# A SYSTEMATIC REVIEW OF TRENDS IN RESEARCH ON SEABIRD BEHAVIORAL FLEXIBILITY

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**ABSTRACT**

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There has been an increase in interest in the study of behavioral flexibility for its role in how organisms face disturbances and changes in their environment. However, there is not much research on this topic for seabirds, whose conservation status is affected by multiple issues related to changes in their environment. The goal of this paper was to analyze research on seabird behavioral flexibility and to identify knowledge gaps. A systematic review was conducted using academic search engines that included articles published from 1986 to 2022. In the 143 articles that were analyzed, the following were identified: publication date, family and species being studied, annual cycle period, research context and focus, behavioral flexibility components studied, and related environmental issues. The results show that the study of the issue in seabirds increased between 1986 and 2022, especially for the Spheniscidae, Alcidae, and Laridae families. Most studies were conducted in the field during the reproductive period in a parental-care context, mainly focusing on behavioral diversity and personality. In the studies that focused on behavioral flexibility mechanisms, the most-studied components were neophobia and exploration, whereas in the mixed-approach studies, the study of boldness prevailed. The environmental issue that was examined the most was global climate change. Our review shows that, even if the number of studies on seabird behavioral flexibility has increased in the last decade, few of them focus on the links between specific behavioral flexibility components, conservation status, and the environmental issues pertaining to the places where the species live.

**Key words:** behavioral ecology, boldness, conservation, environmental issue, neophobia, marine birds, personality

## INTRODUCTION

Behavioral flexibility implies adjusting a learned behavior in response to changes in local environmental conditions (Coppens *et al.* 2010, Stamps 2016). It allows organisms to build adaptive responses to new environmental conditions (Ricklefs 2004, Sol *et al.* 2005a), and it is a key factor in their capacity to successfully adapt to novel settings and expand their distribution range (Sol *et al.* 2005a, Griffin & Guez 2014, Chow *et al.* 2016). In this sense, research on behavioral flexibility is key to developing management and conservation proposals for species whose conversation status is critical or otherwise requires attention (Caro 2007, Greggor *et al.* 2014).

Behavioral innovation is an expression of behavioral flexibility (Sol *et al.* 2005a), in which several processes and traits determine whether an innovation takes place and how it is established (Tebbich *et al.* 2016). Among these are the capacity for individual and social learning, as well as personality traits such as audacity, neophobia level, and explorative behavior (Reader & Laland 2003, Smith & Blumstein 2008, Cole & Quinn 2012, Griffin & Guez 2014, Tebbich *et al.* 2016). These processes and traits are related to ecological plasticity, which is defined as the capacity of an organism to adapt to a wide array of resources and environmental conditions (Hutchinson 1957, Klopfer & MacArthur 1960). This plasticity can take place through variations in physiology, morphology, and/or behavior according to environmental conditions (Greenberg 1990). In this sense, the adaptation to new niches first takes the form of behavioral changes before morphological adaptations can be adjusted in the population through natural selection. These variations in behavior are more likely to appear in ecologically plastic species (Greenberg & Mettke-Hofmann 2001).

The previously mentioned set of processes and traits reflects the ability of the organisms to respond to changes in food availability, environmental degradation, competitive scenarios, and the presence of a new resource (Greenberg 1990, Sih 2013). Investigating the different aspects of behavioral flexibility allows us to determine how species adjust to changes generated by anthropogenic activities (Greenberg & Droege 1999, Sih *et al.* 2011) and to the resulting new environmental constraints (Sol *et al.* 2005a, 2020). Different studies have shown relationships between a species' capacity for innovation and other attributes like reproductive strategy (Sol *et al.* 2002; Overington *et al.* 2011; Cauchard *et al.* 2013, 2017), trophic generalism (Overington *et al.* 2011), the use of urban environments (Sol *et al.* 2020), and taxa diversification (Nicolakakis *et al.* 2003, Sol *et al.* 2005b).

For the last decade of the study period, there was a noticeable increase in research examining different aspects of behavioral flexibility (Smith & Blumstein 2008, Audet & Lefebvre 2017). However, few of the existing studies focus on seabirds, which include species that have been greatly affected by both global and climate change, which in turn is strongly related to anthropogenic activities (Paleczny *et al.* 2015, Wilcox *et al.* 2015, Paz *et al.*

2018, Carmona *et al.* 2021, Pais de Faria *et al.* 2021, Sydeman *et al.* 2021, Recabarren-Villalón *et al.* 2023). Seabirds include a large number of species categorized as globally threatened, and in the last few decades, they have shown severe population decrease (Butchart *et al.* 2004, Croxall *et al.* 2012, Paleczny *et al.* 2015, Grémillet *et al.* 2018). Chronic deterioration of marine and coastal habitats as well as marine resources has had—and will continue to have—long-term effects on seabirds. Many studies refer to urbanization and deforestation of the marine-coastal environment as the cause of severe changes in coastal ecosystems. Nevertheless, activities such as fishing and unregulated human presence can, for instance, lead to birds abandoning reproductive sites (Yorio *et al*. 2001), being more exposed to predators (Yorio *et al.* 2001), and even stopping the use of winter and replenishment areas (Copello *et al.* 2014). On this basis and considering the implications that behavioral flexibility studies can have on managing and preserving fauna groups, this study aims to analyze research studies on seabird behavioral flexibility and shed light on the main knowledge gaps for this topic.

## METHODS

We conducted a systematic search for peer-reviewed articles on seabird behavioral flexibility, which included publications from March 1986 to December 2022. Three electronic academic search engines were used: SciELO, SCOPUS, and Google Scholar. The search employed the following terms: “seabird” (or “seabirds”) AND “behavioral flexibility” OR “behavioral plasticity”. The search was repeated using “seabirds”. Suitable records were selected using the processing phases for systematic revision established in the PRISMA declaration (Moher *et al.* 2010). The following were discarded: duplicated records, grey literature (books, book chapters, theses, dissertations), scientific reviews, and those articles that did not deal with seabird behavioral flexibility (i.e., articles that used the concept of behavioral flexibility only to define or discuss aspects of the species being studied).

From each selected publication, the following information was extracted for analysis (Table 1): publication year, study location,

**TABLE 1**
**Information selected to characterize publications on seabird behavioral flexibility**

| Variable | Categories | Description |
|---|---|---|
| Publication year | | Year when the article was published |
| Study location | | Country where the study took place |
| Taxon | Family | Seabird family for which behavioral flexibility was analyzed |
| | Species | Seabird species for which behavioral flexibility was analyzed |
| Methodological approach | Field | Studies conducted in reproductive colonies or winter sites |
| | Captivity | Studies that conducted experiments on behavioral flexibility in captivity (i.e., experimental aviaries) |
| Annual cycle period | Reproductive | Studies conducted during the species’ reproductive period |
| | Non-reproductive | Studies conducted during the species’ non-reproductive period |
| Research context | Parental care | Studies that analyzed behavioral flexibility during an incubation or offspring feeding period |
| | Feeding | Studies that analyzed behavioral flexibility in the feeding cycle for individuals |
| | Migration | Studies that analyzed behavioral flexibility during individual migration |
| Approach | Behavioral diversity | Studies that analyzed differences and/or changes in the behavioral patterns of individuals when facing different environmental conditions (i.e., adapting to changes in climate conditions, food availability, and nesting sites) |
| | Behavioral flexibility mechanisms | Studies that analyzed specific components of behavioral flexibility (i.e., neophobia, exploration, individual learning, and innovation) |
| | Mixed | Studies that related behavioral diversity to specific components of behavioral flexibility |
| Components of behavioral flexibility that were studied | Behavioral innovation | Studies that analyzed new behavior acquisition or modification of existing ones |
| | Individual learning | Studies that analyzed individual learning capacity |
| | Personality | Studies that included research on boldness, neophobia, and exploration |
| Related environmental issue | Global and climate change | Studies that related behavioral diversity to variations in the environment as a consequence of global and climate change (i.e., variation on prey availability and habitat because of climate conditions changing) |
| | Urbanization | Studies that focused on behavioral diversity or components of behavioral flexibility in individuals within urban environments |
| | Interaction with anthropogenic activities | Studies that focused on behavioral diversity or components of behavioral flexibility in individuals that are interacting with anthropogenic activities (i.e., fisheries and touristic activities) |

taxon (i.e., family and species being studied), methodological approach (i.e., field or captivity study), the birds' annual cycle period (reproductive or non-reproductive), and the research context in which the study was done (i.e., parental care, feeding, or migration). We also classified the articles into three categories according to the method used to study behavioral flexibility: (1) if they analyzed behavioral diversity (i.e., differences and/or changes in behavioral patterns of individuals when facing different environmental conditions), (2) if they analyzed behavioral flexibility mechanisms, or (3) if they used a mixed approach relating the behavioral differences and/or changes to specific behavioral flexibility components. For the latter two categories, it was also determined which of the following components of behavioral flexibility were studied in each: behavioral innovation, individual learning, and personality. Moreover, in those studies that dealt with personality characteristics, we examined whether the researchers investigated boldness, neophobia, or exploration. Finally, we ascertained whether these attributes were studied in relation to environmental issues (i.e., climate change, urbanization, or interaction with anthropogenic activities).

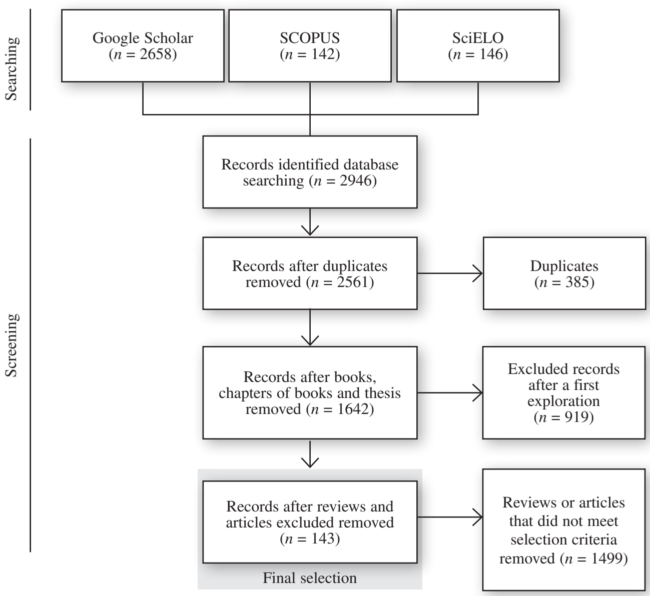


**Fig. 1.** Phases of the systematic review for articles found in the literature search.

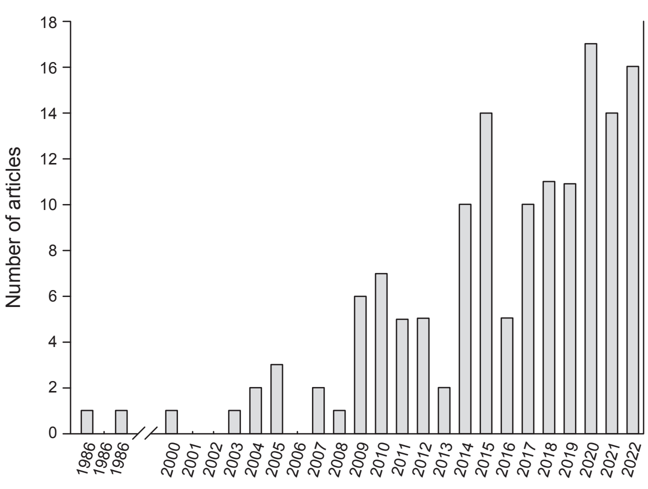


**Fig. 2.** Frequency of published articles on seabird behavioral flexibility between 1986 and 2022. No articles were published between 1989 and 1999.

## RESULTS

A total of 143 articles (out of an original set of 2946) met the selection criteria (Fig. 1; Tables A1 and A2 in Appendix 1, available online). The first article was published in 1986, and there was an increase in the production of articles on this topic over time, with the highest publication rate taking place in 2020 (*n* = 17; Fig. 2).

### Location and taxon

The studies were concentrated in the Northern Hemisphere, mainly in Canada (*n* = 18), the United States (*n* = 14), and the United Kingdom (*n* = 12). For the Southern Hemisphere, they were most frequent in Australia (*n* =11), Antarctica (*n* = 8), and Argentina (*n* = 8; Fig. 3). The most-studied families were Spheniscidae (20.8%, *n* = 33), Alcidae (20.1%, *n* = 32), and Laridae (19.5%, *n* = 31; Fig. 4). Particularly, out of the 75 recorded species, the most frequent were Common Murre *Uria aalge* (*n* = 12), Little Penguin *Eudyptula minor* (*n* = 7), Lesser Black-backed Gull *Larus fuscus* (*n* = 7), and Northern Gannet *Morus bassanus* (*n* = 7).

### Methodological approach, annual cycle period, and research context

The studies occurred mainly in the field (99.3%, *n* = 142) and during the reproductive period (86.0%, *n* = 123). The most common contexts were parental care (79.0%, *n* = 113), feeding (16.1%, *n* = 23), and migration (4.9%, *n* = 7). Studies during the reproductive period were done in the context of parental care (91.9%, *n* = 113), and feeding (8.1%, *n* = 10). The studies conducted during the non-reproductive period (14.0%, *n* = 20) were done in the contexts of feeding (65.0%, *n* = 13) and migration (35.0%, *n* = 7).

### Approach

The main approach in the studies was behavioral diversity (86.0%, *n* = 123), followed by behavioral flexibility mechanisms (7.7%,

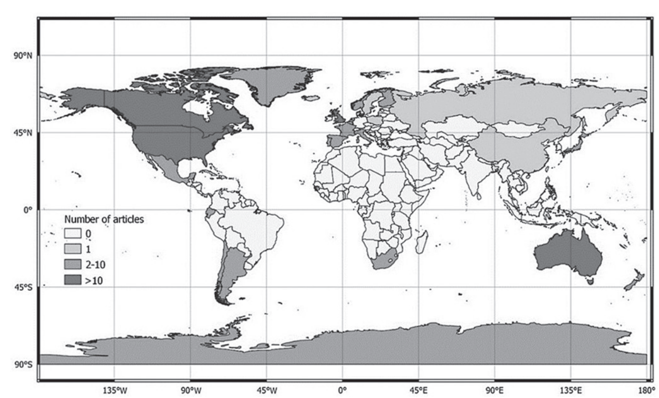


**Fig. 3.** Geographical distribution of the seabird behavioral flexibility studies analyzed in this review.

*n* = 11) and mixed approaches (6.3%, *n* = 9). The most-studied components of behavioral flexibility were personality (69.2%, *n* = 18), innovation (15.4%, *n* = 4), and individual learning (15.4%, *n* = 4). Of the studies about personality, 38.4 % (*n* = 10) focused on the analysis of boldness, 30.8% focused on neophobia (*n* = 8), and 30.8% examined exploration (*n* = 8).

Among the studies that investigated behavioral flexibility mechanisms, neophobia and exploration were studied the most (both at 25.0%, *n* = 5). Among those with a mixed approach, the study of boldness prevailed (50.0%, *n* = 7; Fig. 5).

In the three contexts that were studied (parental care, feeding, and migration), the behavioral-diversity approach prevailed overall. During feeding, the second most frequent approach was the study of behavioral flexibility mechanisms (26.1%, *n* = 6). During migration and parental care, the second most frequent approach was the mixed one, which represented 14.3% (*n* = 1) and 6.2% (*n* = 7) of the studies, respectively (Fig. 6).

### Components of behavioral flexibility

While examining flexibility components in the different contexts, the greatest number of recorded behavioral flexibility components was seen in the analysis of parental care and feeding. In parental care, boldness was the most-studied component (50.0%, *n* = 9). For feeding, the most frequent components were neophobia (31.3%, *n* = 5) and exploration (25.0%, *n* = 4). The only component evaluated for migration was boldness (Fig. 7).

### Related environmental issue

Finally, 59.0% (*n* = 84) of the studies dealt with behavioral flexibility as related to an environmental issue. Most studies analyzed the effects of global change and climate change (83.3%, *n* = 70) in relation to individual behavioral diversity (97.1%, *n* = 68). A lower percentage analyzed urbanization (11.9%, *n* = 10) and its link to food resources and habitat use through the study of behavioral diversity (31.3%, *n* = 5) and behavioral mechanisms like neophobia (25.0%, *n* = 4), exploration (25.0%, *n* = 4), innovation (12.5%, *n* = 2), and individual learning (6.3%, *n* = 1). Finally, studies examining how seabirds interact with anthropogenic activities (4.8%, *n* = 4) most often approached the question by assessing boldness (75.0%, *n* = 3).

## DISCUSSION

The study of seabird behavioral flexibility has increased in the last 35 years, particularly between 2012 and 2022. This growth is related to the general increase in the study of behavioral flexibility in a wide variety of taxa (Smith & Blumstein 2008). Moreover, in a context in which marine and coastal areas are affected by several environmental issues simultaneously, there is a need for information about how fauna respond to these changes, which can be acquired by analyzing their behavior (Smith & Blumstein 2008, Audet & Lefebvre 2017).

In this review, we found that behavioral flexibility has been analyzed in a wide range of seabird families; the most frequent were Spheniscidae, Alcidae, and Laridae. The penguin and auk families contain a number of vulnerable species affected by current environmental issues (Croxall *et al.* 2012, Fort *et al.* 2013, Paleczny *et al.* 2015, Grémillet *et al.* 2018, Amélineau *et al.* 2019, Hodges *et al.* 2022). One result of this, especially for penguins, is that some species are protected by extensive conservation programs (Hickcox *et al.* 2019, Ropert-Coudert *et al.* 2019, García-Borboroglu *et al.* 2022), which would explain the interest in and access to study the behavior of these groups. The frequency of studies on Laridae could be due to their being a generalist and opportunist group: they are very much present in urban areas, they are strongly linked to anthropogenic activities in many parts of the world, and they include species that have had population increases in recent years (Yorio *et al.* 2016, Feng & Liang 2020, Stewart *et al.* 2020, Carmona *et al.* 2021, Pais de Faria *et al.* 2021, Coccon *et al.* 2022). This is why, at the same time, Laridae is one of the most common and easily accessed groups for study in coastal environments. In these species, given their close association with humans, studying behavioral flexibility allows identification of their capacity to profit from anthropogenic resources (i.e., shelter and food) and the conflicts it might bring about (Sol *et al.* 2020).

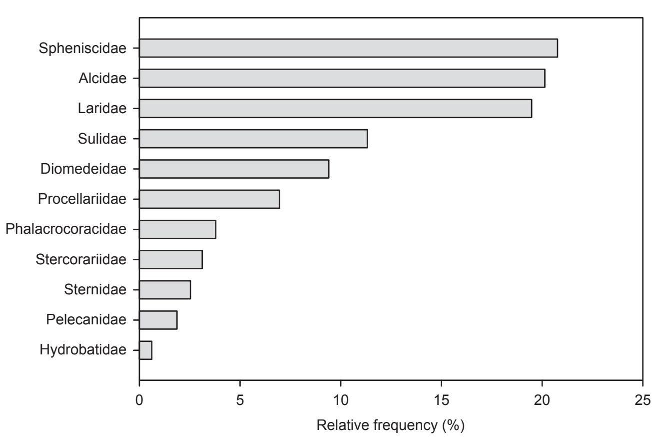


**Fig. 4.** Relative frequency of the seabird families studied in the articles on behavioral flexibility.

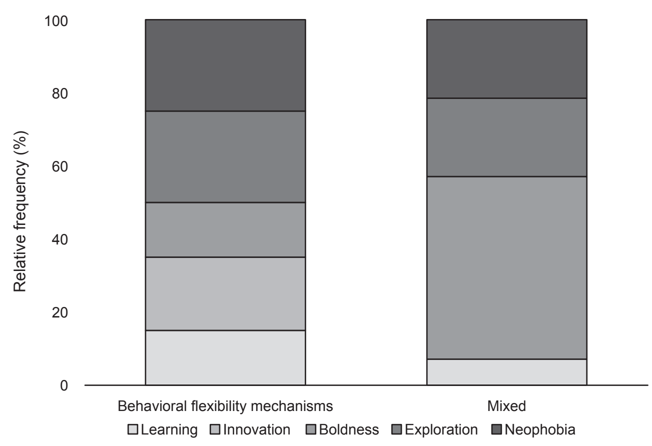


**Fig. 5.** Relative frequency of the behavioral flexibility components assessed in studies using the behavioral flexibility mechanisms approach or the mixed approach in the articles analyzed.

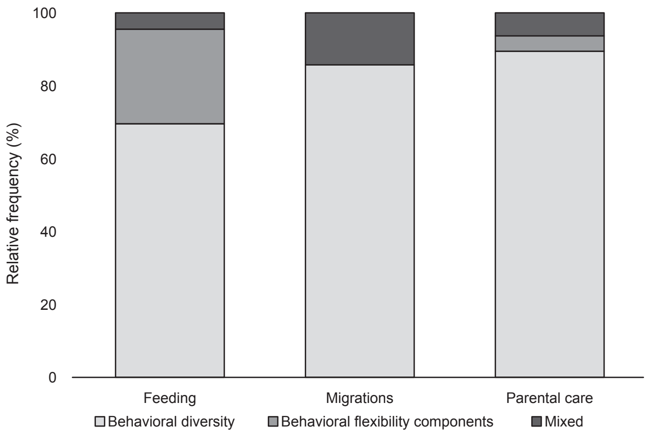


**Fig. 6.** Relative frequency of the approaches used, as compared to the research context in which the study was done.

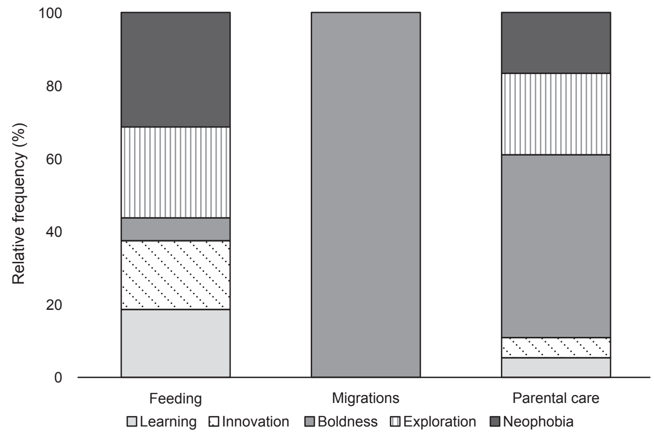


**Fig. 7.** Relative frequency of the behavioral flexibility components studied, as compared to the research context in which the study was done.

Other families studied, such as Diomedeidae and Procellariidae, also include species of special conservation status (Phillips *et al.* 2016). Although they were less represented in the studies, possibly as a result of their particular nesting habitat (i.e., in burrows or cavities and on very remote islands), their presence could point to interest in using behavioral flexibility as another tool to identify and analyze the effects of global and climate change and of environmental variations on these groups. Understanding the influence of flexibility on the individuals' behavioral responses in the face of anthropogenic changes in the environment is crucial for assessing the vulnerability of a population and quantifying the effects of these changes on specifics behaviors (Piatt *et al.* 2007, Sydeman *et al.* 2012, Wong & Candolin 2015).

The most frequently studied seabird families were concentrated in the United States, Canada, and the United Kingdom, where the main families studied were Laridae and Alcidae. The most well-studied penguin species were concentrated in Antarctica, Argentina, and Australia, with the locations being somewhat remote. The most frequent studies were confined to the reproductive period and took place in the context of parental care. Gulls, auks, and penguins are most easily accessed during this period, which facilitates observations, field experiments, and tracking (e.g., Gómez-Laich *et al.* 2015, Williams *et al.* 2020).

As our results show, there are many ways of studying behavioral flexibility. While the term "behavioral flexibility" is widely used in the study of behavior, including both behavioral ecology and experimental psychology, there are differences in its definition and study criteria (Audet & Lefebvre 2017). This is reflected in the different approaches used among the studies analyzed here. Two main approaches to behavioral flexibility were identified. The approach used most frequently was behavioral diversity, in which variation was assessed among individuals for a particular behavior related to changes in one or more environmental variables. In this way, these studies dealt with flexibility as the ability to modify behaviors adaptively for different contexts and circumstances (Duckworth 2010, Ydenberg & Prins 2012, Holekamp *et al.* 2013). This promotes an understanding of the way species use their feeding, reproduction, and chick-rearing strategies according to environmental variations (i.e., prey availability, climate conditions, and niche site characteristics; Green *et al.* 2005, Lopes *et al.* 2015, Beever *et al.* 2017, Amélineau *et al.* 2019). Other studies analyzed behavioral flexibility in terms of components such as innovation, individual learning, and personality, thus allowing the identification of differences among individuals in their response to a new environment and relating them to other cognitive abilities (Stamps 2016). In these studies, researchers most frequently analyzed personality, assessing seabird capacity for exploration, neophobia, and boldness. These behavior studies are key to identifying the effects of anthropogenic environmental changes, since personality would play an essential role in the way organisms respond to new stimuli (Garamszegi *et al.* 2008, Cole & Quinn 2014). In turn, this would affect how individuals search for new sources of food and shelter and/or change their reproductive strategies.

The mixed approach was the least frequent method used in the studies and assessed different components of behavioral flexibility (i.e., personality, innovation, and learning). It allowed researchers to identify and associate individual characteristics to how different species deal with environmental challenges in nesting, feeding, and migration. The majority of the studies using the mixed approach analyzed boldness as a personality trait related to environmental changes. Relative to these effects of habitat alterations, boldness is associated with coping strategies in dynamic situations (Koolhaas *et al.* 2010). For example, differentiating causes and consequences for these changes in feeding strategies during the breeding period, which predominated in the analyzed studies, is crucial because predicting the location and distance to feeding and reproduction sites can largely determine the reproductive success of the birds in the colony (Harding *et al.* 2013).

## Final considerations

Though the studies that analyze behavioral flexibility in seabirds have increased in the last 10 years, a low percentage of that research focused on the specific components of individual behavioral flexibility related to seabird conservation status and/or environmental issues where they live. Increasing this type of study would deepen the understanding of how seabird species adjust to the consequences of anthropogenic changes in their habitats and food sources (Greenberg & Droege 1999, Beever *et al.* 2017, Vardi & Berger-Tal 2022). The conservation status of seabirds is affected by several issues (i.e., invasive species, incidental capture, climate change, overfishing, pollution, and environmental changes; Dias *et al.* 2019), and monitoring their behavioral adjustments is important for assessing how they adapt to environmental changes (Wong & Candolin 2015). Therefore, it is essential to incorporate the study of specific behavioral flexibility mechanisms into the development of effective management and conservation strategies in seabirds.

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