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Size-assortative mating in a long-lived monogamous seabird

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Abstract

Mate choice is a key process in animals to optimize the fitness benefits of reproduction, and it is generally guided by phenotypic features of potential partners that mirror reproductive abilities. Assortative mating occurs when there is within-pair selection for specific functional traits that can confer fitness benefits. Assortative mating can be positive if mates are more similar, and negative if they are more dissimilar than expected by chance. Mate choice is particularly important in long-lived species with biparental care, such as procellariforms that form long term monogamous bonds. We assessed the mating strategy of a sexually dimorphic Mediterranean procellariform, the Scopoli's Shearwater (*Calonectris diomedea*), by testing for assortative mating according to bill (in accordance with previous studies on a sister species) and tarsus size (proxy of body size). We found that shearwaters adopted a positive size-assortative mating by tarsus length, while mating for bill size was random. Moreover, tarsus length was positively correlated with the duration of incubation shifts, when individuals are fasting on eggs. The observed assortative mating could be the results of choice by similarity between individuals, likely because partners with similar relative size have similar tolerance to fasting. Alternatively, the observed pattern could be the product of mutual mate choice, with a selection for large size that could confer competitive abilities in nest selection, defense, foraging aggregations and fasting ability. While our data suggest strong assortative mating in the Scopoli’s Shearwater (R = 0.4), we cannot fully disentangle the multiple processes at play acting on mate choice.

Keyword: bill depth, *Calonectris diomedea*, mate choice, reproductive behaviour, Scopoli’s Shearwater, tarsus length

Zusammenfassung

Größen-assortative Paarung bei einem langlebigen, monogamen Seevogel

Die Partnerwahl ist ein wichtiger Prozess bei Tieren, um die Fitnessvorteile der Fortpflanzung zu optimieren, und sie wird im Allgemeinen von phänotypischen Merkmalen potenzieller Partner geleitet, die die Fortpflanzungsfähigkeiten widerspiegeln. Assortative Paarung tritt auf, wenn innerhalb eines Paares eine Selektion auf bestimmte funktionale Merkmale stattfindet, die Fitnessvorteile bringen können. Assortative Paarung kann positiv sein, wenn sich die Partner ähnlicher sind, und negativ, wenn sie unterschiedlicher sind als zufällig erwartet. Die Partnerwahl ist besonders wichtig

bei langlebigen Arten mit biparentaler Pflege, wie z. B. bei Sturmtauchern, die langfristige monogame Bindungen eingehen. Wir untersuchten die Paarungsstrategie eines geschlechtsdimorphen mediterranen Sturmtauchers, des Gelbschnabel-Sturmtauchers (*Calonectris diomedea*), indem wir auf assortative Paarung nach Schnabel- (in Übereinstimmung mit früheren Studien an einer Schwesterart) und Tarsuslänge (stellvertretend für die Körpergröße) prüften. Wir fanden, dass Sturmtaucher eine positive größen-assortative Paarung nach Tarsuslänge zeigen, während die Verpaarung nach Schnabellänge zufällig war. Darüber hinaus korrelierte die Tarsuslänge positiv mit der Dauer der Inkubationsschichten, wenn die Individuen auf den Eiern fasten. Die beobachtete assortative Paarung könnte das Ergebnis einer Auswahl nach Ähnlichkeit zwischen den Individuen sein, wahrscheinlich, weil Partner mit ähnlicher relativer Größe eine ähnliche Toleranz gegenüber dem Fasten haben. Alternativ könnte das beobachtete Muster das Ergebnis einer gegenseitigen Partnerwahl sein, bei der eine Selektion auf Größe erfolgt, die Wettbewerbsvorteile bei der Nestwahl, der Verteidigung, bei der Bildung von Futtergruppen und beim Fasten mit sich bringt. Während unsere Daten auf eine starke assortative Paarung beim Gelbschnabel-Sturmtaucher (R = 0,4) hindeuten, können wir die verschiedenen Prozesse, die bei der Partnerwahl eine Rolle spielen, nicht vollständig entschlüsseln.

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Introduction

Mate choice is an important process in wild animals which optimizes individual fitness by successfully producing as many high-quality offspring as possible. Mate choice can be defined as any pattern of behaviors that leads members of one sex to be more likely to mate with specific members of the opposite sex than with others (Bateson 1983). Mate choice is less likely to occur in polygamous species, where one or both sexes try to mate with as many partners as possible to increase their reproductive success, or when the costs of evaluating the partner are higher than the payoff of choosing a preferred partner (Rosenthal 2017). On the contrary, when constraints acting on reproductive success are more severe (e.g. number of eggs that can be produced, parental care, genetic compatibility), mates should adopt a different strategy leading to a non-random mate choice, since individual mating success is affected by the quality of the partner (Bateman 1948; Kvarnemo 2018; Schneider and Fromhage 2010). In mutually monogamous species, where both partners mate only with the highest quality mate possible (Kvarnemo 2018), the choice of partner is key for successful reproduction (Bateson 1983).

It is difficult to fully understand which drivers modulate mate choice (Ryan et al. 2007), but generally it is based on specific traits in the opposite sex that signal their reproductive qualities (Andersson and Simmons 2006). When a nonrandom mating strategy is driven by a specific feature (e.g., related to age, rank, phenotypes, or physiological conditions), and when there is a correlation of such features within the pair, then assortative mating occurs (Schreiber and Burger 2001). Assortative mating can be positive (often known simply as assortative mating) if mates have similar traits, or negative (often termed dissortative mating) if specific traits are more different between pair members than expected by chance (Burley 1983). Assortative mating can provide fitness benefits and shape the genetic structure of populations. Indeed, negative assortative mating may increase heterozygosity and maintain genetic variation in a population, while positive assortative mating may increase within-locus homozygosity and inflate the variance of quantitative traits (Jiang et al. 2013; Lynch and Walsh 1998). Negative assortative mating has been observed in both mammals (e.g., *Canis lupus occidentalis*, Hedrick et al. 2016) and birds (e.g., *Zonotrichia albicollis*, Hedrick et al. 2018; *Calonectris borealis*, Nava et al. 2014), but it is actually relatively rare and might result from type I errors occurring across studies (Jiang et al. 2013). Conversely, positive assortative mating has been observed more frequently (Jiang et al. 2013), based for example on morphological (Einoder et al. 2008), behavioural (Podos 2010), or physiological traits (Caillaud and Via 2000). However, the apparent ubiquity of assortative mating in animal populations has been recently questioned. Indeed, assortative mating might emerge even when it is not a product of mate choice, but rather an artifact of measurement error or experimental design. Wang et al. (2019) showed, for instance, that assortative mating can disappear when both partners are measured by independent observers and, thus, that a robust methodological approach is crucial.

Research on mate choice in birds has attracted a great deal of attention, partly because many birds form monogamous pair bonds (Mock and Fujioka 1990), and share parental care, which implies that an individual's reproductive success strongly depends on its partner's investment in reproduction. Mate choice is particularly important in long-lived species with long-term monogamous pair bonds, like seabirds. Accordingly, previous studies on seabirds have shown the occurrence of mate choice, e.g. positive assortative mating for age (e.g., *Sterna hirundo*, Bouwhuis et al. 2015), colour morph (e.g., *Sula dactylatra*, Rull et al. 2016), size (e.g., *Stercorarius longicaudus*, Seyer et al. 2020; *Rissa tridactyla*, Helfenstein et al. 2004) and body condition (e.g. *Sula nebouxii*; González-Medina et al. 2020). Good candidates to test for assortative mating in seabirds are procellariforms, a group of highly pelagic seabirds comprising albatrosses, petrels and shearwaters, in which breeders generally have high inter-annual fidelity to both the mate and the nest site (Bried et al. 2003). During incubation, breeding individuals generally undertake long lasting foraging trips (i.e., from 1 to 3 weeks, depending on the species) while the partner is incubating the egg, fasting, and waiting for the changeover. Since they share parental care, interaction of both partner's body mass plays an important role in the coordination of incubation shifts (Gillies et al. 2022), and a good synchronization between mates is crucial, because the partner that is not attending the nest must find enough food for its maintenance and still return before its mate has exhausted body reserves and left the nest unattended (Bried and Jouventin 2001). Therefore, we could expect that body size plays an important role in the selection of an optimal partner in procellariforms.

Here, we investigated the mating strategy of Scopoli's Shearwater (*Calonectris diomedea*), a long-lived (> 20 years, Fransson et al. 2017) sexually size-dimorphic Mediterranean procellariform species with biparental care and long-term pair bonds. There are no previous studies on the mating strategy of this species, but there are two on its sister species, which breeds in the Atlantic Ocean, the Cory's Shearwater (*C. borealis*). The mating strategy of the Cory's Shearwater is controversial since both assortative mating and random mating strategies have been found when investigating preferences for bill size in two different colonies (Mougin 2000; Nava et al. 2014). In our study, we assessed the mating strategy of breeders from three colonies, investigating the preference for both bill and tarsus sizes. We examined bill in accordance with former studies and tarsus size since is considered as a proxy of body size (Peck et al. 2006; Senar and Pascual 1997).

Materials and Methods

Study species and areas

The Scopoli’s Shearwater is a medium size procellariform species breeding only in the Mediterranean basin and feeding mainly on small pelagic fish, crustaceans, and squids (Grémillet et al. 2014); they also feed opportunistically on discard from fishing vessels (Cecere et al. 2015; Cianchetti-Benedetti et al. 2018). The species shows sexual dimorphism, with males being ca. 20% heavier than females, and having larger skeletal size and higher wing loading (De Pascalis et al. 2020). It does not show sexual dimorphism in plumage, but calls can be used to reliably sex individuals. Typically, males have a high-pitched call, while females make lower calls (Curé et al. 2016). Data were collected in three colonies located around the Italian Peninsula over 13 years: Linosa Island (Pelagie Archipelago) in 2008, 2009 and 2012, Tremiti Archipelago in 2009 and 2010, and La Maddalena Archipelago from 2011 to 2021 (Fig.1).

Biometric measures and sex identification

During the breeding season, breeders were caught by hand at burrows and ringed with a unique alphanumeric metal ring for individual identification. For each individual, we measured tarsus length, bill length and bill depth using a dial caliper (± 0.1 mm). Overall, we collected morphometric data from 95 pairs (Linosa: 55; Tremiti: 17; La Maddalena: 23). Individuals were measured by two different researchers, and members of the pair were often measured in different years, limiting the possible biases identified by Wang et al. (2019) in the assessment of assortative mating. Birds were sexed using individual or partner vocalization (Curé et al. 2009). Individuals that did not vocalize during capture or handling were sexed according to the sex of the partner or comparing morphometric measures and body mass of the two pair members. Molecular sexing of 38 individuals using polymerase chain reaction (PCR) confirmed our initial sex assignment in 100% of those cases (Ilahiane et al. 2022), demonstrating that our morphometric and vocalization-based sexing methods were highly reliable. To assess the sex, PCRs were performed using the CHD1F/CHD1R primer set (Çakmak et al. 2017), following the thermal cycling protocol suggested by Ilahiane et al. (2020).

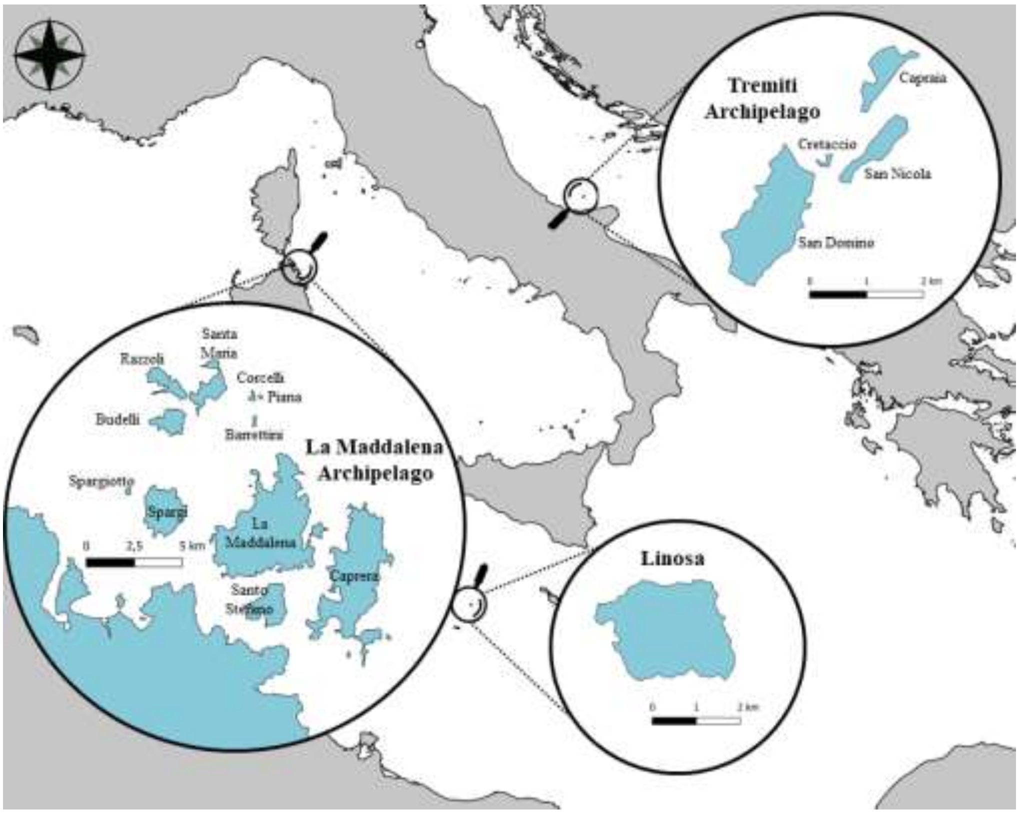

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Fig. 1. Map of the three study areas: Linosa, hosting 10.000 Scopoli's Shearwater pairs, Tremiti Archipelago hosting 300-400 pairs (Baccetti et al. 2009) and La Maddalena Archipelago hosting 200-500 pairs (Morinay et al.2022).

Incubation shift length

During breeding, Scopoli's Shearwaters from the three studied colonies perform long-lasting foraging trips (up to 20 days, Cecere et al. 2013, Cecere et al. 2014), implying prolonged fasting. Since fasting capacity is generally positively correlated with body size in birds (Barbraud and Chastel 1999; González-Solís et al. 2000), we tested if larger individuals performed longer shifts (i.e. longer fasting) to interpret the role of body-size in fasting capacity and discuss its possible consequences on mate choice. We measured the length of a single incubation shift in 57 individuals (Linosa: 13 individuals, 01/06-15/07 2008; Tremiti: 26 individuals, 24/06-11/07 2009 and 15/06-07/07 2010; La Maddalena: 18 individuals 04/06-04/07 2011), each from a different pair. Scopoli's Shearwaters attend the colony only at night, avoiding moonlight conditions and leaving the breeding site at night or just before the sunrise (Rubolini et al. 2015). All monitored nests were easily reachable, consisting of shallow burrows and crevices, and each one was checked during the day to assess the identity of the incubating bird. To aid individual recognition and avoid unnecessary handling for reading metal rings, we marked all of the incubating birds with a yellow non-toxic marker (picric acid) on the chest. Then, nests were visited every day and when the partner was found incubating, we caught it and marked it with purple picric acid. The monitoring continued until the next change-over. The individuals marked in purple were the ones for which we measured the incubation shift length, since we knew the exact day of nest arrival.

Statistical analyses

To check and quantify the reliability of morphometric measures (i.e., tarsus length, bill length and bill depth), we checked their repeatability, benefitting from multiple measures of the same individual collected in different years. We fitted Linear Mixed Models (LMM) with one of the three body measures as a dependent variable and bird identity as a random effect, without entering any fixed effect. Then, we assessed the repeatability (i.e., the relative partitioning of variance into within- and between-individual source of variance) using the "rptR" R package (Stoffel et al. 2017). To test for assortative mating (positive or negative) vs. random mating, we assessed the correlation of each body measure between pair members using Pearson correlation tests, separately for each colony since we cannot rule out density dependent effects on mate choice (i.e. different mating strategies according to the number of breeding individuals in a colony; Bried et al. 2021). However, the test for the significance of differences between correlations performed using "cocor" R package (Diedenhofen and Musch 2015), showed no differences between colonies either for tarsus length or bill (p always > 0.05). Therefore, we pooled together data from different colonies, and we ran a new Pearson correlation test.

To test if the length of the incubation shift depended on individual body size, we fitted a Linear Model (LM) with the length of incubation shift as the dependent variable, and tarsus length (proxy of body size), sex, colony and day of the year as independent variables. Tarsus length was centred by sex to account for sexual differences in size and thus collinearity with sex. The day of the year was included to account for difference in movement patterns according to the progress of the incubation stage (foraging trips are shorter close to hatching, Ramos et al. 2003). Due to logistic constrains we did not record the exact dates of egg-laying, however Scopoli's Shearwaters are quite synchronous in laying (Cramp and Simmons 1977, Cachia-Zammit and Borg 1987), allowing us to use the day of the year as a proxy of the laying day. In this model, bird identity was not entered as a random effect since we recorded only one incubation shift for each individual. We also tested the effect of the two-way interaction between sex and tarsus length (and colony and tarsus length as well), but they were removed from the final models because not being significant.

LMs were run using the 'stats' R package (R Core Team 2021). All model assumptions were carefully inspected for each fitted model using the 'performance' R package (Lüdecke et al. 2021). All analyses were performed using R 4.1.1. (R Core Team 2021).

Results

Both tarsus length and bill depth were highly repeatable, with $R_{pt} = 0.80$ and $R_{pt} = 0.82$ respectively. The repeatability of bill length was low ($R_{pt} = 0.62$) and for this reason the measure was considered less reliable and not used in the following analyses. Tarsus length was positively correlated between pair members ($R = 0.4$, $p < 0.0001$, $N = 93$), while bill depth was not ($R = -0.17$, $p = 0.11$; $N = 89$) (Fig. 2). However, a positive assortment for size may also result from individuals of different sizes reaching the breeding grounds at different times, as the Scopoli's Shearwater is a migratory species (Campioni et al. 2022). To rule out this hypothesis, we analysed migratory tracks from individuals tagged with geolocators and assessed whether arrival date at the colony was correlated with individual body size (See Supplementary Materials). We did not find any correlation between body size and of date of arrival, although some care must be taken in the interpretation of this result, given the small sample size (n=14). Finally, the length of incubation shifts was positively correlated with tarsus length, when controlling for colony and sex (Table 1).

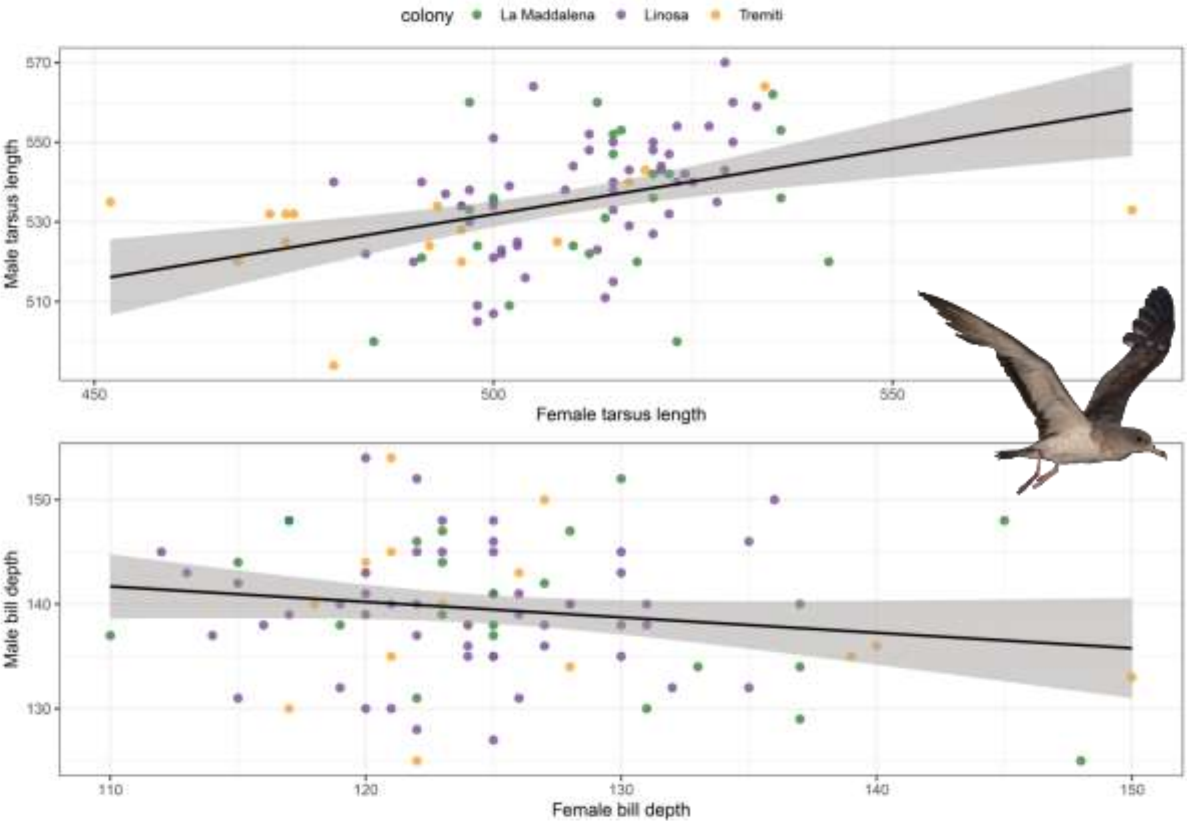

Fig. 2. Relationships between tarsus lengths (mm) of pair members (Person test: $R = 0.4$, $P < 0.0001$, $N = 93$), in the upper panel, and between bill depths (mm) of pair members ($R = -0.17$, $P = 0.11$; $N = 89$), in the lower panel, considering all data from the three studied colonies: Linosa island, Tremiti archipelago and La Maddalena archipelago (see Fig. 1). Although for our analyses we used a correlative approach, since we did not assume a cause-effect

relationship, to plot the correlation we used a LM for graphical reasons. Photo of Scopoli's Shearwater by A. Benvenuti.

Table 1: Results of the fitted Linear Model to test the effect of body size (tarsus length) on the length of incubation shifts (N = 57, days). The model includes data from the three colonies (Linosa, La Maddalena archipelago and Tremiti archipelago; see Fig. 1), with only one measure for each individual.

Predictor	***Estimate* ± *SE***	***T***	***P***
Intercept	9.13±7.05	1.29	0.20
Sex (female)	0.72± 0.64	1.12	0.26
Tarsus centred by sex	0.07 ± 0.01	4.25	**< 0.001**
Colony (La Maddalena)	2.22 ± 1.01	2.19	**< 0.03**
Colony (Tremiti)	-0.46 ± 0.98	-0.46	0.64
Day of the year	-0.01 ± 0.03	-0.28	0.77

Discussion

We investigated the existence and nature of assortative mating in the Scopoli's Shearwater, a seabird with long-term monogamous pair bonds. Using only highly repeatable, and thus reliable, morphometric measurements from three different colonies, we found that Scopoli's Shearwaters adopt a positive assortative mating strategy by body size, with a correlation of tarsus length, but not bill depth, between pair members. Moreover, tarsus length positively correlated with the duration of incubation shifts while it was likely not correlated with the spring arrival date at the colony.

Mixed evidence on the existence of assortative mating has been observed for the Cory's Shearwater (*C. borealis*), the Atlantic sister species of the Scopoli's Shearwater. Indeed, both random (Mougin 2000) and negative assortative mating by bill size (Nava et al. 2014) have been described for birds breeding in two distinct colonies. Moreover, the latter study found no evidence of assortative mating by tarsus and wing length (Nava et al. 2014). Such differences between studies and between the two *Calonectris* species might be colony or species-specific or they could be due to differences in how measures have been collected. Differently to what has been observed in the black-legged kittiwake (Helfenstein et al. 2004), we found no effect of tarsus length on the arrival date at the colony, although some care must be taken given the small sample size of this analysis. Hence, it is likely that the observed size-assortative mating is not a byproduct of higher encounter rates in spring among individuals which are similar in relative size, and we argue that it is likely a product of mate choice.

Positive assortative mating (hereafter just assortative mating) by size, as we observed, is a widespread and relatively common phenomenon among long-lived monogamous birds (Helfenstein et al. 2004; Seyer et al. 2020). Two general hypotheses have been proposed to explain its occurrence (Jiang et al. 2013). The first one suggests that assortative mating is an adaptive response to direct or indirect selective pressures, that can act on the fitness of individuals and/or their offspring. Alternatively, assortative mating can be an incidental consequence of specific constraints (e.g., spatio-temporal barriers) that drive individuals with similar attributes to mate. The correlation of tarsus length between partners that we observed was relatively strong (0.4) compared to the mean correlation between partners for positive assortative mating (0.28) reported in the meta-analysis by Jiang et al. (2013), suggesting that a mechanism generating strong assortative mating is at play. However, the identification of such a mechanism is extremely difficult, particularly without an experimental approach.

In our study system, a mechanism of choice by similarity could be at play. In this case, the advantage of having similar relative body-sizes could be a matching in fasting abilities. Fasting ability is crucial in coordinating shifts, and it should be well matched within the pair to increase shift alignment, or divergences can occur if birds are not able to adjust their foraging trips to account for each other's fasting ability, leading to a mismatch and subsequent breeding failure (Chaurand and Weimerskirch 1994; Pinaud and Weimerskirch 2002). We speculate that pairs with individuals of similar relative size (relative within sex, i.e., large females and large males, small females and small males) likely are capable of fasting for similar timespans, decreasing the likelihood of egg neglect and increasing fitness. For example, a large female and a large male, despite the absolute differences in size, are likely to have comparable fasting abilities (also considering their differences in metabolism and physiology, Navarro et al. 2007), reducing the mismatch that would be present in a pair composed of individuals with different relative sizes. This hypothesis is supported by the positive effect of tarsus length (i.e., a proxy of body size, Peck et al. 2006; Senar and Pascual 1997) on the duration of incubation shifts (and therefore fasting periods). However, direct selection favoring trait-matched mate pairs have been documented but is rare (Jiang et al. 2013).

The observed assortative mating could as well be the result of mutual mate choice, a more common process, where birds have a preference for large-sized individuals. In this case, the preference for large partners is often coupled with a size-dependent competitive exclusion, that leads larger and more competitive individuals to obtain the preferred partner, while smaller and inferior competitors are forced to choose a suboptimal one (Baldauf et al. 2009, Taborsky et al. 2009). In the Scopoli’s Shearwater, mating with a large partner could confer a set of crucial advantages. For example, large individuals could be more competitive in the interactions with conspecifics and heterospecifics, resulting in a higher quality nest-site selection and defense (Werner et al. 2014) and dominance in foraging aggregations (González-Solís et al. 2000). Larger body size could also improve egg thermoregulation, and since it is related to fasting ability, it could confer additional buffer time when fasting. Finally, large individuals could have a higher food load capacity, resulting in a better provisioning of chicks and therefore an increased fitness.

Overall, we suggest that, in accordance with Jiang et al. (2013) first hypothesis, assortative mating by size could confer a fitness advantage to individuals. However, the mechanisms underlying the observed assortative mating cannot be fully disentangled. It is likely which, given the ecology of the species, the choice of an optimal partner is influenced by its competitive and fasting abilities, that are a product of body size. However, several other selective processes act on body size and sexual dimorphism in seabirds, making the full picture even more complex. Correlative approaches can provide valuable insights into these processes, but ultimately experimental approaches are needed to gain a deep understanding of mate choice.

Declarations

Ethical approval

Our work was undertaken following the international, national and institutional ethical guidelines on the care and use of captured animals. Birds were caught, ringed, handle, and equipped with leg-mounted geolocators by the Italian Institute for Environmental Protection and Research (ISPRA), under the authorization of Law 157/1992 [Art.4(1) and Art 7(5)], which regulates research on wild bird species in Italy.

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