, Spain

<sup>3</sup>Marine Apex Predator Research Unit, Department of Zoology, Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha, South Africa

<sup>4</sup>Institute of Zoology, Zoological Society of London, London, UK

**Correspondence**

Junhyuk Keum  
Email: [jhk109@naver.com](mailto:jhk109@naver.com)

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**Abstract**

1. Understanding the mechanisms that increase a species resilience to climate change is central to predicting how they are likely to respond.
2. One determinant of vulnerability to climate change identified in multiple taxa is the thermal range of a species' distribution. In this context, species with narrow thermal ranges are reportedly more vulnerable to climate change. One paradigm for predicting the range of environmental conditions that a species can occupy is the 'cognitive buffer hypothesis'. The cognitive buffer hypothesis predicts that species with larger brain sizes (relative to body mass) display greater behavioural flexibility and are more able to persist and thrive within variable environmental conditions. Following the theory, we expect that species with larger relative brain sizes will occupy broader thermal ranges and be less vulnerable to climate change.
3. In this study, we collate species-specific information for 206 species of seabird. We then use phylogenetic generalised least squares regression and path analysis to quantify and identify linkages connecting relative brain size, thermal range, migration pattern, hand-wing index, foraging behaviour, vulnerability to climate change and extinction risk while controlling for shared ancestry between species. We focused our study on seabirds, a highly threatened group that displays large variation in these variables. Previous work has also proposed that seabird species with a narrower thermal range across their geographic distribution are more likely to be impacted by climate change.
4. Consistent with the cognitive buffer hypothesis, we found that seabird thermal range increases with relative brain size. We also found that having a larger relative brain size or being a long-distance migrant may indirectly reduce extinction risk through a species' thermal range. Additionally, we found that having a higher hand-wing index and employing generalist foraging behaviours reduces seabird vulnerability to climate change and extinction risk.
5. Our study suggests that having a larger relative brain size, being a long-distance migrant, employing generalist foraging behaviour and having a higher hand-wing index can lower extinction risk. Identifying the ecological traits that promote

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species resilience is crucial for determining which species are most at risk of population declines to direct species conservation.

#### KEYWORDS

cognitive buffer hypothesis, extinction risk, relative brain size, seabirds, thermal range

## 1 | INTRODUCTION

Identifying species most vulnerable to climate change is crucial for developing effective conservation strategies to protect biodiversity for the future. Resilience to climate change varies significantly among species, and a growing body of evidence has identified species-specific traits linked to climate change vulnerability (e.g., Graham et al., 2016; Richards et al., 2021). However, as yet, the underlying mechanistic connections between these traits and extinction risk remain largely untested.

The 'cognitive buffer hypothesis' proposes that having a larger brain size, relative to body mass, enables species to survive in novel or unpredictable environments (Allman et al., 1993; Sol, 2009). In birds, a larger relative brain size has been linked to an increased ability to persist and thrive under variable environmental conditions (Fristoe et al., 2017; Sayol, Maspons, et al., 2016; Vincze, 2016). For example, non-migratory passerines inhabiting seasonal fluctuations in climate conditions have larger relative brain sizes than migratory species that move to maintain year-round favourable conditions (Sol et al., 2010). This evidence suggests that birds with larger relative brain sizes may possess greater resilience and adaptive capacity in response to environmental threats (Baldwin et al., 2022; Sih et al., 2011). In agreement, farmland birds with smaller relative brain sizes are more likely to experience population declines following land-use changes (Shultz et al., 2005). Similarly, seabirds with smaller relative brain sizes appear more vulnerable to climate change impacts, potentially due to having lower rates of natal dispersal (Constanti Crosby et al., 2023).

Relative brain size may influence vulnerability to climate change through various ecological mechanisms. Species with larger brains often exhibit generalist niches, such as diverse foraging behaviours, a wide range of prey preferences and broad habitat adaptability (Ducatez et al., 2015; Lefebvre & Sol, 2008). These traits enable them to flexibly adapt their strategies to mitigate adverse conditions (Cooke et al., 2019). In seabirds, species with narrower thermal ranges (i.e. the range of temperatures across their geographic distribution) are considered more likely to be impacted by climate change (Orgeret et al., 2021). Investigating the ecological traits that influence seabird thermal range could therefore support the identification of the key mechanisms underpinning species resilience to future environmental change.

Seabirds represent a highly diverse assemblage of birds that have evolved a wide array of strategies to adapt to environmental variability. These species exhibit considerable variation in range

sizes, from exclusively coastal distributions to trans-equatorial migrations. Likewise, their foraging behaviours vary widely, spanning specialised diving to restricted aerial feeding. Their wing morphology also includes a broad range of structures, from long and narrow to short and broad, highlighting further variations in flight efficiency and dispersal ability (Table S1; Billerman et al., 2022). Seabirds are also among the most threatened avian groups globally, with nearly half of all species (48%) experiencing population declines (BirdLife International, 2022). Climate change poses an increasingly significant threat to these birds (Dias et al., 2019), and previous studies have identified that seabird vulnerability to climate change may be linked to species-specific traits, such as relative brain size (Constanti Crosby et al., 2023) and thermal range (Orgeret et al., 2021). However, the relationships connecting relative brain size, thermal range, migration patterns, and vulnerability to climate change, along with their connection to extinction risk, have yet to be examined within a single, unified framework. Testing these relationships could provide valuable insights into the mechanisms driving seabird resilience or susceptibility to environmental changes.

In this study, we compiled species-specific data on relative brain size, thermal range, migration pattern, foraging behaviour, hand-wing index, vulnerability to climate change and extinction risk for 206 species of seabirds. We first examined the relationship between seabird ecological traits and thermal range. We then employed path analysis to investigate the interplay between different traits, climate change vulnerability and extinction risk. Based on the cognitive buffer hypothesis, our expectation is that species with broader thermal ranges will have larger relative brain sizes and adopt more diverse foraging behaviours. These traits, in turn, are expected to reduce species vulnerability to climate change and lower extinction risk.

## 2 | MATERIALS AND METHODS

### 2.1 | Species data

#### 2.1.1 | Brain size and body mass

We obtained brain size (ml) and body mass (g) estimates for 206 species of seabird. Here, we define seabirds as avian species that rely on the marine environment, including Sphenisciformes, Procellariiformes, Phaethontiformes, Pelecaniformes, Suliformes (excluding darters), certain Charadriiformes (including auks, skuas,

gulls and terns) and certain Gaviiformes (including divers). We collated published brain size estimates for 158 species of seabird (Boire & Baron, 1994; Crile & Quiring, 1940; Franklin et al., 2014; Fristoe et al., 2017; Iwaniuk et al., 2004; Iwaniuk & Nelson, 2003; Ksepka et al., 2020; Mlikovsky, 1989; Sayol et al., 2018; Speroni & Carezzano, 1995; Tsuboi et al., 2018) and collected new brain size estimates for a further 48 species (across 10 families). All estimates were obtained from adult skull specimens using the endocast method (Nelson & Iwaniuk, 2002). This involved filling the cranial cavity of empty skulls with glass micro-balloons via the foramen magnum. The micro-balloons were weighed to provide a value for skull volume that was converted to an estimate of brain size (ml). In birds, a larger relative brain size has been shown to reflect a disproportionate enlargement of pallial regions and an increased proportion of pallial neurons (Sayol, Lefebvre, et al., 2016; Sol et al., 2022), both of which are linked to enhanced behavioural plasticity (Overington et al., 2009; Sol et al., 2016).

All brain sizes were collated as single species-specific mean values. To account for the allometric relationship between brain and body mass, we also obtained available species-specific body mass values (g) associated with the museum specimens used to measure brain size. For specimens where body mass data was unavailable, we obtained species mean values from the Handbook of Avian Body Masses (Dunning, 2008) and Birds of the World (Billerman et al., 2022).

## 2.1.2 | Thermal range

To define the thermal ranges of seabird species, we first identified their geographic distributions using polygons derived from distribution maps provided by BirdLife International (2024). Within these polygons, we excluded the passage areas that reflect migration between breeding and non-breeding ranges. We then extracted and averaged sea surface temperature (SST) data for each  $1^{\circ} \times 1^{\circ}$  grid cell within a species range. We obtained SST data from the Marine Copernicus global reanalysis dataset (phy-001-026 product: <https://catalogue.marine.copernicus.eu/>) for the period January 1993 to December 2018, following Orgeret et al. (2021). For each species, we calculated the 5th and 95th percentiles of SST values across their distribution. The difference between these percentiles was used to define the thermal range (Stuart-Smith et al., 2015).

## 2.1.3 | Migration pattern

To account for potential inflation in the thermal range of migrants associated with the method used to estimate thermal range, we collated data on species-specific migration patterns. We compiled published migration classifications identifying individual species as either 'migrant' or 'resident' (Keogan et al., 2018). Species classified as migrants include long-distance trans-equatorial migrants

and those that spend the winter outside the ocean sector in which they breed. By contrast, we classified species that remain within the same ocean sector year-round as 'residents' (Keogan et al., 2018). Ocean sectors were defined as North Atlantic, Mediterranean, South Atlantic, Southern Ocean–Atlantic, North Pacific, South Pacific, Southern Ocean–Pacific, Indian and Southern Ocean–Indian (Keogan et al., 2018). For species without published migration classifications, we assigned migration patterns based on the distribution maps employed for thermal range estimation (BirdLife International, 2024). For our binary migration pattern variable, residents were assigned a value of 0 and migrants a value of 1.

## 2.1.4 | Hand-wing index

To investigate additional traits that may influence a species' thermal range, we collated data on species-specific hand-wing index from the AVONET database (Tobias et al., 2022). Hand-wing index is a morphological metric associated with wing aspect ratio (Lockwood et al., 1998) that is widely used as a proxy for avian flight efficiency and dispersal ability (Sheard et al., 2020). Among seabirds, diving species such as penguins and cormorants tend to have lower hand-wing index values, reflecting absent or reduced flight efficiency, whereas gliding species like terns and albatrosses typically exhibit higher hand-wing index values. We hypothesise that seabird species with lower hand-wing index values are less mobile and, as a result, their spatial distribution will have a narrower thermal range.

## 2.1.5 | Foraging behaviour

To examine additional drivers potentially influencing a species' thermal range, we collated data on species-specific foraging behaviour. Evidence suggests that generalist foragers are better adapted to highly variable environments (Dehnhard et al., 2019). Based on this, we hypothesise that seabird species employing diverse foraging behaviour could exploit broader thermal ranges. Using descriptions from Birds of the World (Billerman et al., 2022), we identified species as employing one or more of the following four dominant foraging strategies: aerial snatching, plunge diving, surface foraging or surface diving (Pigot et al., 2020). We translated qualitative descriptions into semi-quantitative scores following the methods used in the EltonTraits database (Wilman et al., 2014). For each foraging behaviour, percentage scores were assigned to reflect relative use. Species with a single foraging behaviour accounting for at least 60% of their activity were classified as 'specialist foragers', while those using multiple strategies, with no single behaviour exceeding 60% were classified as 'generalist foragers'. For our binary foraging behaviour variable, specialist foragers were assigned a value of 0 and generalist foragers a value of 1. Full definitions and example species for each foraging behaviour are provided in the Supporting Information (Table S1).

## 2.1.6 | Species vulnerability to climate change and extinction risk

To examine the effects of relative brain size, thermal range and vulnerability to climate change on species-level extinction risk, we extracted vulnerability and threat status data from the IUCN Red List database ([iucnredlist.org](http://iucnredlist.org); IUCN, 2023). Using the Threats Classification Scheme (V. 3.3, IUCN, 2023), we identified whether species are affected by 'Climate Change & Severe Weather' threats. We classified species as vulnerable to climate change if this threat was listed as 'ongoing'. For our binary climate change vulnerability variable, unaffected species were assigned a value of 0 and affected species received a value of 1. To define a species extinction risk, we grouped species into two categories based on IUCN Red List classifications. Species listed as Critically Endangered (CR), Endangered (EN), Vulnerable (VU) and Near Threatened (NT) were classified as 'threatened', while those listed as Least Concern (LC) were classified as 'non-threatened' (Ali et al., 2023). For our binary extinction risk variable, non-threatened species were assigned a value of 0 and threatened species a value of 1. We also repeated our analyses by reclassifying NT species in the 'non-threatened' group, following Constanti Crosby et al. (2023). This adjustment did not qualitatively alter our results, except that it removed a pathway between foraging behaviour and extinction risk indicating that NT seabird species provide support for a link between specialist foraging behaviour and increased threat of extinction (Figure S3).

## 2.2 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Species	206

## 2.3 | Statistical analysis

We conducted all statistical analyses using the program R (v. 4.4.1, R Core Team, 2024).

### 2.3.1 | Relative brain size

To account for the allometric relationship between body mass and brain size, we calculated species-specific relative brain size as the residuals from a log-log regression between brain and body mass (Figure S1). Although there are multiple methods to estimate relative brain size, the use of residuals from a log-log regression between brain and body mass has emerged as one of the most common (e.g., Minias & Podlaszczuk, 2017; Sayol, Maspons, et al., 2016; Sol et al., 2007). This approach also enables the effect of body mass on brain size to be accounted for when including brain size alongside other explanatory variables. The alternative method of using both

brain and body mass as predictors could cause issues of collinearity and thus a failure to account for the effect of body mass on the predictors (Smeele, 2022; Sol et al., 2016). We visually checked that this analysis met the assumptions of a linear model using the 'ncvTest' and the 'durbinWatsonTest' functions from the R package 'car' (v. 3.1.2, Fox & Weisberg, 2019) and the shapiro.test function from the 'stats' package in base R (R Core Team, 2024).

### 2.3.2 | Relationship between relative brain size and thermal range

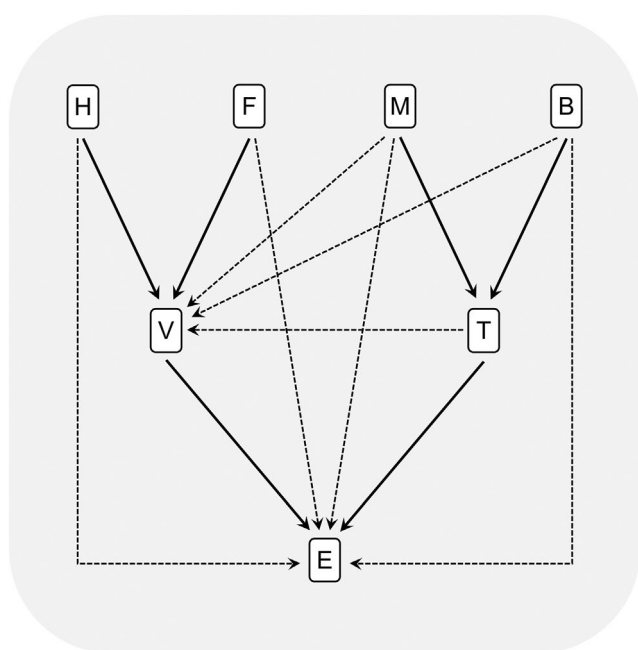
To examine the ecological traits related to seabird thermal range, we used a phylogenetic generalised least squares (PGLS) regression (Grafen, 1989) fitted using the R package 'caper' (v. 1.0.2, Orme et al., 2023). We included relative brain size, migration pattern, hand-wing index and foraging behaviour as explanatory variables. Migration pattern was also included as an interaction effect with relative brain size to test for differences in this relationship between migration strategies. By using a PGLS regression, we were able to account for any phylogenetic non-independence between species (Orme et al., 2013). Here, the expectation was that closely related species are phenotypically more similar and therefore have distributions with similar thermal ranges. We used a maximum clade credibility tree with the Ericson backbone from the complete distribution of trees (10,000 trees) at birdtree.org (Jetz et al., 2012). We pruned the tree to include only the species of interest using the R package 'phytools' (v. 1.9-16, Revell, 2012). We measured the strength of the phylogenetic signal on the relationship between relative brain size and thermal range using Pagel's lambda ( $\lambda$ ) value calculated using maximum likelihood provided by the PGLS regression (Pagel, 1999).

To identify influential explanatory variables in the PGLS regression, we conducted model selection using the R package 'MuMIn' (v. 1.47.5, Barton, 2024). This procedure considered 32 candidate models nested within the initial model that was constructed to have the largest number of explanatory variables (hereon referred to as the 'global model'). The best model was selected based on the second-order Akaike information criterion (AICc) (Burnham & Anderson, 2002). Here, a difference of more than two AICc units was taken to indicate strong support for the model with the lower AICc score (Burnham & Anderson, 2002). To test the influence of migrant species on identified relationships, we also repeated the PGLS regression and model selection process using only resident species ( $n=171$ ). This adjustment did not qualitatively alter our results (Table S4).

### 2.3.3 | Drivers of climate change vulnerability and extinction risk

We examined the relationships connecting the ecological traits (seabird relative brain size, thermal range, migration pattern, hand-wing index and foraging behaviour) to climate change vulnerability and

extinction risk using a multi-level path analyses that also controlled for phylogenetic non-independence (von Hardenberg & Gonzalez-Voyer, 2013). We tested 128 candidate models that included both direct and indirect effects of ecological traits on climate change vulnerability and extinction risk (Figure 1). We included all significant relationships identified in the PGLS regression in the candidate models. We also retained variables that were found to be insignificant in the PGLS regression to test for any potential direct links to climate change vulnerability and extinction risk. In the path analysis, positive relationships between continuous (i.e. relative brain size, thermal range, hand-wing index) and binary variables (i.e. migration pattern, foraging behaviour, climate change vulnerability and extinction risk) indicate that as the continuous variable increases, there is an increased tendency towards the binary factor assigned a value of



**FIGURE 1** The general framework illustrating all candidate models embedded in the path analysis. We ran 128 models; solid arrows indicate pathways that were included in all models, and dotted arrows indicate pathways that were included in different combinations. Variable notation: hand-wing index (H), foraging behaviour (F), migration pattern (M), relative brain size (B), vulnerability to climate change (V), thermal range (T) and extinction risk (E).

**TABLE 1** Model selection based on AICc identified one best candidate phylogenetic generalised least squares regression model for describing seabird thermal range (Model 1). Models within 2 AICc units of the best candidate model are shown. The global model, including all explanatory variables, was not within 2 AICc units of the best model.

Model no.	Model	df	Log likelihood	AICc	$\Delta$ AICc	Weight
1	B + M	3	-169.766	345.7	0.00	0.250
2	B + M + B $\times$ M	4	-169.139	346.5	0.83	0.165
3	B + M + F	4	-169.204	346.6	0.96	0.155
4	B + M + H	4	-169.547	347.3	1.64	0.110

Note: Notation: relative brain size (B), migration pattern (M), interaction between relative brain size and migration pattern (B  $\times$  M), foraging behaviour (F) and hand-wing index (H). df is degrees of freedom and  $\Delta$ AICc is the difference in AICc units from the best candidate model.

1. For migration pattern, this was 'migrants'; for foraging behaviour, this was 'generalist foragers'; for vulnerability to climate change, this was species identified as 'vulnerable'; and for extinction risk, this was species categorised as 'threatened'.

The path analysis was conducted in program R using the package 'phylopath' (v. 1.1.3, van der Bijl, 2018). We used the d-separation method to filter out disqualified candidate models. We combined the *p*-values of the conditional independencies in each candidate model to quantify Fisher's C statistic that reflects the goodness-of-fit to the data according to methods in Shipley (2000). The Fisher's C statistic can be approximated to a  $\chi^2$  distribution with  $2k$  degrees of freedom, where  $k$  is the number of conditional independencies in the model. Thus, a C statistic with a *p*-value  $>0.05$  indicates that the conditional independencies are met, and the model can be considered a candidate model (Shipley, 2000). We then compared the remaining different, non-nested models using the means of the C statistic information criterion (CIC; von Hardenberg & Gonzalez-Voyer, 2013). The CIC is analogous to the AIC, whereby the smallest CIC value represents the best candidate model. The explanatory power of the links between variables was calculated by standardised path coefficients. Slopes were averaged by the weight of the model following the standardisation of all variables, and variables that did not display a link in a given model were assigned a value of zero (Symonds & Moussalli, 2011). We display the best candidate model, and for comparison, we also detail the averaged model from models within 2 CICc units of the best candidate model and some sensitivity testing in the Supporting Information (Figure S2).

### 3 | RESULTS

#### 3.1 | Relationship between relative brain size and thermal range

The best candidate PGLS regression model for describing inter-specific variation in seabird thermal range retained relative brain size and migration pattern (Table 1, model 1). The sum of model weights confirmed the high importance of migration pattern (AICc sum of weights = 1, Table 2), as well as relative brain size (AICc sum of weights = 0.94, Table 2). We identified that species with broader thermal ranges were likely to be migrants and have larger relative brain sizes (Table 3; Figure 2). The value of Pagel's lambda indicated a moderate phylogenetic signal ( $\lambda = 0.42$ ).



TABLE 2 Relative importance for each variable within the phylogenetic generalised least squares regression models.

	Migration pattern	Relative brain size	Foraging behaviour	Relative brain size × migration pattern	Hand-wing index
Sum of weights	1.00	0.94	0.37	0.36	0.31
Number of models containing variable (max=32)	12	12	10	4	10

TABLE 3 Effect sizes for the explanatory variables retained in the best candidate phylogenetic generalised least squares regression model describing interspecific variation in seabird thermal range (Model 1, Table 1). Estimates are unstandardised effect sizes.

Variable	Estimate	Standard error	t-Value	p-Value
Intercept	2.31	0.16	14.43	<0.001
Migration	0.53	0.11	4.93	<0.001
Relative brain size	0.66	0.25	2.66	<0.01
Adjusted $R^2 = 0.12$ , $p$ -value < 0.001				

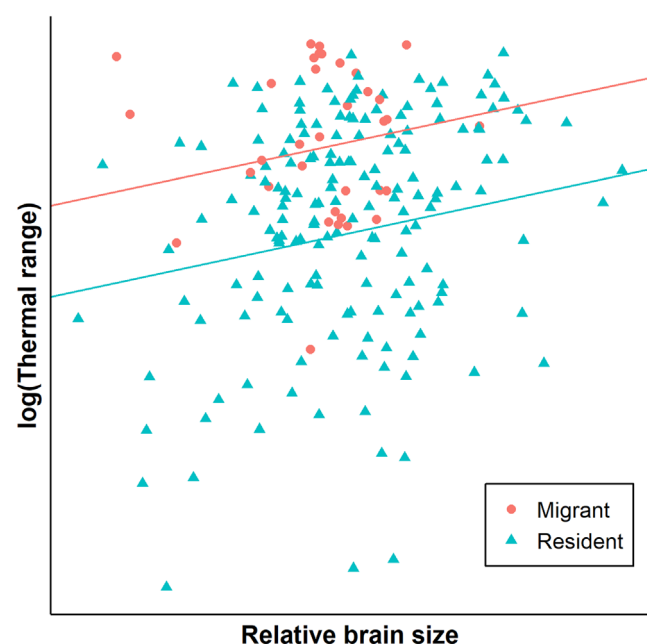
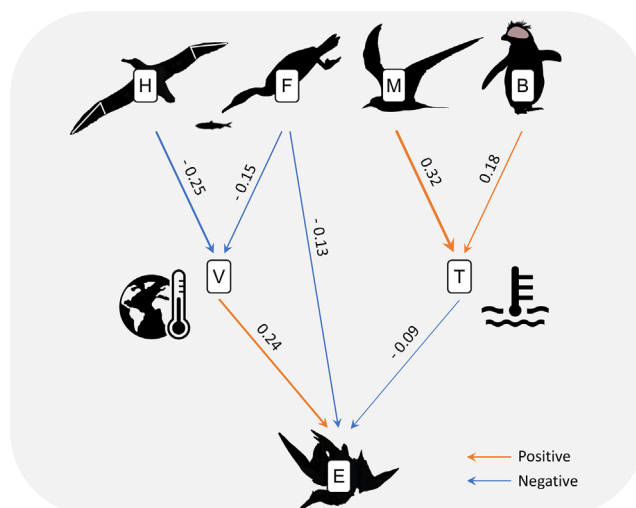


FIGURE 2 Seabird thermal range was positively related to relative brain size and migration pattern. Each data point reflects a seabird species. Orange circles indicate resident species, blue triangles indicate migrant species.

### 3.2 | Drivers of climate change vulnerability and extinction risk

The phylogenetic path analysis identified that migrant species and species with larger relative brain sizes have broader thermal ranges, confirming the results from the PGLS (Figure 3). Results from the path analysis also suggest that the migration pattern may have a stronger correlation with thermal range, compared with relative brain size

FIGURE 3 The best candidate model from the multi-level path analysis. Numbers adjacent to arrows indicate the standardised path coefficients. Variable notation: hand-wing index (H), foraging behaviour (F), migration pattern (M), relative brain size (B), vulnerability to climate change (V), thermal range (T) and extinction risk (E). Arrow thickness reflects the strength of the relationship based on the slope coefficient ( $\beta$ ):  $-0.09 \leq \beta \leq 0.09$  (thin);  $-0.19 \leq \beta \leq -0.10$  or  $0.1 \leq \beta \leq 0.19$  (medium);  $-0.29 \leq \beta \leq -0.20$  or  $0.2 \leq \beta \leq 0.29$  (thick);  $\beta \leq -0.3$  or  $\beta \geq 0.3$  (extra thick). Arrow colour reflects the direction of the relationship: blue—negative, orange—positive.

(Figure 3; Table 3). Having a broad thermal range was also weakly associated with a lower extinction risk, such that the migration pattern and relative brain size are potentially indirectly linked to extinction risk through thermal range. Here, migrant species and those with larger relative brain sizes have broader thermal ranges, which are associated with a lower extinction risk. We did not identify a significant relationship between thermal range and climate change vulnerability. By contrast, the variables not identified as significantly affecting thermal range in the PGLS regression (i.e. hand-wing index and foraging behaviour) were significantly correlated with climate change vulnerability. Here, species with a higher hand-wing index and employing generalist foraging behaviours were identified as being less vulnerable, with hand-wing index potentially providing greater explanatory power. Climate change vulnerability was also positively linked to extinction risk, such that hand-wing index and foraging behaviour are potentially indirectly linked to extinction risk through climate change vulnerability (Figure 3). Additionally, we found a weak direct relationship between foraging behaviour and extinction risk, such that species employing generalist foraging behaviours are potentially less threatened (Figure 3).

## 4 | DISCUSSION

In this study, we investigated the ecological traits that influence seabird thermal range and examined the ecological pathways potentially connecting seabird relative brain size, thermal range, migration pattern, hand-wing index and foraging behaviour to climate change vulnerability and extinction risk. We found that seabird thermal range increases with relative brain size and is larger for migrant species. We also found that having a larger relative brain size and being a long-distance migrant may indirectly reduce a species' extinction risk by contributing to a broader thermal range. Additionally, we found that employing generalist foraging strategies and having a larger hand-wing index may indirectly reduce a species' extinction risk via vulnerability to climate change. These findings indicate key ecological traits and relationships that can aid in imputing missing trait data (e.g. Horswill et al., 2019, 2021) and assessing the conservation status of 'Data Deficient' species ([iucnredlist.org](https://www.iucnredlist.org/); IUCN, 2023), as well as those that are difficult to monitor empirically, such as the Pincoya storm petrel (*Oceanites pincoyae*) and white-vented storm petrel (*Oceanites gracilis*) (Kindsvater et al., 2018).

Finding a positive correlation between seabird thermal range and relative brain size aligns with the predictions of the cognitive buffer hypothesis that species with larger relative brain sizes are better equipped to deal with variable environmental conditions (Sayol, Maspons, et al., 2016; Schuck-Paim et al., 2008; Sol, 2009; Sol et al., 2010). However, the combination of larger thermal ranges and larger brain sizes for migratory species contrasts with previous findings in passerines, where non-migratory species inhabiting seasonal climates tend to have larger relative brain sizes compared to migratory species that move to maintain favourable year-round conditions (Sol et al., 2010). In our study, we used the range of temperatures across a species' geographic distribution as a proxy for its thermal range (following Orgeret et al., 2021). It is important to note that long-distance migratory species do not inhabit their entire geographic range year-round and therefore may not experience the full thermal range of SST values. Reassuringly, re-testing the relationship between seabird relative brain size and thermal range using only resident species ( $n=171$ ) strengthened the identified positive correlation between these traits (Table S4.3). However, the method used to define residency, that is, species that remain within the same ocean sector year-round (Keogan et al., 2018), means that the resident group includes coastal species, such as most cormorants (Phalacrocoracidae), as well as species that migrate within ocean sectors, like penguins (Spheniscidae). Further research distinguishing seasonal thermal ranges and incorporating measures of longitudinal and latitudinal range extent is therefore recommended to provide a more nuanced understanding of the relationships connecting relative brain size, thermal range and migration pattern.

In our path analysis, we tested the hypothesis that having a larger relative brain size supports species to have a distribution spanning a broader thermal range (Figure 1). Alternatively, it is possible that a larger relative brain size is a consequence of species travelling greater distances and expanding their thermal ranges. That the

ecological traits showed direct and indirect pathways leading to extinction risk not only reflects the complex nature of the mechanisms underlying seabird adaptations to environmental variability but also suggests that future research testing additional variables could provide valuable insights into the evolutionary factors driving brain size variation.

We were unable to identify a link between seabird thermal range and climate change vulnerability. This result contrasts with previous comparative work on marine vertebrates that suggests species with narrower thermal ranges are more impacted by climate change (Orgeret et al., 2021). The prior study analysed a subset of the species and data included in our study, making ours the most comprehensive investigation to date. However, potential dataset biases still warrant consideration. In our analysis, climate change vulnerability was classified as a binary variable, which may oversimplify this complex phenomenon. Species vulnerability to climate change can encompass multiple aspects, including phenotypic plasticity (Sheridan & Bickford, 2011), dispersal ability (Freeman et al., 2018; Hitch & Leberg, 2007) and genetic diversity (Alberto et al., 2013). We find that hand-wing index, as a proxy for dispersal ability, is associated with seabird resilience to climate change. However, seabird dispersal ability may also reflect plasticity in philopatry, migration pattern, and foraging range (Constanti Crosby et al., 2023; Dunn et al., 2022; Horswill et al., 2017, 2022). Moreover, while 31% of seabird species are listed as vulnerable to climate change (Dias et al., 2019), only 16.5% (34 out of 206) of species in our dataset were classified as such. This bias may limit the ability to identify traits associated with climate change vulnerability, such that a priority for future research is to obtain brain and body size estimates for seabird species that are vulnerable to climate change and that currently lack published data. Finally, climate change is one of five major pressures impacting this group of species (Dias et al., 2019). Future work may benefit from examining the pathways that link ecological traits to vulnerability in other threats, including invasive alien species (Oppel et al., 2022), bycatch in fisheries (Horswill & Manica, 2019; Ramírez et al., 2024), overfishing (Ratcliffe et al., 2015; Sherley et al., 2018) and harvesting (Inch et al., 2024).

We found evidence that species with a higher hand-wing index, that is, soaring species such as albatrosses and terns were less likely to exhibit vulnerability to climate change. This supports the expectation that species with greater dispersal ability are better equipped to mitigate adverse conditions (Freeman et al., 2018; Hitch & Leberg, 2007). However, natal and adult philopatry vary substantially among seabird species with high hand-wing index values (e.g. albatrosses are highly philopatric compared with terns; Constanti Crosby et al., 2023). Incorporating dispersal and philopatry data, where available, could provide a more nuanced understanding of the relationship between hand-wing index and climate change vulnerability. In addition, we found that generalist foragers, which employ a range of foraging behaviours, are more resilient to climate change and have a lower risk of extinction compared with specialist foragers. This finding aligns with previous research on seabirds (Dehnhard et al., 2019; Richards et al., 2021) and other avian groups (Ducatez

et al., 2020), highlighting the adaptive advantage of foraging flexibility in changing environments.

In this study, we found that seabird thermal range increases with relative brain size and that having a larger relative brain size and being a long-distance migrant may indirectly reduce extinction risk through their influence on a species thermal range. Additionally, we found that a higher hand-wing index and employing generalist foraging behaviours reduce vulnerability to climate change and extinction risk. Understanding the ecological traits that enhance species resilience to environmental change is critical for identifying species most at risk of population decline under future climate change scenarios. These findings are essential for predicting changes in species diversity and prioritising conservation efforts for vulnerable species.

## AUTHOR CONTRIBUTIONS

Junghyuk Keum, Catharine Horswill, and Ferran Sayol conceived the ideas and designed the methodology; Junghyuk Keum, Ferran Sayol, and Florian Orgeret collected the data; Junghyuk Keum and Ferran Sayol analysed the data; Junghyuk Keum and Catharine Horswill led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

## DATA AVAILABILITY STATEMENT

Our study brings together data from a number of different sources, including published literature and museum specimens. Data deposited in the Dryad Digital Repository: <http://doi.org/10.5061/dryad.95x69p8wc> (Keum et al., 2025).

## ORCID

Junghyuk Keum  <https://orcid.org/0009-0007-8987-6701>

Ferran Sayol  <https://orcid.org/0000-0003-3540-7487>

Florian Orgeret  <https://orcid.org/0000-0002-1940-7797>

Catharine Horswill  <https://orcid.org/0000-0002-1795-0753>

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## SUPPORTING INFORMATION

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

**Figure S1.** Seabird brain size was positively related to body size.

**Figure S2.** The best candidate model identified by the path analysis shown with the averaged model estimated from models within 2 CICc units of the best candidate model.

**Figure S3.** Path analysis with 'Near threatened' species reclassified as 'non-threatened'.

**Table S1.** Definitions used to assign specialist foraging strategies.

**Table S2.** Number of seabird species with data for each trait.

**Table S3.** List of seabird species in the study.

**Table S4.** Result of phylogenetic generalised least squares regression for resident species.

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