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11 Size-assortative mating in a long-lived monogamous seabird

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29 Abstract

30 Mate choice is a key process in animals to optimize the fitness benefits of reproduction, and it is generally guided by 31 phenotypic features of potential partners that mirror reproductive abilities. Assortative mating occurs when there is 32 within-pair selection for specific functional traits that can confer fitness benefits. Assortative mating can be positive if 33 mates are more similar, and negative if they are more dissimilar than expected by chance. Mate choice is particularly 34 important in long-lived species with biparental care, such as procellariforms that form long term monogamous bonds. 35 We assessed the mating strategy of a sexually dimorphic Mediterranean procellariform, the Scopoli's Shearwater 36 (Calonectris diomedea), by testing for assortative mating according to bill (in accordance with previous studies on a 37 sister species) and tarsus size (proxy of body size). We found that shearwaters adopted a positive size-assortative 38 mating by tarsus length, while mating for bill size was random. Moreover, tarsus length was positively correlated with 39 the duration of incubation shifts, when individuals are fasting on eggs. The observed assortative mating could be the 40 results of choice by similarity between individuals, likely because partners with similar relative size have similar 41 tolerance to fasting. Alternatively, the observed pattern could be the product of mutual mate choice, with a selection for 42 large size that could confer competitive abilities in nest selection, defense, foraging aggregations and fasting ability. 43 While our data suggest strong assortative mating in the Scopoli's Shearwater (R = 0.4), we cannot fully disentangle the 44 multiple processes at play acting on mate choice.

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

46 Zusammenfassung

47 Größen-assortative Paarung bei einem langlebigen, monogamen Seevogel

48 Die Partnerwahl ist ein wichtiger Prozess bei Tieren, um die Fitnessvorteile der Fortpflanzung zu optimieren, und sie

- 49 wird im Allgemeinen von phänotypischen Merkmalen potenzieller Partner geleitet, die die Fortpflanzungsfähigkeiten
- 50 widerspiegeln. Assortative Paarung tritt auf, wenn innerhalb eines Paares eine Selektion auf bestimmte funktionale
- 51 Merkmale stattfindet, die Fitnessvorteile bringen können. Assortative Paarung kann positiv sein, wenn sich die Partner
- 52 ähnlicher sind, und negativ, wenn sie unterschiedlicher sind als zufällig erwartet. Die Partnerwahl ist besonders wichtig

53 bei langlebigen Arten mit biparentaler Pflege, wie z. B. bei Sturmtauchern, die langfristige monogame Bindungen 54 eingehen. Wir untersuchten die Paarungsstrategie eines geschlechtsdimorphen mediterranen Sturmtauchers, des 55 Gelbschnabel-Sturmtauchers (Calonectris diomedea), indem wir auf assortative Paarung nach Schnabel- (in 56 Übereinstimmung mit früheren Studien an einer Schwesterart) und Tarsuslänge (stellvertretend für die Körpergröße) 57 prüften. Wir fanden, dass Sturmtaucher eine positive größen-assortative Paarung nach Tarsuslänge zeigen, während die 58 Verpaarung nach Schnabellänge zufällig war. Darüber hinaus korrelierte die Tarsuslänge positiv mit der Dauer der 59 Inkubationsschichten, wenn die Individuen auf den Eiern fasten. Die beobachtete assortative Paarung könnte das 60 Ergebnis einer Auswahl nach Ähnlichkeit zwischen den Individuen sein, wahrscheinlich, weil Partner mit ähnlicher 61 relativer Größe eine ähnliche Toleranz gegenüber dem Fasten haben. Alternativ könnte das beobachtete Muster das 62 Ergebnis einer gegenseitigen Partnerwahl sein, bei der eine Selektion auf Größe erfolgt, die Wettbewerbsvorteile bei der 63 Nestwahl, der Verteidigung, bei der Bildung von Futtergruppen und beim Fasten mit sich bringt. Während unsere Daten 64 auf eine starke assortative Paarung beim Gelbschnabel-Sturmtaucher (R = 0,4) hindeuten, können wir die verschiedenen 65 Prozesse, die bei der Partnerwahl eine Rolle spielen, nicht vollständig entschlüsseln.

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78

80 Introduction

81 Mate choice is an important process in wild animals which optimizes individual fitness by successfully producing as 82 many high-quality offspring as possible. Mate choice can be defined as any pattern of behaviors that leads members of 83 one sex to be more likely to mate with specific members of the opposite sex than with others (Bateson 1983). Mate 84 choice is less likely to occur in polygamous species, where one or both sexes try to mate with as many partners as 85 possible to increase their reproductive success, or when the costs of evaluating the partner are higher than the payoff of 86 choosing a preferred partner (Rosenthal 2017). On the contrary, when constraints acting on reproductive success are 87 more severe (e.g. number of eggs that can be produced, parental care, genetic compatibility), mates should adopt a 88 different strategy leading to a non-random mate choice, since individual mating success is affected by the quality of the 89 partner (Bateman 1948; Kvarnemo 2018; Schneider and Fromhage 2010). In mutually monogamous species, where 90 both partners mate only with the highest quality mate possible (Kvarnemo 2018), the choice of partner is key for 91 successful reproduction (Bateson 1983).

92 It is difficult to fully understand which drivers modulate mate choice (Ryan et al. 2007), but generally it is 93 based on specific traits in the opposite sex that signal their reproductive qualities (Andersson and Simmons 2006). 94 When a nonrandom mating strategy is driven by a specific feature (e.g., related to age, rank, phenotypes, or 95 physiological conditions), and when there is a correlation of such features within the pair, then assortative mating 96 occurs (Schreiber and Burger 2001). Assortative mating can be positive (often known simply as assortative mating) if 97 mates have similar traits, or negative (often termed dissortative mating) if specific traits are more different between pair 98 members than expected by chance (Burley 1983). Assortative mating can provide fitness benefits and shape the genetic 99 structure of populations. Indeed, negative assortative mating may increase heterozygosity and maintain genetic variation 100 in a population, while positive assortative mating may increase within-locus homozygosity and inflate the variance of 101 quantitative traits (Jiang et al. 2013; Lynch and Walsh 1998). Negative assortative mating has been observed in both 102 mammals (e.g., Canis lupus occidentalis, Hedrick et al. 2016) and birds (e.g., Zonotrichia albicollis, Hedrick et al. 103 2018; Calonectris borealis, Nava et al. 2014), but it is actually relatively rare and might result from type I errors 104 occurring across studies (Jiang et al. 2013). Conversely, positive assortative mating has been observed more frequently 105 (Jiang et al. 2013), based for example on morphological (Einoder et al. 2008), behavioural (Podos 2010), or 106 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 107 108 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.

111 Research on mate choice in birds has attracted a great deal of attention, partly because many birds form 112 monogamous pair bonds (Mock and Fujioka 1990), and share parental care, which implies that an individual's 113 reproductive success strongly depends on its partner's investment in reproduction. Mate choice is particularly important 114 in long-lived species with long-term monogamous pair bonds, like seabirds. Accordingly, previous studies on seabirds 115 have shown the occurrence of mate choice, e.g. positive assortative mating for age (e.g., Sterna hirundo, Bouwhuis et 116 al. 2015), colour morph (e.g., Sula dactylatra, Rull et al. 2016), size (e.g., Stercorarius longicaudus, Seyer et al. 2020; 117 Rissa tridactyla, Helfenstein et al. 2004) and body condition (e.g. Sula nebouxii; González-Medina et al. 2020). Good 118 candidates to test for assortative mating in seabirds are procellariforms, a group of highly pelagic seabirds comprising 119 albatrosses, petrels and shearwaters, in which breeders generally have high inter-annual fidelity to both the mate and the 120 nest site (Bried et al. 2003). During incubation, breeding individuals generally undertake long lasting foraging trips (i.e., 121 from 1 to 3 weeks, depending on the species) while the partner is incubating the egg, fasting, and waiting for the 122 changeover. Since they share parental care, interaction of both partner's body mass plays an important role in the 123 coordination of incubation shifts (Gillies et al. 2022), and a good synchronization between mates is crucial, because the 124 partner that is not attending the nest must find enough food for its maintenance and still return before its mate has 125 exhausted body reserves and left the nest unattended (Bried and Jouventin 2001). Therefore, we could expect that body 126 size plays an important role in the selection of an optimal partner in procellariforms.

127 Here, we investigated the mating strategy of Scopoli's Shearwater (*Calonectris diomedea*), a long-lived (> 20 128 years, Fransson et al. 2017) sexually size-dimorphic Mediterranean procellariform species with biparental care and 129 long-term pair bonds. There are no previous studies on the mating strategy of this species, but there are two on its sister 130 species, which breeds in the Atlantic Ocean, the Cory's Shearwater (C. borealis). The mating strategy of the Cory's 131 Shearwater is controversial since both assortative mating and random mating strategies have been found when 132 investigating preferences for bill size in two different colonies (Mougin 2000; Nava et al. 2014). In our study, we 133 assessed the mating strategy of breeders from three colonies, investigating the preference for both bill and tarsus sizes. 134 We examined bill in accordance with former studies and tarsus size since is considered as a proxy of body size (Peck et 135 al. 2006; Senar and Pascual 1997).

136

137 Materials and Methods

138 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).

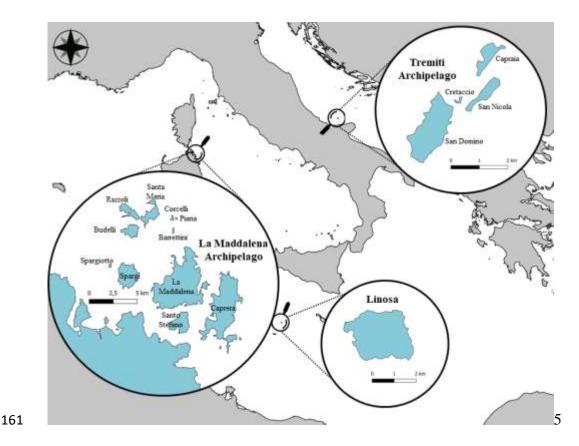


Fig. 1. Map of the three study areas: Linosa, hosting 10.000 Scopoli's Shearwater pairs, Tremiti Archipelago hosting
300-400 pairs (Baccetti et al. 2009) and La Maddalena Archipelago hosting 200-500 pairs (Morinay et al.2022).

164

166 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 167 168 correlated with body size in birds (Barbraud and Chastel 1999; González-Solís et al. 2000), we tested if larger 169 individuals performed longer shifts (i.e. longer fasting) to interpret the role of body-size in fasting capacity and discuss 170 its possible consequences on mate choice. We measured the length of a single incubation shift in 57 individuals (Linosa: 171 13 individuals, 01/06-15/07 2008; Tremiti: 26 individuals, 24/06-11/07 2009 and 15/06-07/07 2010; La Maddalena: 18 172 individuals 04/06-04/07 2011), each from a different pair. Scopoli's Shearwaters attend the colony only at night, 173 avoiding moonlight conditions and leaving the breeding site at night or just before the sunrise (Rubolini et al. 2015). All 174 monitored nests were easily reachable, consisting of shallow burrows and crevices, and each one was checked during 175 the day to assess the identity of the incubating bird. To aid individual recognition and avoid unnecessary handling for 176 reading metal rings, we marked all of the incubating birds with a yellow non-toxic marker (picric acid) on the chest. 177 Then, nests were visited every day and when the partner was found incubating, we caught it and marked it with purple

¹⁶⁵ Incubation shift length

- 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.

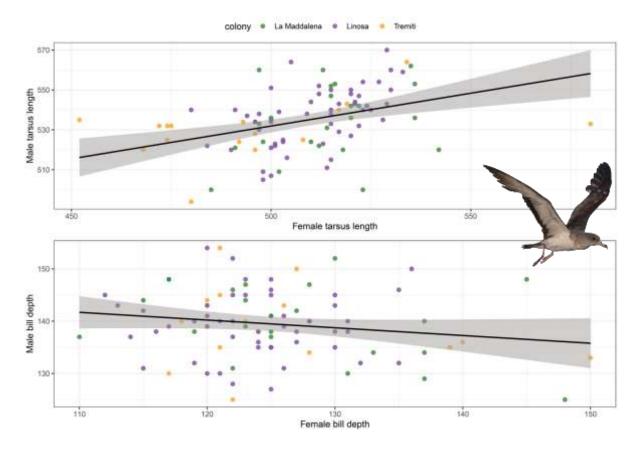
194 To test if the length of the incubation shift depended on individual body size, we fitted a Linear Model (LM) with the length of incubation shift as the dependent variable, and tarsus length (proxy of body size), sex, colony and day 195 196 of the year as independent variables. Tarsus length was 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.

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).

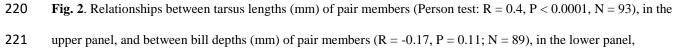
207 Results

208 Both tarsus length and bill depth were highly repeatable, with $R_{pt} = 0.80$ and $R_{pt} = 0.82$ respectively. The repeatability 209 of bill length was low ($R_{pt} = 0.62$) and for this reason the measure was considered less reliable and not used in the 210 following analyses. Tarsus length was positively correlated between pair members (R = 0.4, p < 0.0001, N = 93), while 211 bill depth was not (R = -0.17, p = 0.11; N = 89) (Fig. 2). However, a positive assortment for size may also result from 212 individuals of different sizes reaching the breeding grounds at different times, as the Scopoli's Shearwater is a 213 migratory species (Campioni et al. 2022). To rule out this hypothesis, we analysed migratory tracks from individuals 214 tagged with geolocators and assessed whether arrival date at the colony was correlated with individual body size (See 215 Supplementary Materials). We did not find any correlation between body size and of date of arrival, although some care 216 must be taken in the interpretation of this result, given the small sample size (n=14). Finally, the length of incubation 217 shifts was positively correlated with tarsus length, when controlling for colony and sex (Table 1).

218



219



considering all data from the three studied colonies: Linosa island, Tremiti archipelago and La Maddalena archipelago

223 (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.
- 225 Benvenuti.
- 226

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	Τ	Р
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)	$\textbf{-0.46} \pm 0.98$	-0.46	0.64
Day of the year	-0.01 ± 0.03	-0.28	0.77

230

231 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.

237 Mixed evidence on the existence of assortative mating has been observed for the Cory's Shearwater (C. 238 borealis), the Atlantic sister species of the Scopoli's Shearwater. Indeed, both random (Mougin 2000) and negative 239 assortative mating by bill size (Nava et al. 2014) have been described for birds breeding in two distinct colonies. 240 Moreover, the latter study found no evidence of assortative mating by tarsus and wing length (Nava et al. 2014). Such 241 differences between studies and between the two Calonectris species might be colony or species-specific or they could 242 be due to differences in how measures have been collected. Differently to what has been observed in the black-legged 243 kittiwake (Helfenstein et al. 2004), we found no effect of tarsus length on the arrival date at the colony, although some 244 care must be taken given the small sample size of this analysis. Hence, it is likely that the observed size-assortative

245 mating is not a byproduct of higher encounter rates in spring among individuals which are similar in relative size, and 246 we argue that it is likely a product of mate choice.

247 Positive assortative mating (hereafter just assortative mating) by size, as we observed, is a widespread and 248 relatively common phenomenon among long-lived monogamous birds (Helfenstein et al. 2004; Seyer et al. 2020). Two 249 general hypotheses have been proposed to explain its occurrence (Jiang et al. 2013). The first one suggests that 250 assortative mating is an adaptive response to direct or indirect selective pressures, that can act on the fitness of 251 individuals and/or their offspring. Alternatively, assortative mating can be an incidental consequence of specific 252 constraints (e.g., spatio-temporal barriers) that drive individuals with similar attributes to mate. The correlation of tarsus 253 length between partners that we observed was relatively strong (0.4) compared to the mean correlation between partners 254 for positive assortative mating (0.28) reported in the meta-analysis by Jiang et al. (2013), suggesting that a mechanism 255 generating strong assortative mating is at play. However, the identification of such a mechanism is extremely difficult, 256 particularly without an experimental approach.

257 In our study system, a mechanism of choice by similarity could be at play. In this case, the advantage of having 258 similar relative body-sizes could be a matching in fasting abilities. Fasting ability is crucial in coordinating shifts, and it 259 should be well matched within the pair to increase shift alignment, or divergences can occur if birds are not able to 260 adjust their foraging trips to account for each other's fasting ability, leading to a mismatch and subsequent breeding 261 failure (Chaurand and Weimerskirch 1994; Pinaud and Weimerskirch 2002). We speculate that pairs with individuals of 262 similar relative size (relative within sex, i.e., large females and large males, small females and small males) likely are 263 capable of fasting for similar timespans, decreasing the likelihood of egg neglect and increasing fitness. For example, a 264 large female and a large male, despite the absolute differences in size, are likely to have comparable fasting abilities 265 (also considering their differences in metabolism and physiology, Navarro et al. 2007), reducing the mismatch that 266 would be present in a pair composed of individuals with different relative sizes. This hypothesis is supported by the 267 positive effect of tarsus length (i.e., a proxy of body size, Peck et al. 2006; Senar and Pascual 1997) on the duration of 268 incubation shifts (and therefore fasting periods). However, direct selection favoring trait-matched mate pairs have been 269 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.

287

288 Declarations

289 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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