Sex-specific mate choice and mate change based on MHC-IIB dissimilarity in a genetically monogamous seabird

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Acknowledgments

We thank the Middleton fieldworkers who collected data, as well as the undergraduate students who helped with molecular analyses.

Authors' contributions

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Ethics

The experiment was conducted under the approval of the U.S. Geological Survey Alaska Science Center, the University of Alaska Institutional Animal Care and Use Committees, and the Institut Paul-Emile Victor Ethical Committee, in accordance with United States laws and under permits from the U.S. Fish and Wildlife Service and the State of Alaska.

Conflict of interest

The authors declare that they have no conflict of interest.

Funding

This work was supported by the French Polar Institute Paul-Emile Victor (IPEV "Programme 1162" to ED and SL) and the Fondation Fyssen (to SL). This study is part of the "Laboratoire d'Excellence" (LABEX) entitled TULIP (ANR-10-LABX-41). LR was supported by an EUR TULIP Ph.D. grant obtained through SEVAB postgraduate school.

Data availability statement

Data available from the Zenodo Repository: https://doi.org/10.5281/zenodo.14523780.

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Abstract

Among species reproducing sexually, mating strategies represent a major component of individual fitness. The Major Histocompatibility Complex (MHC) is an extremely diverse set of genes responsible for immunological recognition and defense against pathogens. Although MHC-dissimilarity between mates has been proposed to drive mate choice through increased offspring pathogen resistance, evidence is mixed, and evidence for other MHC-based mating strategies remains rare. We investigated whether MHC-IIB dissimilarity is associated with mate choice and mate change in the genetically monogamous black-legged kittiwake (*Rissa tridactyla*). We found that first-time male breeders are paired with females more MHC-IIB dissimilar to them than expected by chance. After a successful reproduction, the more males are MHC-IIB dissimilar to their mate, the less likely they are to change mate. When males change their mate, they tend to be more MHC-IIB dissimilar to the new mate compared to the previous mate. However, males are not more MHC-IIB dissimilar to their new mate than expected by chance. We did not find evidence for an effect of MHC-IIB dissimilarity on mating strategies when considering the female's perspective. Male mate choice should not be overlooked in species with bi-parental care in which the male performs a significant part of parental care.

Keywords: Black-legged kittiwake, *Rissa tridactyla*, Divorce, Reproduction, Major Histocompatibility Complex, Disassortative mate choice

Introduction

Mating strategies are the set of behavioural patterns used by individuals to attract, select, change or retain mates to promote individual fitness. Understanding their driving factors has long been a major topic in evolutionary biology ([1]; [2]; [3]; [4]). For instance, mate choice has repeatedly been shown to rely on traits that honestly reflect the quantity or quality of resources, the care or the genes that the mate can provide ([5]; [6]; [7]). In addition, in several species, individuals preferentially choose mates who are more genetically or behaviourally compatible to avoid inbreeding or to enhance behavioural coordination or task complementation between mates ([8]; [9]; [10]; [11]; [12]). However, individuals may face energetic, time or spatial constraints in choosing mates ([13]). In such circumstances, individuals are forced to choose within a limited pool of mates and to potentially accept suboptimal mates. A possible response to this limitation in iteroparous species is divorce, defined as one breeding individual changing partner for a new mate while the previous mate is still alive ([14]). Theoretical studies have suggested that individuals should divorce when pairing with a higher-quality or more compatible mate increases their lifetime reproductive success [15]. Accordingly, divorce is common after a reproductive failure ([16]; [17]; [18]), and usually leads to increased reproductive success ([19]; [20]; [17]). Like mate choice, divorce may be associated with the quality of the ornaments of the mate or the genetic or behavioural compatibility of the pair (e.g. [21]; [22]; [23]).

Concerning the genetic component of the pool of heritable factors that can affect mating strategies, the major histocompatibility complex (MHC, called HLA in humans) has been the focus of much research ([24]; [25]; [26]). The MHC, one of the most polymorphic sets of genes in vertebrates, encodes cell-surface proteins that are essential for immunological recognition and defense against pathogens. Because each MHC molecule can bind a limited set of antigens ([27]), higher MHC-diversity increases the number of antigens recognized,

49 thereby providing resistance to a wider range of parasites ([28]; [29]). Accordingly, several
50 studies have found that higher MHC-diversity increases health, reproductive success and
51 survival ([30]; [31]; [32]; [33]; [34]). Because the MHC allelic composition of the offspring
52 results from the combination of those of the parents, numerous studies have found evidence
53 for MHC-based mate choice ([35]; [36]; [37]; [38]; [39]; [40]; [41]). Although there is
54 evidence that the parental MHC-composition also influences other reproductive strategies
55 (e.g. cryptic female choice, [42]; extra-pair copulation, [43]), to our knowledge, a single
56 study on Seychelle warblers (*Acrocephalus sechellensis*) explored how parental MHC-
57 similarity is associated with divorce rate and found no evidence for such an association
58 ([44]).
59 Here we tested whether mate choice and mate change (defined as the probability to
60 observe an individual with a new mate, whether the previous mate is seen alive or not)
61 depend on dissimilarity at MHC class-II B (hereafter MHC-IIB) in the black-legged kittiwake
62 (*Rissa tridactyla*), a long-lived genetically monogamous seabird with no extra-pair copulation
63 ([45]). In kittiwakes, divorce is quite common (i.e., 15% - 50% of the pairs), and more
64 frequent among first-time breeders and after reproductive failure ([46]; [47]; [48]). Coulson
65 ([46]) suggested therefore that some kinds of "incompatibility" between mates results in
66 unsuccessful breeding, thereby providing costs that select for divorce. In black-legged
67 kittiwakes, MHC-IIB similarity between mates results in reduced offspring MHC-IIB
68 diversity ([49]), which incurs costs for female chicks in terms of slower growth, poor tick
69 clearance and lower survival ([50]). We therefore hypothesised that, in this species, mating
70 strategies based on MHC-IIB dissimilarity between mates may have evolved to maximise the
71 MHC-IIB diversity of the offspring.
72 First, we expected individuals to preferentially choose an MHC-IIB dissimilar mate.
73 In several seabirds, including the black-legged kittiwake, young or inexperienced individuals

arrive later to the breeding ground than older or more experienced breeders, which may limit the pool of potential partners ([51]; [52]; [53]). Inexperienced breeders may also be less efficient in sampling mates and less able to make mating discrimination or to anticipate alternative choices ([54]). For instance, in grey mouse lemurs (*Microcebus murinus*), young females in their first mating season do not express mate choice, while experienced females prefer MHC-IIB dissimilar males ([41]). The mate choice of first-time breeders may thus be more constrained than that of experienced breeders. We therefore tested the existence of MHC-IIB dependent mate choice in first-time breeders and experienced breeders separately. Second, if mate change allows individuals paired with a suboptimal mate to increase the MHC-IIB diversity of their future offspring, we expected the rate of mate change to increase with MHC-IIB similarity between mates. Third, we expected that, after a mate change, the new pair should be more MHC-IIB dissimilar than the previous one. In black-legged kittiwakes, although both mates participate fairly equally in incubation and chick rearing, sexes slightly differ in energetic investment in reproduction ([55]; [56]). We thus tested these predictions separately in males and females to explore potential sex differences in mating strategies.

Materials and methods

Study area and population

This study was conducted between 1996 and 2021 in a colony of black-legged kittiwakes nesting in an abandoned U.S. Air Force radar tower on Middleton Island (59°26'N, 146°20'W), Gulf of Alaska, located approximately 100 km south of the mainland. Individuals were tagged with a unique combination of coloured and metal bands for long-term monitoring ([57]). About 400 nest sites were monitored on the tower each year. All these sites were checked daily to record the identity of the individual(s) occupying the nests. For

each individual of the study, sex was determined, in order of priority, by: 1) molecular assessment (n = 746 individuals, [58]); 2) behavioural observations (n = 413 individuals, [59]); and 3) comparison of the relative size of both members of a pair, the largest bird being considered male (n = 16 individuals). When only one individual of a pair was sexed, we attributed the opposite sex to its mate (n = 112 individuals).

Like many populations monitored in the long term, our population has been subjected to several treatments during the study period (e.g. supplemental feeding, brood manipulation, feather clipping, use of anti-copulatory devices). These treatments can affect reproductive success ([57]; [60]; [61]) and therefore pair stability. To limit any bias (e.g. artificial increase of reproductive success, and thus decreased mate change probability due to supplemental feeding), we removed pairs that were subjected to experiments from certain analyses (see below).

We defined a pair as two individuals of opposite sex attending the same nest and laying at least one egg during the reproductive season. Individuals usually remain and breed in the same colony during their whole life ([46]). We thus defined the first mate choice as the pair formed during the first observed breeding attempt. Each individual of the population was involved in on average 4.57 ± 3.61 (SE) reproductive events (range = 1 - 21, Supporting information 1) over the course of the study.

To study mate change, we focused on individuals that were observed with an identified mate during at least one year and that re-mated with a new mate the next year, whether its former mate was re-observed or not. In the studied population, the proportion of pairs in which the two mates were both seen alive in the years after pair splitting was very low (i.e. strict divorce; 6% of all pairs) compared to the proportion observed in other populations of kittiwakes (25% in [46]; between 13 % and 47 % in [47]; 19.1 % on average in [48]). On Middleton island, numerous kittiwakes nest on other man-made structures than

124 the tower ([57]). These sites were not monitored, except for occasional demographic surveys
125 for certain years. It therefore limited our ability to observe alive birds who changed nesting
126 sites, and thus to detect strict divorces. Therefore, we focused our analyses on mate change,
127 which was defined as the situation of an individual being seen with a different mate in year n
128 and n+1, whether the mate of the year n was observed or not in the studied population during
129 the year n+1 and subsequent. Our definition of mate change thus applies to a larger context
130 than strict divorce, and may include widowed birds. However, we also present analyses on
131 the probability of strict divorce in the supplementary material.
132
133 *Molecular analysis*
134 We focused on the MHC class II which exhibits stronger selection than the MHC class I in
135 non-passerines such as the black-legged kittiwake ([62]). Dissimilarity at MHC-IIB was
136 assessed following the methods described in Pineaux et al. ([50]; [63]). Briefly, DNA was
137 extracted from blood with the blood and tissue DNA extraction kit (Qiagen), and a 258-pb
138 fragment of exon 2 of MHC-IIB was amplified using specific primers (forward: 5′-
139 GCACGAGCAGGGTATTTCCA, and reverse: 5′-GTTCTGCCACACACTCACC).
140 Amplicons were then sequenced with an Illumina MiSeq platform, using the 2 x 300-bp
141 protocol (Fasteris SA, Switzerland). Amplicon sequences were analysed with ampliSaS, a
142 three-step pipeline that consists of read demultiplexing, unique sequence clustering and
143 erroneous sequence filtering (substitution errors, 1 %; indel errors, 0.001 %; minimum
144 frequency with respect to dominant, 33 %; minimum amplicon sequence frequency, 2.5 %,
145 [64]). We calculated the MHC-IIB functional distance between individuals based on amino
146 acid variations in the peptide-binding region (PBR) inferred from Leclaire et al. ([65]).
147 We described the chemical binding properties of each amino acid in the PBR with
148 Sandberg's five physicochemical descriptors (z-descriptors, [66]) and computed a Sandberg's

149 distance matrix between sequences using the DistCalc function of the MHCTools package in
150 R ([67]). Then, we calculated an UPGMA dendrogram of sequences (hclust function in R),
151 which represents clusters of functionally similar MHC-IIB sequences (hereafter,
152 "supertypes"). The MHC-IIB functional distance between a male and a female was estimated
153 using the tree distance (treedist function in the package vegan, [68]), which is found by
154 combining sequences in a common dendrogram and calculating how much of the dendrogram
155 height is shared and how much is unique. In addition, we calculated the difference in MHC-
156 IIB supertype sharing between mates by calculating the difference in supertype sharing
157 following the definition of Strandh et al. ([40]):

158 $$100 \times Nb_{supertypes\ pair} / (Nb_{supertypes\ female} + Nb_{supertypes\ male}),$$

159 where $Nb_{supertypes\ female}$ corresponds to the number of supertypes possessed by the female,
160 $Nb_{supertypes\ male}$ corresponds to the number of supertypes possessed by the male, and $Nb_{supertypes}$
161 $_{pair}$ corresponds to the total number of supertypes possessed by the female and the male
162 together (shared supertypes count as 1). This variable thus varies between 50 for individuals
163 sharing no supertype and 100 for individuals sharing all their supertypes. Overall, we
164 identified 15 supertypes, among which 3 were very common (possessed by more than 47 %
165 of the sequenced population), 6 were common, and 6 were rare (possessed by less than 7 %
166 of the sequenced population, Supporting information 2). The MHC-IIB functional distance
167 was highly correlated with the difference in MHC-IIB supertype sharing (Spearman
168 correlation test: $P < 0.01$, $\rho = 0.77$). We found similar results when studying MHC-IIB
169 functional distance and difference in MHC-IIB supertype sharing, except for one analysis
170 (i.e. the analysis on mate choice in first-time male breeders, see below).

171 Mate choice for MHC-IIB dissimilarity may not only be governed by evolutionary
172 processes that specifically target these genes, but may also be affected by mechanisms
173 operating at the level of the entire genome (e.g. inbreeding avoidance). To test whether

174 associations between MHC-IIB dissimilarity and mate choice might be driven by genome-
175 wide relatedness, we used RAD sequencing (n = 92 individuals) to estimate genome-wide
176 relatedness between individuals (Supporting information 3). We found that genome-wide
177 relatedness was weakly correlated with functional MHC-IIB similarity (Mantel test: r = 0.09,
178 P = 0.04), and not correlated with MHC-IIB supertype similarity (Mantel test: r = 0.04, P =
179 0.14). These associations were not significant when excluding the four individuals involved
180 in a first-degree family relationship (siblings or parents-chicks; Mantel tests: r = 0.05, P =
181 0.16 and r = 0.02, P = 0.33).
182
183 *Statistical analysis*
184 To test for potential differences between sexes, we conducted all analyses on males and
185 females separately (see sex-specific sample sizes and details of the analyses in Supporting
186 information 4). We performed all analyses using the R software (R Core Development Team
187 2023, version R 4.4.0). All datasets and code used in the analyses are available from the
188 Zenodo Repository (https://doi.org/10.5281/zenodo.14523780).
189 To test whether males and females selected a more MHC-IIB dissimilar mate than
190 under random mating, we used bootstrapping to generate random pairs, where we let each
191 individual choose randomly 10000 times between all available opposite-sex mates of the
192 same year, without replacement (i.e. one mate can be selected only once during a given year,
193 [69]). An individual was considered to be available for mating in year n if it was seen in the
194 colony during that year, unless it was observed with the same mate in both the previous year
195 n-1 and the current year n. We also ran the same analyses when considering all opposite-sex
196 mates of the same year, and found similar results (Supporting information 5). We calculated
197 p-values as the proportion of iterations in which the random MHC-IIB dissimilarity mean
198 was superior or equal to the observed MHC-IIB dissimilarity mean (one-tailed test). We

199 tested MHC-IIB based mate choice for: i) first-time breeders only (n = 487 males and n = 485
200 females), and ii) all the breeders of the population experiencing a mate change (n = 220
201 events in males and n = 233 events in females). Because of a lack of available mates of
202 known MHC-IIB composition to generate random re-matings for the females in 2004, we
203 excluded the 2004 data in the mate choice analysis (n = 13 reproductive events).
204 To test whether mate change probability (1 = mate change between the year n and
205 n+1, 0 = faithful pair between the year n and n+1) varied with the MHC-IIB dissimilarity of
206 the pair during the year n in males (n = 1104) and females (n = 1094), we used Generalised
207 Linear Mixed Models (GLMM) with a binomial distribution of error and a logit link (glmer
208 function of the lme4 package, [70]). We tested the effect of the MHC-IIB dissimilarity (fixed
209 effect) in two different models, after a reproductive success and after a reproductive failure.
210 Indeed, the MHC-IIB dissimilarity might influence the reproductive outcome, which is also
211 known to influence the probability of divorce in black-legged kittiwakes ([48]). We defined
212 the reproductive outcome as a binary variable recording the presence (i.e. "success") or
213 absence (i.e. "failure") of at least one chick fledged at the end of the reproductive season. In
214 the models, we set the nAGQ argument (number of points per axis for evaluating the adaptive
215 Gauss-Hermite approximation to the log-likelihood) of the glmer function to 0 to help for
216 convergence when necessary ([71]). We tested the effect of individual identity and year as
217 random intercepts with the ranef function of the lme4 package ([70]) and removed these
218 variables when they had no effect. We removed pairs that were subjected to experiments
219 from this analysis. As we used GLMM with binomial data, we provided the log odd (and its
220 standard error), which is equivalent to the coefficient of the slope in a linear model (i.e.
221 estimate in the model summary), i.e. the probability of an event in the log scale, which is the
222 transformed scale to satisfy the assumptions of a linear model for GLMM with binomial data.
223 When using mixed models, we calculated the confidence intervals on the fixed effects using

224 the predictInterval function of the merTools package (n iterations = 10000, [72]). We
225 conducted the same analysis when considering only the pairs for which both mates were seen
226 during the years n and n+1 (Supporting information 6). This dataset, although smaller than
227 the original one (n = 1022 events in males, and n = 1034 events in females) particularly
228 regarding the number of pair splitting (n = 50 (37 after breeding failure, 13 after breeding
229 success) versus 132 events in males, n = 62 (41 after breeding failure, 21 after breeding
230 success) versus 122 events in females), served as a refined dataset focusing on strict divorce.
231 However, as the individual monitoring focused mostly on individuals breeding in the tower,
232 this dataset might exclude individuals involved in a strict divorce but breeding elsewhere on
233 the island.

234 If individuals changed mate, we tested whether their new mate was more MHC-IIB
235 dissimilar to them compared to the previous one (n = 165 males, n = 179 females) using
236 Linear Models (LM). The response variable was the MHC-IIB dissimilarity gain, i.e. the
237 difference between the MHC-IIB dissimilarity to the previous mate and the MHC-IIB
238 dissimilarity to the new mate. Using the gain in a LM framework allowed us to estimate if the
239 difference between the MHC-IIB dissimilarity to the previous mate and the new mate was
240 significantly different from 0. Additionally, it allowed us to include individual and year as
241 random effects. Each individual possesses its own MHC-IIB composition, which can be rare
242 or common, and it is easier for an individual with a rare MHC-IIB composition to find a new
243 mate which is MHC-IIB dissimilar compared to an individual with a common MHC-IIB
244 composition. Depending on the year, the MHC-IIB composition of the individuals available
245 in the population might change and affect the ability to find MHC-IIB dissimilar mates.
246 These phenomena can create individual and year patterns, and the use of random effects
247 allows us to account for this potential source of variability. We tested the effect of individual
248 identity and year as random intercepts with the ranef function of the lme4 package ([70]) and

249 removed these variables when they had no effect. Similarly to the previous analysis, we used
250 two different models: after a reproductive failure and after a reproductive success. We used
251 the 0.5 quantile of a Quantile Regression Model (lqm function of the lqmm package, [73])
252 instead of LM when we encountered problems of non-normality and/or heteroscedasticity of
253 the residuals (tested with the simulateResiduals function of the DHARMa package, [74]).
254

255 **Results**

256 *Analyses from the point of view of the males*

257 First-time male breeders paired with a female which had a higher MHC-IIB supertype
258 sharing than expected by chance (P = 0.01). This result was not significant when considering
259 MHC-IIB functional distance (P = 0.08, Fig. 1).

260 Mate change probability varied differently with the MHC-IIB dissimilarity of the pair
261 depending on the reproductive output (Fig. 2). After a successful reproduction (n = 620
262 reproductive events), males were less likely to change mates if they were more MHC-IIB
263 dissimilar to the female (functional distance: log odd ± SE = -0.22 ± 0.09, P = 0.02;
264 difference in supertype sharing: log odd ± SE = -0.03 ± 0.01, P = 0.05). Mate change
265 probability was higher after a breeding failure (n = 484 reproductive events) than after a
266 breeding success (107 % increase in the probability of mate change compared to after a
267 breeding success). However, after a breeding failure, mate change probability did not vary
268 with the MHC-IIB dissimilarity of the pair (functional distance: log odd ± SE = 0.02 ± 0.06,
269 P = 0.73; difference in supertype sharing: log odd ± SE = 0.00 ± 0.01, P = 0.65). When
270 considering only pairs in which both mates were seen during the years n and n+1 (i.e., strict
271 divorce only), the MHC-IIB dissimilarity did not affect the probability of mate change,
272 neither after a reproductive failure (functional distance: log odd ± SE = 0.10 ± 0.10, P = 0.31;
273 difference in supertype sharing: log odd ± SE = 0.00 ± 0.01, P = 0.80; Supporting

274 information 6), nor after a reproductive success (functional distance: log odd ± SE = -0.20 ±
275 0.15, P = 0.18; difference in supertype sharing: log odd ± SE = -0.02 ± 0.02, P = 0.28;
276 Supporting information 6).
277 When mate change occurred after a reproductive success, the MHC-IIB functional
278 distance between the male and the new female was higher compared to that between the male
279 and the previous female (mean ± SE = 0.51 ± 0.23, P = 0.03; difference in MHC-IIB
280 supertype sharing: P = 0.05; Fig. 3). In contrast, after a reproductive failure, there was no
281 difference in MHC-IIB functional distance between the new and the previous pair (mean ±
282 SE = -0.23 ± 0.25, P = 0.35; Fig. 3; difference in MHC-IIB supertype sharing: P = 0.91).
283 However, males did not re-mate with a female who had a higher MHC-IIB functional
284 distance than expected under random mating, neither after a reproductive success (P = 0.31;
285 difference in MHC-IIB supertype sharing: P = 0.24) nor after a reproductive failure (P = 0.22,
286 Fig. 4; difference in MHC-IIB supertype sharing: P = 0.20).
287
288 *Analyses from the point of view of the females*
289 Females did not mate with a more MHC-IIB dissimilar male than expected under random
290 mating, neither for their first breeding attempt (functional distance: P = 0.33, Fig. 5a;
291 difference in supertype sharing: P = 0.20), nor when they were experienced breeders
292 (functional distance: P = 0.20; Fig. 5b; difference in supertype sharing: P = 0.08).
293 In females, mate change probability did not vary with the MHC-IIB dissimilarity of
294 the pair, neither after a reproductive failure (functional distance: P = 0.31; difference in
295 supertype sharing: P = 0.44), nor after a reproductive success (functional distance: P = 0.66;
296 difference in supertype sharing: P = 0.78). We found similar results when considering only
297 pairs for which both mates were seen in the years n and n+1 (Supporting information 6).
298 However, as expected, the probability to change mate was higher after a reproductive failure

299 than after a reproductive success (49 % increase in the probability of mate change compared
300 to after a breeding success). The difference in MHC-IIB dissimilarity between the new and
301 the previous male mate was not different from 0 (functional distance: mean ± SE = 0.03 ±
302 0.17, P = 0.86; difference in supertype sharing: P = 0.95).
303

304 **Discussion**

305 In this study, we tested whether the mating strategies (i.e. mate choice and mate change) of
306 black-legged kittiwakes depend on the MHC-IIB dissimilarity between mates. We found sex-
307 specific patterns.
308 First-time male breeders were paired with more MHC-IIB dissimilar females than
309 expected by chance. Like several other species (e.g. [75]; [76]; [28]; [77]; [78]), including
310 birds ([79]; [80]), black-legged kittiwakes are able to recognize MHC-IIB dissimilarity using
311 body odors ([63]). In this species, the recognition of MHC-IIB dissimilarity might have
312 evolved as a mechanism to select MHC-IIB dissimilar mates to produce offspring with high
313 MHC-IIB dissimilarity ([49]), and therefore to increase female offspring growth, tick
314 clearance and survival ([50]). Similarly, in the domestic cat (*Felis catus*), mating with MHC-
315 IIB dissimilar mates increases offspring survival and thus probably parental fitness ([81]). In
316 contrast to first-time breeding males, we did not find evidence for MHC-IIB dissimilarity
317 based mate choice when considering first-time breeder females. Our analysis design does not,
318 however, allow us to determine whether these results are driven by males' choice or females'
319 choice. For instance, first-time male breeders may preferentially choose MHC-IIB dissimilar
320 females, or females may preferentially choose MHC-IIB dissimilar males when they have to
321 mate with a first-time male breeder. Similarly, in bluethroats (*Luscinia svecica*), only pairs
322 including females with a young male are more MHC-compatible than expected from random
323 pairing ([82]). In kittiwakes, the breeding experience is an important factor determining

324 reproductive success ([83]). Females paired with young inexperienced males might thus
325 compensate for the lack of experience of their mate by choosing MHC-IIB dissimilar males.
326 Males paired with a more MHC-IIB similar female had a higher probability of
327 changing mate in the next breeding season than males paired with a more MHC-IIB
328 dissimilar female. However, this result was significant only for pairs that reproduced
329 successfully. In pairs that failed to reproduce, mate change probability was higher than in
330 pairs that reproduced successfully, but it did not vary with the MHC-IIB dissimilarity
331 between mates. Hence, besides reinforcing the known role of breeding success on mate
332 change in black-legged kittiwakes ([47]; [84]; [48]), our results reveal the importance of
333 MHC-IIB dissimilarity in mate change in this species. However, we did not detect an effect
334 of MHC-IIB dissimilarity on mate change probability when considering females who were
335 observed changing mate, or when focusing on strict divorces. These results suggest that the
336 splitting pairs in which the males were seen alive in the studied population differ from those
337 in which the female or both mates were seen alive in the studied population after splitting.
338 Accordingly, in these former pairs, only 14 % of the females were seen alive in the studied
339 population. Low sample size coupled with potential sampling bias can affect the conclusions
340 of the analyses when studying the role of MHC-IIB composition in mating strategies (e.g. in
341 randomisation tests, [85]). Thus, the structure of our dataset limits our ability to conclude on
342 the absence of an effect of the MHC-IIB dissimilarity on the probability of divorce.
343 Nevertheless, in black-legged kittiwakes, females invest more than males in
344 reproduction ([55]; [56]), and they adjust their parental care to chick requirements more than
345 males ([86]; [87]). In pairs that reproduced successfully, females of MHC-IIB similar pairs
346 might have invested more energy in parental care than females of more MHC-IIB dissimilar
347 pairs to compensate for the deleterious effects of reduced MHC-IIB diversity of the offspring.
348 This higher investment rate might have reduced their survival at sea during the next winter

349 and explain the lower re-observation rate ([86]). It could eventually have forced their male
350 partner to mate with a new female. Non-exclusively, either mate might have chosen to
351 divorce. In kittiwakes, females are the dispersing sex ([88]) and they are less faithful to the
352 nesting site than males ([47]). Accordingly, in our dataset, females were less often re-
353 observed in the studied population after a mate change compared to males (n = 14 % of
354 females re-observed versus 21 % of males re-observed among splitting pairs). Therefore, the
355 females mated with a MHC-IIB similar male might have dispersed away from the tower, or
356 even from the colony, which forced the male to re-mate with a new partner. Under this latter
357 scenario, the reproductive success, as measured by the successful fledging of a chick, would
358 not be the only determinant of divorce in black-legged kittiwakes. For instance, not only the
359 presence of a fledgling, but also its quality (sensu [89]), which is shaped in part by its MHC-
360 IIB diversity and thus the MHC-IIB dissimilarity of the parents ([50]; [49]), might be a
361 determinant of the probability of female changing mates and nesting site. A previous study in
362 black-legged kittiwakes showed that MHC-IIB similar parents preferentially produce males
363 rather than females, probably to mitigate the cost of producing a female chick with low
364 MHC-IIB diversity ([49]).

365 Our study suggests that mate change might be another parental strategy to reduce the
366 deleterious effect of mating with a MHC-IIB similar mate. To which extent these potential
367 strategies translate into fitness benefits requires further studies. The lack of association
368 between MHC-IIB dissimilarity and mate change probability when considering females seen
369 alive in the studied population suggests that these females have changed mate for other
370 reasons than high MHC-IIB similarity. These reasons may include the death of the male, late
371 arrival of the male at its usual breeding site, or the intrusion of a third individual ousting the
372 male ([90]; [91]).

We found that although males who changed mate tended to pair with a new female not more MHC-IIB dissimilar to them than a random female, the new female was more MHC-IIB dissimilar to them than the previous one. Even though our results cannot ascertain the existence of an active mate choice of males when remating, they suggest that even random mate choice is sufficient to pair with a more MHC-IIB dissimilar female compared to the previous one. Interestingly, we found that males involved in MHC-IIB similar pairs tended to have very common MHC-IIB genotypes (Supporting information 2), thereby probably limiting their possibility to mate with a female which is highly MHC-IIB dissimilar to them.

The contrasting results between males and females likely illustrate sex-specific mating strategies. In long-lived monomorphic species in which males and females equally share parental care, such as the black-legged kittiwake ([61]), mate choice has been suggested to be mutual ([92]). However, males and females may have different preference criteria ([93]; [94]). In the Leach's storm-petrel (*Oceanodroma leucorhoa*), males show MHC-IIB based disassortative mate choice, whereas females' choice does not differ from random mating ([95]). The intrinsic quality of the parent, such as its ability to provide good genes ([96]; [97]), but also good parental care ([98]) or good-quality territory ([99]), may be more important factor for one sex than the other. In kittiwakes, females invest more in reproduction than males ([55]; [56]) and males may thus benefit from choosing a mate in good health or condition more than females. Future studies are needed to investigate whether mate choice based on MHC-IIB dissimilarity trades off with mate choice for other criteria and it varies with sexes. For instance, in a cichlid fish, while genetic similarity is a more important criteria for mate choice than body size for females, the opposite is true for males ([10]).

A previous study on the same population of black-legged kittiwakes showed that pairs have a higher genetic dissimilarity (as measured by microsatellites) than expected by chance,

398 and that the resulting increased heterozygosity of their chicks leads to higher fitness ([100]).
399 Although MHC-IIB disassortative mate choice may also participate in limiting inbreeding (
400 [77]; [101]), here we detected only a weak correlation between genome-wide relatedness and
401 MHC-IIB dissimilarity, which was driven by two pairs made of first-degree relatives. These
402 results suggest that MHC-IIB based mating strategies detected in black-legged kittiwakes are
403 probably driven by the MHC rather than resulting from inbreeding avoidance at the genome-
404 wide scale.

405 In conclusion, we found evidence that MHC-IIB dissimilarity influences mate choice
406 in the black-legged kittiwake and that low MHC-IIB dissimilarity between mates increases
407 the probability for males to change mates in the future, even after a reproductive success.
408 These results support the role of the benefits associated with high MHC-IIB dissimilarity in
409 the evolution of mating strategies in this population ([50]). The selective pressures for higher
410 MHC-IIB diversity, such as the level of parasite exposure depending on environmental
411 conditions ([102]), as well as the balance between the benefits of a higher MHC-IIB diversity
412 and those of other mating criteria, can however vary between species, population, ages or
413 sexes, as suggested in the present study. In the latter case, when mate choice is mutual, a
414 sexual conflict over mating strategies can arise ([103]) and may select for a rich repertoire of
415 sex-specific behavioural adaptations ([104]). Our study paves the road for further studies of
416 sex-specific mate choice in species with bi-parental care, a common trait in birds ([105]).

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722 **Figures**

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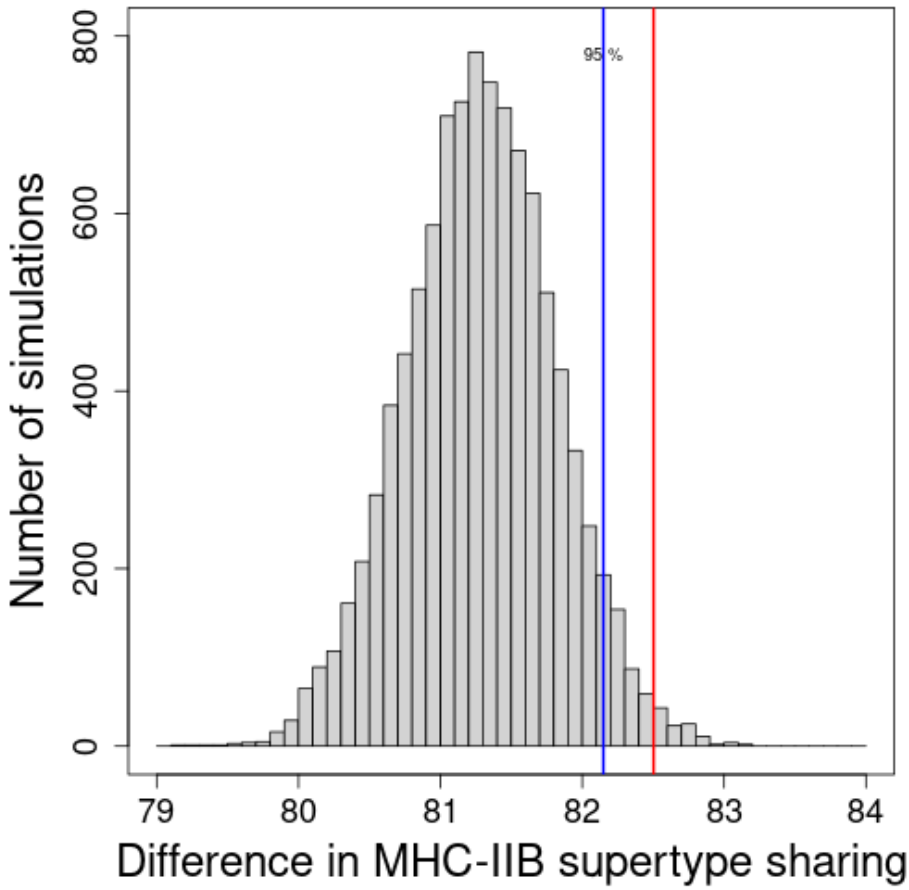

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725 Figure 1: Frequency distribution of difference in MHC-IIB supertype sharing means between
726 first time male breeders and their female mate calculated from 10000 bootstrap
727 randomizations of potential male-female pairs out of the sample studied. The red vertical line
728 is the observed MHC-IIB functional distance. The blue vertical line is the upper 95 %
729 quantile of the simulated distribution.

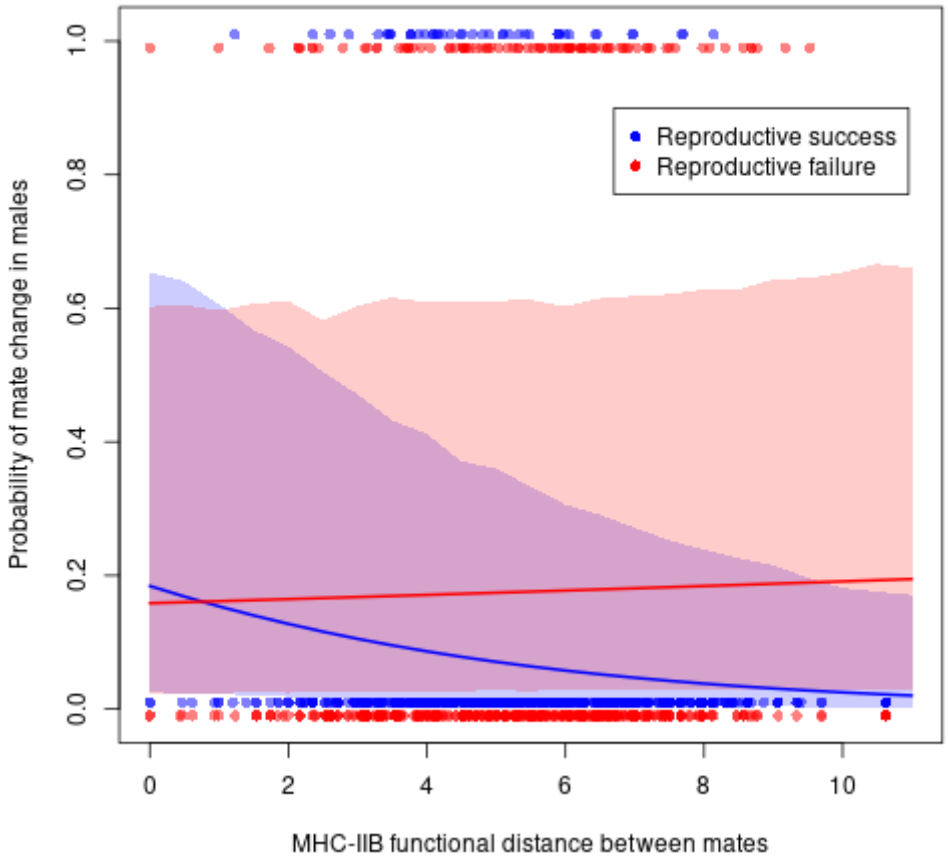

Figure 2: Probability of mate change in males according to the MHC-IIB functional distance with their female mate, when the pair reproduced successfully (in green) or not (in yellow). The yellow and green dots represent the raw observations, and the yellow and green lines represent the predictions of the model. The yellow and green shaded areas represent the 95 % confidence intervals on the fixed effects.

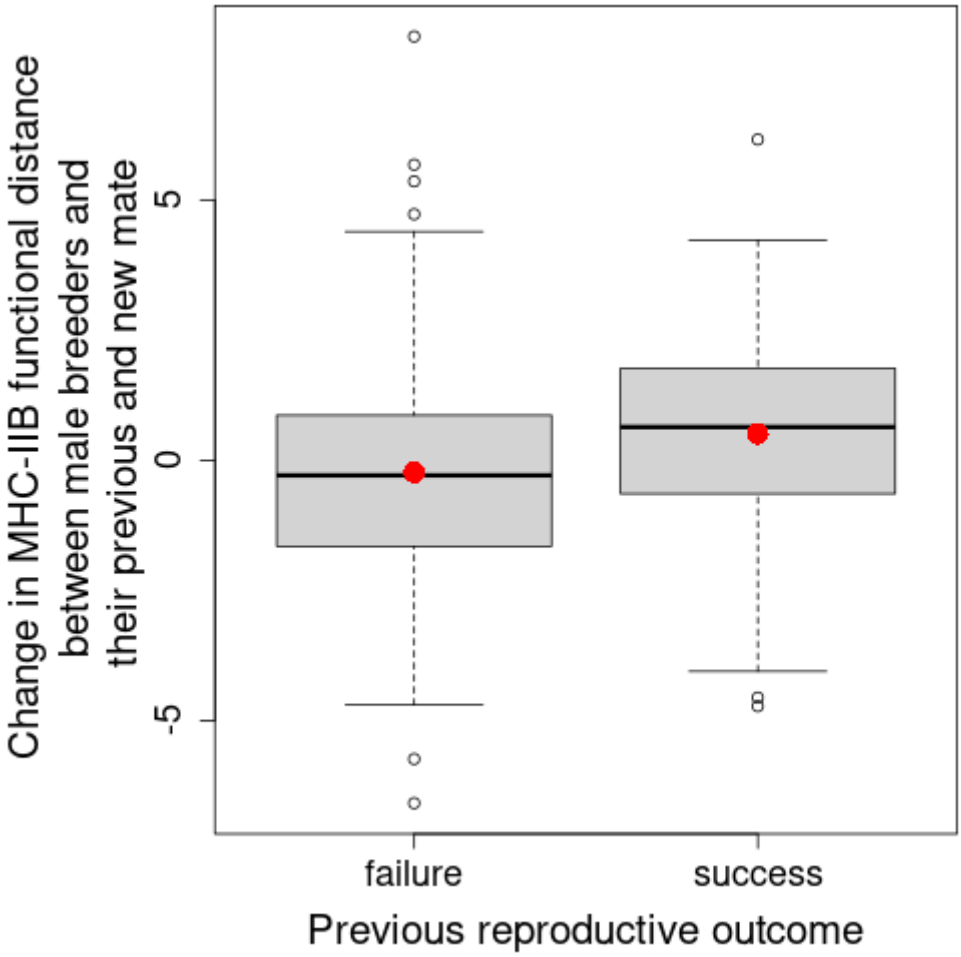

Figure 3: Change in MHC-IIB functional distance between mates in year n+1 compared to year n after the male changed mate following a reproductive success or a reproductive failure. The horizontal black lines represent the medians, the red dots represent the means, the boxes represent the interquartile ranges (IQR) of the distribution, the whiskers extend to the minimum and maximum values within 1.5 times the IQR and the open dots represent the values beyond these limits.

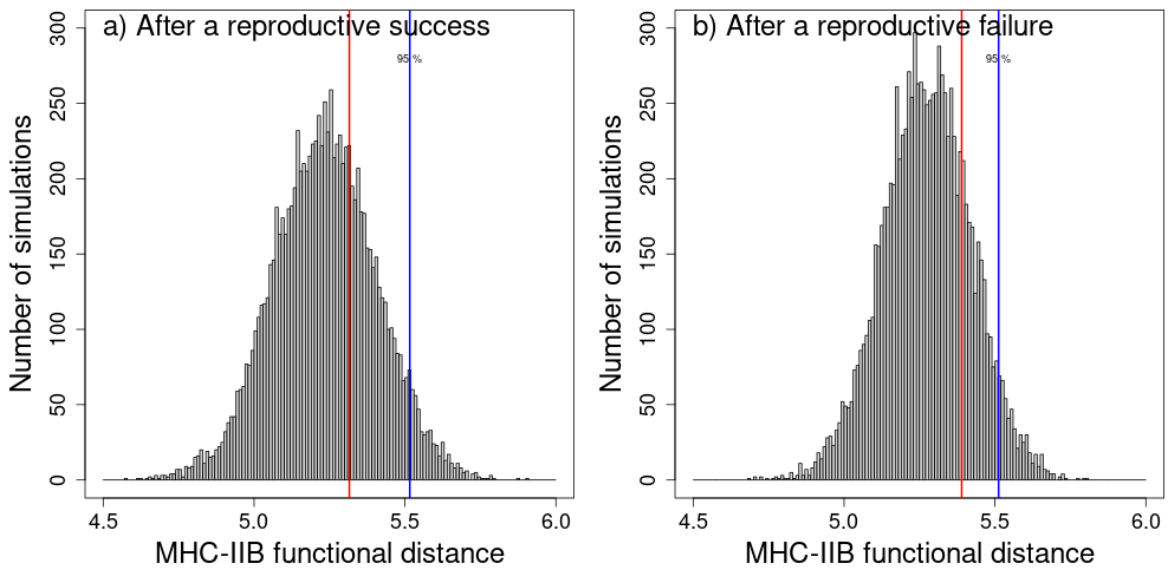

Figure 4: Frequency distribution of MHC-IIB functional distance means between male breeders and their female mate calculated from 10000 bootstrap randomizations of potential male-female pairs out of the sample studied when the previous pair had: a) a reproductive success, b) a reproductive failure. The red vertical line is the observed MHC-IIB functional distance. The blue vertical line is the upper 95 % quantile of the simulated distribution.

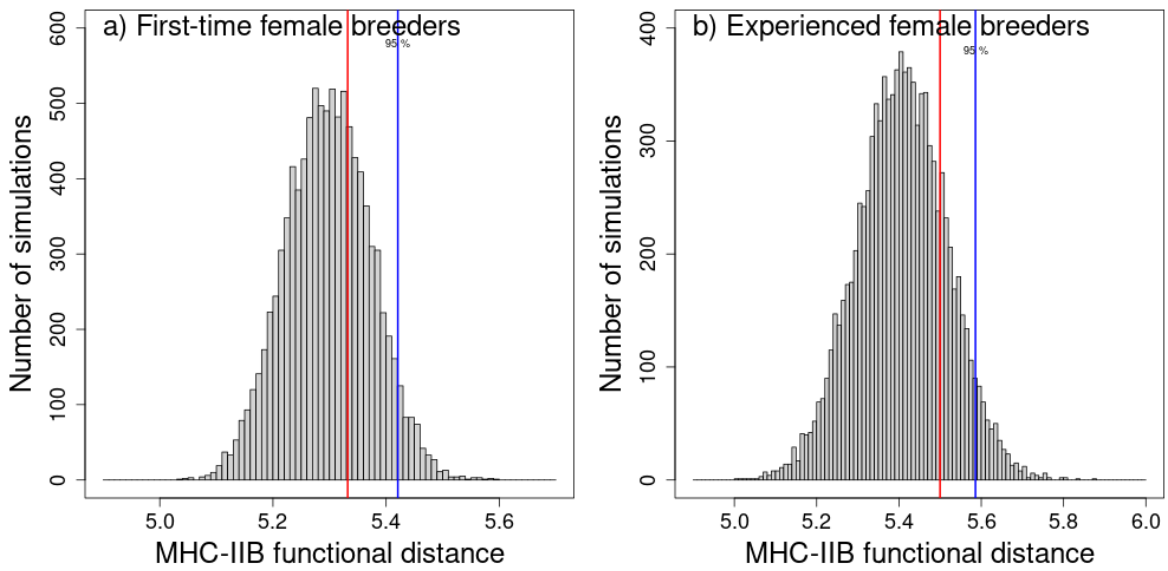

Figure 5: Frequency distribution of MHC-IIB functional distance means between: a) first time female breeders, b) experienced female breeders and their male mate calculated from 10000 bootstrap randomizations of potential male-female pairs out of the sample studied. The red vertical line is the observed MHC-IIB functional distance. The blue vertical line is the upper 95 % quantile of the simulated distribution.