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This is a pre print version of the following article:

Original Citation:

Availability:

This version is available http://hdl.handle.net/2318/1912290 since 2023-06-16T15:23:35Z

Published version:

DOI:10.1007/s10336-023-02063-x

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(Article begins on next page)

01 October 2026

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***This is an author version of the contribution published on**:*
Questa è la versione dell'autore dell'opera:
[Journal of Ornithology, 2023, 10.1007/s10336-023-02063-x]

The definitive version is available at:
La versione definitiva è disponibile alla URL:
https://link.springer.com/article/10.1007/s10336-023-02063-x

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.

Acknowledgments

We thank Alessandro Mazzoleni, Federica Ferrario, Eugenio Carlon, Giacomo dell'Omo, Bruno Massa and Pierandrea Brichetti for the help during fieldwork, and Stefano Focardi and Andrea Pilastro for the useful discussion on preliminary results. A special thanks to Yuri Donno, Mirko Ugo, Antonella Gaio, and Lorenzo Muzzu for the logistic support provided at the La Maddalena Archipelago. We are grateful to three anonymous referees for the valuable suggestions provided. Fieldwork in Linosa 2008 was carried out within the framework of the agreement between LIPU and Ministry for the Ecological Transition (formerly MATTM) signed in 2007; fieldwork in Tremiti and La Maddalena 2011-2013 was funded by LIPU UK; fieldwork in Maddalena 2018-2019-2020-2021 was carried out within the framework of two agreements between Italian Institute for Environmental Protection and Research (ISPRA) and Parco Nazionale dell'Arcipelago di La Maddalena signed in 2018 and 2019 respectively. LC was supported by Marine and Environmental Sciences Center (MARE) (UIDB/04292/2020 and UIDP/04292/2020).

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

139 The Scopoli's Shearwater is a medium size procellariform species breeding only in the Mediterranean basin and feeding
140 mainly on small pelagic fish, crustaceans, and squids (Grémillet et al. 2014); they also feed opportunistically on discard
141 from fishing vessels (Cecere et al. 2015; Cianchetti-Benedetti et al. 2018). The species shows sexual dimorphism, with
142 males being ca. 20% heavier than females, and having larger skeletal size and higher wing loading (De Pascalis et al.
143 2020). It does not show sexual dimorphism in plumage, but calls can be used to reliably sex individuals. Typically,
144 males have a high-pitched call, while females make lower calls (Curé et al. 2016). Data were collected in three colonies
145 located around the Italian Peninsula over 13 years: Linosa Island (Pelagie Archipelago) in 2008, 2009 and 2012, Tremiti
146 Archipelago in 2009 and 2010, and La Maddalena Archipelago from 2011 to 2021 (Fig.1).
147
148 Biometric measures and sex identification
149 During the breeding season, breeders were caught by hand at burrows and ringed with a unique alphanumeric metal ring
150 for individual identification. For each individual, we measured tarsus length, bill length and bill depth using a dial
151 caliper (± 0.1 mm). Overall, we collected morphometric data from 95 pairs (Linosa: 55; Tremiti: 17; La Maddalena:
152 23). Individuals were measured by two different researchers, and members of the pair were often measured in different
153 years, limiting the possible biases identified by Wang et al. (2019) in the assessment of assortative mating. Birds were
154 sexed using individual or partner vocalization (Curé et al. 2009). Individuals that did not vocalize during capture or
155 handling were sexed according to the sex of the partner or comparing morphometric measures and body mass of the two
156 pair members. Molecular sexing of 38 individuals using polymerase chain reaction (PCR) confirmed our initial sex
157 assignment in 100% of those cases (Ilahiane et al. 2022), demonstrating that our morphometric and vocalization-based
158 sexing methods were highly reliable. To assess the sex, PCRs were performed using the CHD1F/CHD1R primer set
159 (Çakmak et al. 2017), following the thermal cycling protocol suggested by Ilahiane et al. (2020).
160

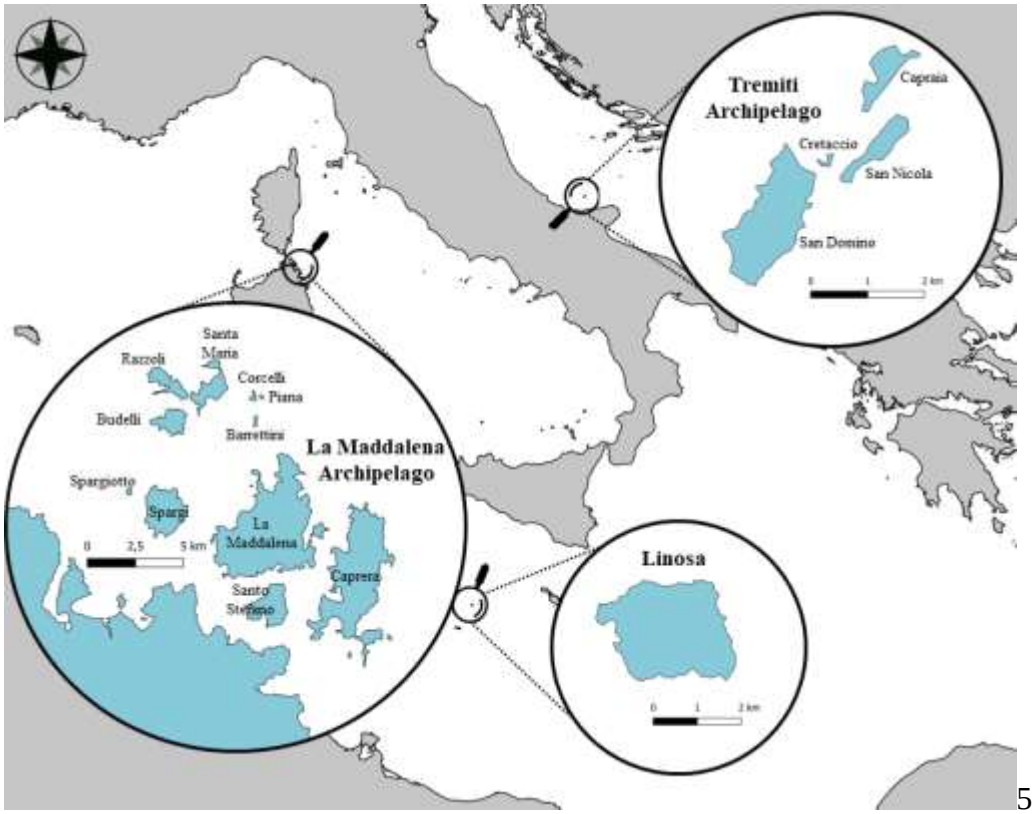

Fig. 1. Map of the three study areas: Linosa, hosting 10.000 Scopoli's Shearwater pairs, Tremiti Archipelago hosting 300-400 pairs (Baccetti et al. 2009) and La Maddalena Archipelago hosting 200-500 pairs (Morinay et al.2022).

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

178 picric acid. The monitoring continued until the next change-over. The individuals marked in purple were the ones for
179 which we measured the incubation shift length, since we knew the exact day of nest arrival.

180

181 Statistical analyses

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

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

204 LMs were run using the 'stats' R package (R Core Team 2021). All model assumptions were carefully inspected for
205 each fitted model using the 'performance' R package (Lüdecke et al. 2021). All analyses were performed using R 4.1.1.
206 (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 = 93) (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).

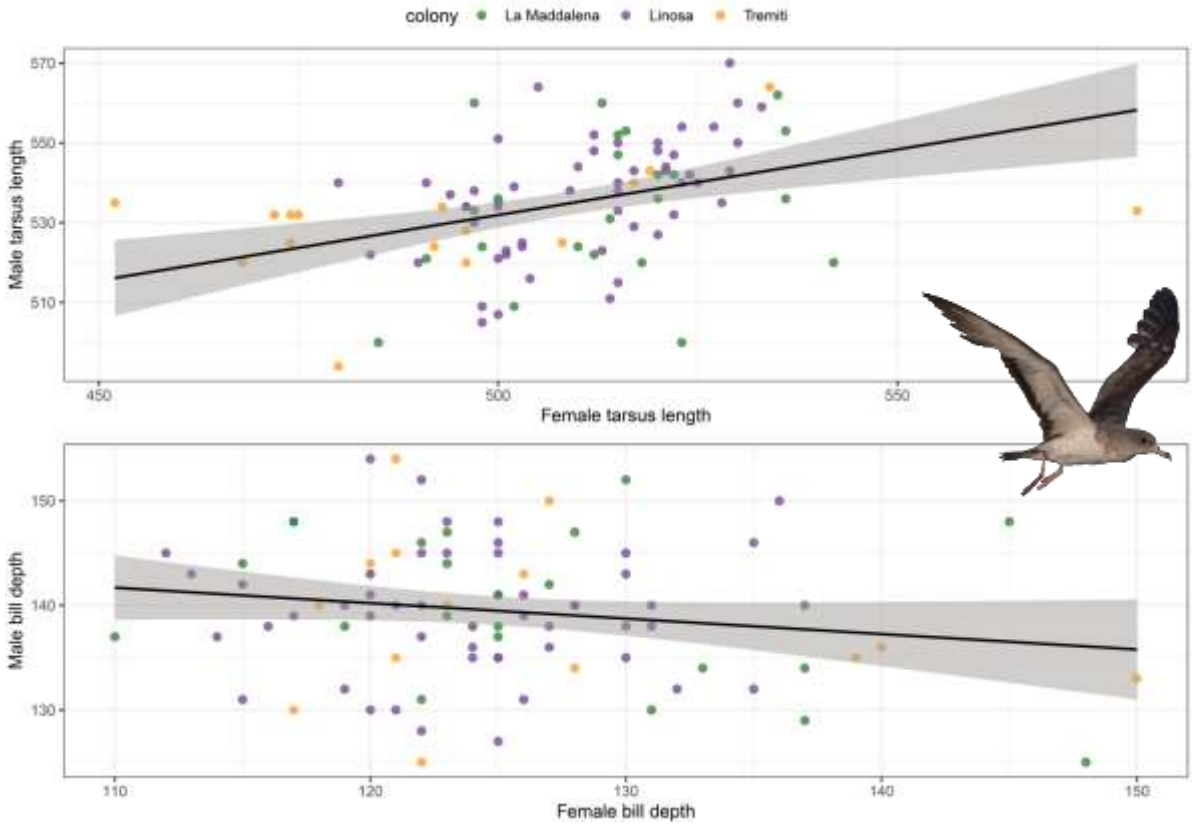

Fig. 2. Relationships between tarsus lengths (mm) of pair members (Person test: R = 0.4, P < 0.0001, N = 93), in the upper panel, and between bill depths (mm) of pair members (R = -0.17, P = 0.11; N = 89), in the lower panel, considering all data from the three studied colonies: Linosa island, Tremiti 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.

294 **References**

295 Andersson M, Simmons LW (2006) Sexual selection and mate choice. Trend Ecol Evol 21:296-302.
296 https://doi.org/10.1016/j.tree.2006.03.015

297 Baccetti N, Capizzi D, Corbi F, Massa B, Nissardi S, Spano G, Sposimo P (2009) Breeding shearwaters on Italian
298 islands: population size, island selection and co-existence with their main alien predator, the black rat. Riv Ital
299 Orn 78:83–100

300 Baldauf SA, Kullmann H, Schroth SH, Thünken T, Bakker T (2009) You can't always get what you want: size
301 assortative mating by mutual mate choice as a resolution of sexual conflict. BMC Evol Biol 9:1-9.
302 https://doi.org/10.1186/1471-2148-9-129

303 Barbraud C, Chastel O (1999) Early body condition and hatching success in the snow petrel *Pagodroma nivea*. Polar
304 Biol 21:1–4. https://doi.org/10.1007/s003000050326

305 Bateman AJ (1948) Intra-sexual selection in Drosophila. Heredity 2:349–368. https://doi.org/10.1038/hdy.1948.21

306 Bateson PPG (1983) Mate Choice. Cambridge University Press. Cambridge

307 Bouwhuis S, Vedder O, Becker PH (2015) Sex-specific pathways of parental age effects on offspring lifetime
308 reproductive success in a long-lived seabird. Evolution 69:1760–1771. https://doi.org/10.1111/evo.12692

309 Bried J, Jouventin P (2001) Site and mate choice in seabirds: an evolutionary approach. In: Schreiber EA, Burger J
310 (eds) Biology of Marine Birds. CRC Press, Boca Raton, pp 263–305

311 Bried J, Andris M, Dubois MP, Jarne P (2021) Decreased selectivity during mate choice in a small-sized population of a
312 long-lived seabird. J Avian Biol 52:1–13. https://doi.org/10.1111/jav.02837

313 Bried J, Pontier D, Jouventin P (2003) Mate fidelity in monogamous birds: A re-examination of the Procellariiformes.
314 Anim Behav 65:235–246. https://doi.org/10.1006/anbe.2002.2045

315 Burley N (1983) The meaning of assortative mating. Ethol Sociobiol 4:191–203. https://doi.org/10.1016/0162-
316 3095(83)90009-2

317 Cachia-Zammit R, Borg J (1987) Notes on the breeding biology of the Cory's shearwater in the Maltese Islands. Il-
318 Merill 24:1-9

319 Caillaud MC, Via S (2000) Specialized feeding behavior influences both ecological specialization and assortative

mating in sympatric host races of pea aphids. Am Nat 156:606–621. https://doi.org/10.1086/316991

Çakmak E, Akın Pekşen Ç, Bilgin CC (2017) Comparison of three different primer sets for sexing birds. J Vet Diagn Invest 29:59–63. https://doi.org/10.1177/1040638716675197

Campioni L, Dell'Omo G, Vizzini S, De Pascalis F, Badalamenti F, Massa B, Rubolini D, Cecere JG (2022) Year-round variation in the isotopic niche of Scopoli's shearwater (*Calonectris diomedea*) breeding in contrasting sea regions of the Mediterranean Sea. Mar Environ Res 178:105650 https://doi.org/10.1016/j.marenvres.2022.105650

Cecere JG, Catoni C, Maggini I, Imperio S, Gaibani G (2013) Movement patterns and habitat use during incubation and chick-rearing of Cory' s shearwaters (*Calonectris diomedea*) (Aves : Vertebrata) from Central Mediterranean : influence of seascape and breeding stage. Ita J Zool 80:82-89. https://doi.org/10.1080/11250003.2012.710654

Cecere JG, Catoni C, Gaibani G, Geraldes P, Celada C, Imperio S (2015) Commercial fisheries, inter-colony competition and sea depth affect foraging location of breeding Scopoli's Shearwaters *Calonectris diomedea*. Ibis 157:284–298. https://doi.org/10.1111/ibi.12235

Cecere JG, Gaibani G, Imperio S (2014) Effects of environmental variability and offspring growth on the movement ecology of breeding Scopoli's shearwater *Calonectris diomedea*. Curr Zool 60:622–630. https://doi.org/10.1093/czoolo/60.5.622

Chaurand T, Weimerskirch H (1994) Incubation routine, body mass regulation and egg neglect in the blue petrel *Halobaena caerulea*. Ibis 136:285-290. https://doi.org/10.1111/j.1474-919X.1994.tb01097.x

Cianchetti-Benedetti M, Dell'Omo G, Russo T, Catoni C, Quillfeldt P (2018) Interactions between commercial fishing vessels and a pelagic seabird in the southern Mediterranean Sea. BMC Ecology 18:1–10. https://doi.org/10.1186/s12898-018-0212-x

Cramp S, Simmons KEL (1977) Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the western Palearctic. Ostrich to Ducks, vol 1. Oxford University Press, Oxford

Curé C, Aubin T, Mathevon N (2009) Acoustic convergence and divergence in two sympatric burrowing nocturnal seabirds. Biol J Linn Soc 96:115–134. https://doi.org/10.1111/j.1095-8312.2008.01104.x

Curé C, Mathevon N, Aubin T (2016) Mate vocal recognition in the Scopoli's shearwater *Calonectris diomedea*: Do females and males share the same acoustic code? Behav Processes 128:96–102. https://doi.org/10.1016/j.beproc.2016.04.013

De Pascalis F, Imperio S, Benvenuti A, Catoni C, Rubolini D, Cecere JG (2020) Sex-specific foraging behaviour is affected by wind conditions in a sexually size dimorphic seabird. Anim Behav 166:207–218. https://doi.org/10.1016/j.anbehav.2020.05.014

Diedenhofen B, Musch J (2015) Cocor: A comprehensive solution for the statistical comparison of correlations. PLoS ONE 10:1–12. https://doi.org/10.1371/journal.pone.0121945

Einoder LD, Page B, Goldsworthy SD (2008) Sexual size dimorphism and assortative mating in the short-tailed shearwater *Puffinus Tenuirostris*. Mar Ornithol 36:167–173

Fransson T, Jansson L, Kolehmainen T, Kroon C, Wenninger T (2017) EURING list of longevity records for European birds. http://www.euring.org/data_and_codes/longevity.htm. Accessed 9 May 2022

Gillies N, Padget O, Syposz M, Bond S, Guilford T (2022) Resource allocation underlies parental decision-making during incubation in the Manx Shearwater. Ornithology 139:1-15. https://doi.org/10.1093/ornithology/ukac006

González-Medina E, Castillo-Guerrero JA, Masero JA, Fernández G (2020) Mate selection based on labile traits affects short-term fitness in a long-lived seabird. Proc R Soc Lond B: Biological Sciences 287. https://doi.org/10.1098/rspb.2019.2578

González-Solís J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. Oikos 90:390–398. https://doi.org/10.1034/j.1600-0706.2000.900220.x

Grémillet D, Péron C, Pons JB, Ouni R, Authier M, Thévenet M, Fort J (2014) Irreplaceable area extends marine conservation hotspot off Tunisia: insights from GPS-tracking Scopoli's shearwaters from the largest seabird colony in the Mediterranean. Mar Biol 161:2669–2680. https://doi.org/10.1007/s00227-014-2538-z

Hedrick PW, Smith DW, Stahler DR (2016) Negative-assortative mating for color in wolves. Evolution 70:757–766. https://doi.org/10.1111/evo.12906

Hedrick PW, Tuttle EM, Gonser RA (2018) Negative-Assortative Mating in the White-Throated Sparrow. J Hered 109:223–231. https://doi.org/10.1093/jhered/esx086

Helfenstein F, Danchin E, Wagner RH (2004) Assortative mating and sexual size dimorphism in Black-legged Kittiwakes. Waterbirds 27:350–354. https://doi.org/10.1675/1524-4695(2004)027[0350:AMASSD]2.0.CO;2

Ilahiane L, De Pascalis F, Pisu D, Pala D, Ferrairo F, Cucco M, Rubolini D, Cecere JG, Pellegrino I (2022) No evidence

374 of avian malaria in two Mediterranean endemic seabirds. Mar Ornithol 50:13-17

375 Ilahiane L, Boano G, Pavia M, Pellegrino I, Grussu M, Voelker G, Galimberti A (2020) Completing the genetic puzzle
376 of the reed warbler complex: insights from Italy. Bird Study 67:440–447.
377 https://doi.org/10.1080/00063657.2021.1927980

378 Jiang Y, Bolnick DI, Kirkpatrick M (2013) Assortative mating in animals. Am Nat 181. https://doi.org/10.1086/670160

379 Kvarnemo C (2018) Why do some animals mate with one partner rather than many? A review of causes and
380 consequences of monogamy. Biol Rev 93:1795–1812. https://doi.org/10.1111/brv.12421

381 Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D, (2021) Performance: An R Package for Assessment,
382 Comparison and Testing of Statistical Models. J. Open Source Softw. 6:3139. https://doi.org/10.21105/joss.03139

383 Lynch M, Walsh B, (1998) Genetics and analysis of quantitative traits. Sinauer, Sunderland, MA

384 Mock DW, Fujioka M (1990) Monogamy and long-term pair bonding in vertebrates. Trend Ecol Evol 5:39–43.
385 https://doi.org/10.1016/0169-5347(90)90045-F

386 Morinay J, De Pascalis F, Catoni C, Benvenuti A, Imperio S, Rubolini D, Cecere JG (2022) Assessing important
387 conservation areas for colonial species from individual tracking data: an evaluation of the effects of colony
388 structure and temporal heterogeneity in movement patterns. Front Mar Sci 9:854826.
389 https://doi.org/10.3389/fmars.2022.854826

390 Mougin JL (2000) Pairing in the Cory's Shearwater (*Calonectris diomedea*) of Selvagem Grande. J Ornithol 141:319–
391 326. https://doi.org/10.1007/BF02462241

392 Nava CP, Kim SY, Magalhães MC, Neves V (2014) Do Cory's shearwaters *Calonectris borealis* choose mates based on
393 size? J Ornithol 155:869–875. https://doi.org/10.1007/s10336-014-1070-8

394 Navarro J, González-Solís J, Viscor G (2007) Nutritional and feeding ecology in Cory's shearwater *Calonectris*
395 *diomedea* during breeding. Mar Ecol Prog Ser 351:261-271. https://doi.org/10.3354/meps07115

396 Peck DR, Erwin CA, Congdon BC (2006) Variation in egg-size in the Wedge-tailed Shearwater (*Puffinus pacificus*).
397 Emu 106:227–231. https://doi.org/10.1071/MU05037

398 Pinaud D, Weimerskirch H (2002) Ultimate and proximate factors affecting the breeding performance of a marine top-
399 predator. Oikos 99:141-150

Podos J (2010) Acoustic discrimination of sympatric morphs in Darwin's finches: A behavioural mechanism for assortative mating? Philos Trans R Soc 365:1031–1039. https://doi.org/10.1098/rstb.2009.0289

R Core Team (2021) R: Language and Environment or Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramos JA, Moniz Z, Solá E, Monteiro LR (2003) Reproductive measures and chick provisioning of Cory's Shearwater *Calonectris diomedea borealis* in the Azores. Bird Study 50:47-54. https://doi.org/10.1080/00063650309461289

Rosenthal GG (2017) Mate choice: the evolution of sexual decision making from microbes to humans. Princeton University Pres, Princeton, NJ

Rull IL, Nicolás L, Neri-Vera N, Argáez V, Martínez M, Torres R (2016) Assortative mating by multiple skin color traits in a seabird with cryptic sexual dichromatism. J Ornithol 157:1049–1062. https://doi.org/10.1007/s10336-016-1352-4

Rubolini D, Maggini I, Ambrosini R, Imperio S, Paiva VH, Gaibani G, Saino N, Cecere JG (2015) The effect of moonlight on Scopoli's Shearwater *Calonectris diomedea* colony attendance patterns and nocturnal foraging: A test of the foraging efficiency hypothesis. Ethology 121:284-299. https://doi.org/10.1111/eth.12338

Ryan MJ, Akre KL, Kirkpatrick M (2007) Mate choice. Curr Biol 17:313–316. https://doi.org/10.1016/j.cub.2007.02.002

Schneider J, Fromhage L (2010) Monogynous mating strategies in spiders. In: Kappler P (ed) Animal Behaviour: Evolution and Mechanisms. Springer, Berlin, pp 441–464

Schreiber EA, Burger J (2001) Seabirds in the marine environment. In: Schreiber EA, Burger J (eds) Biology of Marine Birds. CRC Press, Boca Raton, pp 263–305

Senar JC, Pascual J (1997) Keel and tarsus length may provide a good predictor of avian body size. Ardea 85:269–274.

Seyer Y, Gauthier G, Bernatchez L, Therrien JF (2020) Sexing a Monomorphic Plumage Seabird Using Morphometrics and Assortative Mating. Waterbirds 42:380–392. https://doi.org/10.1675/063.042.0403

Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods Ecol Evol 8:1639–1644. https://doi.org/10.1111/2041-210X.12797

Taborsky B, Guyer L, Taborsky M (2009) Size-assortative mating in the absence of mate choice. Anim Behav 77:439-

448. https://doi.org/10.1016/j.anbehav.2008.10.020

Wang D, Forstmeier W, Valcu M, Dingemanse NJ, Bulla M, Both C et al (2019) Scrutinizing assortative mating in birds. PLoS Biol 17: e3000156. https://doi.org/10.1371/journal.pbio.3000156

Werner AC, Paiva VH, Ramos JA (2014) On the “real estate market”: Individual quality and the foraging ecology of male Cory's Shearwaters. Auk 131:265-274. https://doi.org/10.1642/AUK-13-172.1