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RESEARCH ARTICLE

Links between personality, reproductive success and re-pairing patterns in a long-lived seabird

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Abstract

In long-lived monogamous species, the trigger of costly re-pairing is not always clear. Limited research suggests that within-pair behavioural compatibility may be an important driver of partnership success, as cooperation should be enhanced when pair members' decisions complement one another. Animals' decision-making processes are influenced by personality traits – defined as individual differences in behaviour that are stable in time. Despite the potential for the personality trait 'boldness' to (a) directly impact individual willingness to re-pair and (b) indirectly impact re-pairing choices via reproductive success, there is currently little work exploring how re-pairing decisions might be impacted by the pair members' personalities. Using a 13-year dataset, we investigated whether within-pair boldness and its relationship with breeding success explained re-pairing patterns of black-legged kittiwakes (*Rissa tridactyla*), breeding in two Arctic colonies. We found that pairs with dissimilar boldness levels were more likely to experience breeding failure and that failed pairs were more likely to re-pair the following year. Despite this, only one colony displayed evidence of assortative mating by boldness, and there was no indication that re-pairing impacted reproductive success the following season. Neither individual nor pair boldness directly influenced re-pairing probability; however, in both colonies, re-pairing birds chose partners that were slightly more similar to themselves in boldness than their previous mates. These results imply an indirect pathway by which poorer behavioural compatibility within pairs may lead to breeding failure and ultimately re-pairing. Our findings highlight the importance of behavioural compatibility, and possibly personality, in mitigating sexual conflict and its population-specific drivers.

KEYWORDS
behavioural compatibility, boldness, divorce, kittiwake, mate choice, parental care

1 | INTRODUCTION

In order to successfully reproduce, animals must contend with factors both within and outside their control. Many intrinsic factors that are not alterable by the individual, including individual quality and age, may nevertheless influence reproductive success (Fowler, 1995; Wilson & Nussey, 2010). Thus, animals should attempt to make decisions during foraging, habitat selection and mate choice that allow them to employ the best strategy given the hand they have been dealt (Jeffries et al., 2021; Vincze et al., 2017). In biparental care, these decision-making processes have the potential to be extremely complex, as the condition or behaviour of one partner might impact the choices of the other (Barta et al., 2002; Holtmann et al., 2022).

In long-lived monogamous animals that practice biparental care, pair members share lifetime reproductive success (Griffith, 2019; Mariette & Griffith, 2015). As the behaviour of one partner directly affects the reproductive output of the other, exploitation can be unprofitable, and sexual conflict may incur heavy costs (Jones et al., 2002; Royle et al., 2002). Instead, selection should favour mechanisms that encourage equal effort, which may require coordination of behaviour (Johnstone & Savage, 2019). Mate choice is therefore a critical decision, as choosing a behaviourally compatible partner may help resolve sexual conflict and have long-term implications for the quality of the pair's parental care (Bebbington & Groothuis, 2023; Munson et al., 2020).

Examining individual personalities may provide insight into how animals assess their behavioural compatibility with a potential partner. Personality, defined as individual behavioural differences that are consistent over time (Sánchez-Tójar et al., 2022), is an important intrinsic characteristic that influences both behaviour and, in many species, reproductive output (Biro & Stamps, 2008). Bolder animals demonstrate greater risk tolerance and are generally predicted to invest more heavily in their current breeding attempts to counteract a shortened lifespan (Dammhahn & Almeling, 2012; Smith & Blumstein, 2008). In contrast, shy and risk-averse individuals may make more conservative choices and be more willing to adjust their foraging or breeding strategies when conditions change (Cole & Quinn, 2014; Wolf et al., 2008). Because decision-making processes within biparental pairs are inherently linked, the breeding outcomes and behavioural choices of individuals will depend not just on their own personalities, but also those of their partners (Masilkova et al., 2022; Schuett et al., 2010). The interactions between pair members' personalities may contribute to behavioural compatibility and thus reproductive success, as parents with similar personalities may reap fitness benefits from more effective parental care and improved offspring quality (Ihle et al., 2015; Schuett et al., 2011). In contrast, mismatched parents may struggle to coordinate care or find it more challenging to predict each other's behaviour (Fox & Millam, 2014; Spoon et al., 2006; Wolf et al., 2011).

In cases of incompatibility, changing partners is one potential outcome. Sometimes, experienced breeders are forced to find a new partner (for example, after being widowed); however, theory predicts that choosing to divorce (when both partners survive but one or both choose a different partner for subsequent breeding attempts) may incur considerable cost (Choudhury, 1995; Ismar et al., 2010). Re-pairing (defined as a bird breeding with a new mate following divorce or partner death) is uncommon in long-lived, monogamous birds, including many seabird species (Mercier et al., 2021; Sun, Barbraud, et al., 2022; Ventura et al., 2021). High adult survival means seabirds are less likely to be widowed between seasons, and the fitness benefits of fidelity are widely reported in these taxa (Mills, 1973; Moody et al., 2005). The benefits of partner fidelity discourage breeding birds from finding a new mate too quickly if their partner is late to return to the colony when breeding begins, lowering divorce rates (Jeschke & Kokko, 2008). Divorce may also be costly in seabirds because searching for a new mate may cause breeding delays or loss of mate familiarity, leading to high reproductive costs immediately after re-pairing (Ens et al., 1993; Ismar et al., 2010; Seyer et al., 2022).

Not all research supports the claim that re-pairing is maladaptive. As several studies suggest while re-paired individuals may incur short-term costs, divorcing an unsuitable mate in favour of a more compatible one may improve long-term reproductive success (Choudhury, 1995; Wagner et al., 2022). Although divorce is rare in seabirds, when it does occur, it has often been found to follow poor breeding success (Coulson, 1966; Mills, 1973). Mercier et al. (2021) reported that black-legged kittiwakes (*Rissa tridactyla*, *Linnaeus*) (henceforth 'kittiwakes') were more likely to remain faithful between years following the successful rearing of a chick. Similarly, Wagner et al. (2022) found that reproductive failure was positively correlated with the divorce rates of Magellanic penguins (*Spheniscus magellanicus*, *Forster*). Thus, in specific circumstances, divorce may be adaptive if birds are able to improve long-term reproductive success with a new partner (Culina et al., 2015).

Personality has been associated with variation in reproductive output in some seabirds (Collins et al., 2019; Patrick & Weimerskirch, 2014), but the potential link between personality and re-pairing has received less attention. While assortative mating according to personality has been observed in some species (reviewed in Schuett et al., 2010), it is not clear whether the inverse, that disassortative mating leads to re-pairing- is true. To our knowledge, the only study on the impact of personality on re-pairing in non-human animals concerns seabirds (Sun, Van de Walle, et al., 2022). Sun, Van de Walle, et al. (2022) reported that shy male wandering albatrosses (*Diomedea exulans*, *Linnaeus*) exhibited higher rates of divorce because they were less able to compete with extra-pair males. The link between personality and divorce in wandering albatrosses was not influenced by reproductive success (which is extremely high in this species); however, the potential links between personality, reproductive success and re-pairing have yet to be tested in other study systems.

We aimed to examine how these factors (personality, reproductive success and re-pairing patterns) interacted within an Arctic-dwelling population of kittiwakes (Figure 1). Kittiwakes offer an ideal study system to investigate these questions. Individual personality
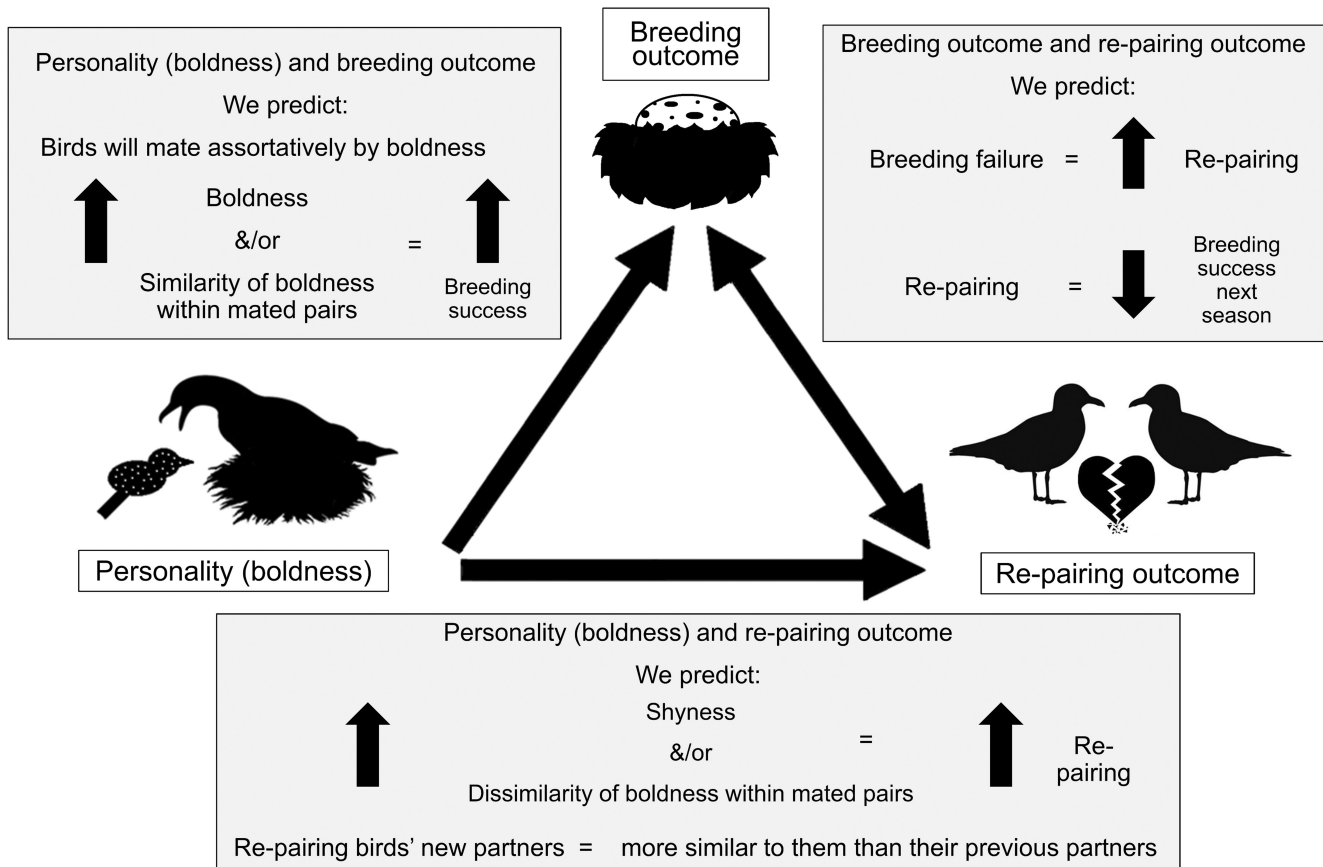
FIGURE 1 Summary of the predicted relationships between personality (the trait 'boldness' is a continuous scale from bold to shy, measured by a novel object), reproductive success and re-pairing in kittiwakes.

(boldness) is measurable and repeatable in this species and is correlated with foraging strategy, reproductive behaviour and reproductive success (Collins et al., 2019; Harris, Descamps, Sneddon, Cairo, et al., 2020). The idea that kittiwake pairs might rely on behavioural compatibility to coordinate their incubation shifts was posited by Coulson (1966), but empirical evidence is lacking. Evidence suggests that they mate assortatively by boldness, and so personality might provide a viable mechanism by which kittiwakes assess behavioural compatibility during mate choice (Collins et al., 2019). How these factors might impact re-pairing has never been explored in this species.

We predicted that bolder birds would have higher reproductive success but that pairs with greater dissimilarity in their personalities would have lower reproductive success (Biro & Stamps, 2008; Munson et al., 2020) (Figure 1). We also predicted that the probability of re-pairing would increase following breeding failure (Coulson, 1966; Mercier et al., 2021). As a result, we predicted that pairs with greater dissimilarity in personality would be more likely to re-pair. Although individuals that fail to breed may benefit from re-pairing in the long term, we predicted this behaviour to cause an initial decline in reproductive success for re-pairing birds compared to faithful couples (Ismar et al., 2010). We predicted that birds would assortatively mate by boldness and that re-pairing birds would choose a new partner more similar to them in boldness than their previous mate (Collins

et al., 2019). Finally, we also predicted that shy birds would be more willing to change their breeding strategy following reproductive failure compared to bolder conspecifics, leading to higher re-pairing probabilities (Wolf et al., 2008) (Figure 1).

2 | METHODS

2.1 | Study population

Data were collected from two separate colonies of kittiwakes in Svalbard: Grumant, Isfjorden (78°10′ N, 15°05′ E) from 2009 to 2018, and Pyramiden, Billefjorden (78°39′ N, 16°19′ E) in 2018, 2019, 2021 and 2022 (Appendix S1).

During the study period, Grumant was occupied by between 20 and 50 breeding pairs of kittiwakes, while Pyramiden was substantially larger, with more than 1000 breeding pairs. The average divorce rate in Grumant has previously been reported as 19.1% but the equivalent figure for Pyramiden is unknown (Mercier et al., 2021). The re-pairing rate, which includes both mortality-induced re-pairing and divorce, is unknown but will be higher than the true divorce rate. Once paired, kittiwake parents share the care of between one and two (rarely three) offspring for around 7 weeks (Barrett & Runde, 1980). They can live beyond the age of 25 (Robinson, 2005)

and adult survival rate in Svalbard has been estimated as 83% (Sauser et al., 2023).

2.2 | Partnership outcome and reproductive success

Colony monitoring took place each year between early and mid-incubation (early/mid-June) until mid-chick-rearing (late July/early August). Incubating adult birds were captured using a noose pole and fitted with a unique metal ring for long-term identification, and a plastic ring with a unique code for identification at a distance. The identities of breeding pair members were established each year using a combination of capture and observation data. Birds were sexed by either molecular sexing (via DNA from blood and feather samples) ($N=99$) or head-bill measurements ($N=284$) (Coulson, 2009) (Appendix S2).

After separating at the end of the breeding season (year t), adults spend the non-breeding season at sea, before returning to colonies to breed in monogamous pairs. At this point (year $t+1$), experienced breeders will choose to either reunite with their previous mate or find a new partner (Coulson, 1966). The variable 're-pairing outcome' was reported as the partnership outcome for year $t+1$. The possible partnership outcomes were listed as 'faithful' or 're-paired'. 'Faithful' was applied when two individuals that had paired together during year t reunited to breed again in year $t+1$. Occasionally, data for year $t+1$ for a specific pair was absent; however, the pair was reported to be breeding together in year t and then again in year $t+2$ ($n=40$ instances). We found no evidence of pairs divorcing, re-pairing for a single year and then reuniting. Thus, these 40 pairs were assumed to have been faithful in year $t+1$.

The term 're-paired' was applied to pairs that bred together in year t, but in year $t+1$, at least one pair member was recorded to be breeding with a different partner. It was not always possible to determine if a re-pairing event had occurred due to the death of one partner or due to a true divorce. The response variable 're-pairing outcome' therefore includes both incidents of widowing and divorces (Mills, 1973; Seyer et al., 2022), thus differing from Mercier et al. (2021), which focused on true divorce. To test whether the ability to disentangle incidents of widowing and divorces affected our results, alternative analyses were conducted containing only true divorces (one partner was breeding with another bird, but both partners were sighted in year $t+1$ or after). These models used the response variable 'divorce outcome' (with the levels 'faithful' or 'divorce') and are reported in the Appendix S3a. The results of these models were similar to those reported in the paper's main body.

In 20 cases (of a total of 121 re-pairing events), pairs were known to have re-paired, but the exact season where the separation took place could not be determined. For example, specific individuals were seen breeding together in year t, were not recorded in year $t+1$ but then bred with different partners in year $t+n$. The variable 'missing seasons' (the number of years since the individuals were last recorded) was created to account for this in analyses that were independent of reproductive success in year t (see M5: boldness_re-pairing outcome below). An analysis excluding these cases was conducted and produced similar results (Appendix S3b). These instances were therefore retained to maximise the sample size.

Breeding outcome was recorded as success or failure. A breeding attempt was defined as a 'success' if at least one chick survived for at least 15 days after hatching. This is the age at which the chicks are ringed and is used as a proxy for fitness in kittiwakes in other studies (Mercier et al., 2021). No breeding outcome data were available for 2019 at Pyramiden.

2.3 | Quantifying boldness

The personality trait 'boldness' was measured during the incubation and brooding periods of 2017 and 2018 (Grumant) and the incubation periods of 2018, 2019 and 2021 (Pyramiden) using novel object testing. This method has been used to quantify personality in multiple seabird species (Grace & Anderson, 2014; Krüger et al., 2019; Patrick & Weimerskirch, 2014), including black-legged kittiwakes, both in the Arctic (Harris, Descamps, Sneddon, Cairo, et al., 2020) and Alaska (Collins et al., 2019). The novel object was a blue plastic penguin toy ($13 \times 10 \times 4.5$ cm; Munchkin®) attached to an extendable (maximum 8 m) pole. The novel object was presented to an individual focal bird for 60 s while its response was recorded by an action camera mounted 30 cm behind the novel object (see Harris, Descamps, Sneddon, Bertrand, et al., 2020 for a full field protocol) (Appendix S4). At Grumant, all boldness tests were conducted by the same tester. Four testers collected video data at Pyramiden: one during 2018, one during 2019 and two during 2021. In 2018, 70 birds from Pyramiden (of the 163 tested) were sampled with videos less than 60 s in length (range = 40–59 s). A subsequent investigation into any potential impact of this discrepancy found that a reduced video length did not make a significant difference to the resulting boldness estimates, so these samples were retained (Appendix S5).

Repeat tests were conducted to assess repeatability within and between years (Nakagawa & Schielzeth, 2010). A total of 307 individuals were tested across 4 years. Of these, 67 individuals were tested in 2 different years, and 36 were tested in 3 years. Overall, 137 birds were tested once, 71 were tested twice, 46 were tested three times and 53 were tested four times or more (max = 7 tests). The number of tests each bird completed was later accounted for when assessing repeatability (see below) and no evidence of habituation was found.

During video analysis, the birds' behaviour was annotated using a set of mutually exclusive behavioural states: (a) sitting on the nest, with the body resting on the nest cup; (b) body raised off the nest cup, but not standing; (c) standing on the nest (legs visible and extending to the base of the nest); (d) off the nest but remaining visible on the ledge close to the nest; and (e) off the ledge (and no longer visible) (Harris, Descamps, Sneddon, Bertrand, et al., 2020). All videos recorded from 2017 and 2018 were analysed using JWatcher v1.0 (Blumstein & Daniel, 2007), while the videos from 2019 and

2021 were analysed using BORIS v7.12.2 (Friard & Gamba, 2016). The same ethogram was used in all years. Four observers processed the personality videos. An intraclass correlation coefficient (ICC) estimate of .99, suggesting excellent inter-rater reliability, was generated using a mean-rating, absolute-agreement, 2-way mixed-effects model (Koo & Li, 2016) via the IRR package (Gamer et al., 2012).

The proportion of time each individual spent in the five behavioural states was calculated. These five proportions were then condensed into a single test score via a principal component analysis (PCA) (Budaev, 2010) using the factoextra package (Kassambara & Mundt, 2020). The PCA scores generated from the first principal component (PC1) were used to test for adjusted repeatability whilst controlling for test date, tester identity, colony, breeding stage and test number (the number of tests that individual had undergone) (Nakagawa & Schielzeth, 2010) using the rptR package (Stoffel et al., 2017). In order to generate a single boldness score for each individual (whilst accounting for potential confounding variables), a linear model was built that fitted the PC1 scores (mean centred by year) as the response variable and colony, test number, tester identity, breeding stage and bird ID as fixed effects. This accounted for potential biases outlined in the STRANGE framework (a tool used to identify potential sampling biases in animal behaviour research) (Webster & Rutz, 2020). The number of tests each bird completed was not significant in this model, suggesting there was no habituation following multiple novel object tests. Parameter estimates for each individual were extracted from this model to serve as individual boldness estimates (Hadfield et al., 2010; Harris, Descamps, Sneddon, Bertrand, et al., 2020). Higher scores were associated with less reactive individuals and so were indicative of increased boldness (Harris, Descamps, Sneddon, Bertrand, et al., 2020; Harris, Descamps, Sneddon, Cairo, et al., 2020). In personality studies, self-selection may lead to a disproportionate number of bold animals being sampled (Carter et al., 2012). Our study included subjects from across the boldness spectrum (Appendix S6), thereby limiting the 'STRANGEness' of our sample (Webster & Rutz, 2020). To quantify the dissimilarity of boldness that existed within each pair, the absolute difference in pair members' boldness score (henceforth 'absolute difference') was calculated. A larger absolute difference was associated with greater dissimilarity in boldness between pair members.

2.4 | Data analysis

All analyses were performed in R 4.2.0 (R Core Team, 2022). The main analyses involved creating global linear mixed models (LMMs) and generalized linear mixed models (GLMMs), before applying an information-theoretic approach to select the top model set containing the best fitting models. While the global models contained all the variables of interest, the best fitting models (the simplest version of models with Δ Akaike's information criterion (AIC) <2, which indicates substantial support) contained only those variables explaining a notable proportion of the variation within the data (Burnham &

Anderson, 2001). The key results of the paper were then drawn from these best fitting models.

To test if kittiwake pairs tended to mate assortatively by boldness, a LMM (M1: female boldness_male boldness, Table 1) was fitted to male boldness (reflected and square root transformed to correct for negative skew) with female boldness as a fixed effect. Although our predictions were not specifically concerned with the effect of colony on this relationship, it was deemed statistically appropriate to control for this factor by including it as a fixed effect. Following the results of subsequent permutation tests (see below), an interaction between colony and female boldness was included to account for the potential differences in mating patterns between colonies. Female ID was included as a random effect to account for repeated measures. For completeness, we conducted an analysis where female boldness was included as the response variable, male boldness as the fixed effect and male ID as a random effect and, achieved similar results (Appendix S3c).

To examine the potential links between boldness, breeding outcome and re-pairing outcome, four GLMMs with a binomial distribution (and a logit link function) were constructed using lme4 (Bates & Maechler, 2010) (Table 1).

The binary response variables were breeding outcome (success=1, failure=0) and re-pairing outcome (re-pair=1, faithful=0) in relation to year t. In terms of fixed effects, the three boldness variables (female boldness, male boldness and absolute difference between pair members) were continuous, scaled (mean 0 ± 1 SD) and checked for evidence of multicollinearity via a traditional variance inflation factor (VIF) threshold (<5) (Appendix S7). The binary variable of colony (Grumant/Pyramiden) accounted for location differences.

M2: boldness_breeding outcome included the response variable of breeding outcome in year t and the fixed effects of the three boldness variables and colony (Table 1). This model contained data collected from both colonies in 2018 (the only year of overlap). These samples were separated into two levels (2018-Pyramiden and 2018-Grumant) to account for the local environmental conditions of each colony in 2018. M3: breeding outcome_re-pairing outcome modelled breeding outcome in year t and colony (as fixed effects) against re-pairing outcome in year $t+1$ as the response variable. In M4: re-pairing outcome_ breeding outcome, breeding outcome in year $t+1$ was the response variable, while sex was included as a separate binary variable. The potential interaction between sex and re-pairing outcome in year $t+1$ was included as a fixed effect to control for the possibility that the fitness consequences of re-pairing may differ between sexes. M5: boldness_re-pairing outcome had a similar structure to M2: boldness_breeding outcome except that the response variable was re-pairing outcome in year $t+n$ (Table 1). It also included 'missing seasons' as a fixed effect to account for the birds' additional chances to re-pair if they went unrecorded between breeding seasons.

In all models, year t was included as a random intercept to act as a proxy for the annual changes to environmental conditions that might influence reproductive success and re-pairing probability (Mercier et al., 2021). Pair ID, female ID and male ID were included as random

TABLE 1 Structure of the global linear mixed model (LMM) and generalised linear mixed models (GLMMs) used to address this study's main hypotheses on the links between boldness, breeding outcome, and re-pairing outcome in kittiwakes.

Global model number: predictor_response	Research question	Model type	Response variable	Explanatory variables	
				Fixed	**Random**
M1: female boldness_ male boldness	Test for assortative mating	LMM	Male boldness (√)	Female boldness	Female ID
				Colony	
				Female boldness × colony	
M2: boldness_breeding outcome	Impact of boldness on breeding outcome	GLMM -binomial distribution	Breeding outcome year t (failure or success)	Female boldness	Year t
				Male boldness	Pair ID
				Absolute difference	Female ID
				Colony	Male ID
M3: breeding outcome_ re-pairing outcome	Impact of breeding outcome on re-pairing probability	GLMM -binomial distribution	Re-pairing outcome year $t+1$ (faithful or re-pair)	Breeding outcome year t (failure or success)	Year t
					Pair ID
				Colony	Female ID
					Male ID
M4: re-pairing outcome_ breeding outcome	Impact of re-pairing outcome on future breeding outcome	GLMM -binomial distribution	Breeding outcome year $t+1$ (failure or success)	Re-pairing outcome year $t+1$ (faithful or re-pair)	Year t
				Colony	Pair ID
				Sex	
				Re-pairing outcome year $t+1$ (faithful or re-pair) × sex	Bird ID
M5: boldness_re-pairing outcome	Impact of boldness on re-pairing probability	GLMM -binomial distribution	Re-pairing outcome year $t+n$ (faithful or re-pair)	Missing seasons	Year t
				Female boldness	Pair ID
				Male boldness	Female ID
				Absolute difference	Male ID
				Colony	

Note: This table contains all variables that were included in the original global models; however, not all of these were retained in the final, best fitting models.

intercepts in M2: boldness_breeding outcome, M3: breeding outcome_re-pairing outcome and M5: boldness_re-pairing outcome to avoid pseudoreplication owing to the repeated measurement of pairs and individuals. In M4: re-pairing outcome_ breeding outcome, the random intercepts were pair and bird ID.

Sample size varied between models (Appendix S8). Goodness of fit (marginal and conditional R^2) (Nakagawa et al., 2017) of the global models was estimated using the MuMIn package (Bartoń, 2020). The information-theoretic model selection procedure involved generating all possible candidate models, and then ranking these by AIC adjusted for small sample size (AIC_C). A group of best-fitting models (Δ AIC < 2) was subsetted and more complex versions of simpler models, which also have an equal or higher AIC_C than the simpler version were removed (Richards et al., 2011). When multiple models were retained, the coefficients of all the best-fitting models are reported and Akaike weights were used as a complementary tool to further assess the relative support for each model. While the best fitting models contained only the variables highlighted as the most important by our model selection criteria, a complete list of models can be found in Appendix S9.

Permutation tests were conducted to assess whether re-pairing (focal) birds selected new partners whose personalities were more similar to the focal bird's than those of their previous mate. The tests quantified whether within-pair differences in boldness were reduced during re-pairing compared to what would be expected if focal birds selected partners randomly from the population. Permutations were carried out using data collected from Grumant ($n=16$ individuals) and Pyramiden ($n=23$ individuals) separately to account for the localised partner options at each location. First, to determine the observed difference in boldness scores between new partnerships and original partnerships, the absolute difference in boldness within each new partnership was subtracted from the absolute difference in boldness within the original partnership. A positive value indicated that the new partner was more similar in boldness to the focal bird than its original partner. These differences were averaged for each population to produce the 'observed mean difference'. The distance of this mean value from zero (in either direction) indicates the strength of the effect at the population level. For example, a large positive mean observed difference in boldness would suggest the re-pairing focal birds were choosing new partners that were

much more similar to themselves than their previous mates. Second, boldness differences were calculated within randomised pairings. Within each permutation, every focal bird in the population was paired with a new partner boldness score, which was randomly sampled from the distribution of boldness scores available within each population. This approach assumes that the boldness distribution of available partners from which the re-pairing birds were selecting new mates was similar to the boldness distribution of the whole population. The absolute difference between the focal birds' boldness and the randomly sampled personalities was calculated and subtracted from the original within-pair difference in boldness. This value (within the original pair difference – within the random pair difference) was then averaged across the population to give a randomised mean difference (difference between the original and randomised pair's absolute difference). This process was repeated 10,000 times per colony. The centre of the distribution (mean) of these 10, 000 randomised mean differences would be the expected observed mean difference if the birds were pairing entirely at random. Finally, to assess the likelihood that the birds' new mate choice was significantly different from random, we measured whether the randomised mean difference in boldness (original partnership–randomised partnership) was smaller than or equal to the observed mean difference (original partnership–new partnership). A one-tailed p-value was therefore calculated as the proportion of randomised partnerships in which boldness differences were greater than the observed difference. To accept the null hypothesis, the randomised mean difference would need to be larger than the observed mean difference in >5% of cases.

2.5 | Ethics and licensing

Permission to conduct fieldwork was granted by the Governor of Svalbard (Sysselmesteren på Svalbard) to project Research in Svalbard (RiS) 361. The capture and boldness testing methods were approved by the Norwegian Food Safety Authority (Mattilsynet) (FOTS IDs 8602, 8616, 27558 and 29584). Field team ringing licenses were issued by the Norwegian Environment Agency (Miljødirektoratet).

3 | RESULTS

3.1 | Boldness, repeatability and assortative mating

Using the scores generated by PC1, birds were found to be highly repeatable in boldness between years ($R = .53$, CI: .51–.64, $p < .001$). Within our sample, the range of boldness scores was −1.57 to 2.62, where higher scores meant increased boldness. Overall, males (Mean = 1.04, SD = .93) were found to be bolder than females (Mean = .84, SD = .94), while birds from Grumant (the smaller colony) (Mean = 1.41, SD = .82) were bolder than those from Pyramiden (Mean = .58, SD = .85) (Appendix S6).

From the global M1: female boldness_male boldness model (marginal $R^2 = .17$, conditional $R^2 = .36$), colony, female boldness and the interaction between these two variables were retained in the best fitting model (Table 2). Male birds from Grumant were paired with females whose boldness scores were positively correlated with their own. This is evidence of assortative mating at Grumant but not at Pyramiden, where mating was weakly disassortative (Figure 2). The second-best fitting model was also retained in the top-model set (Table 2, Appendix S9). Only the variable colony was retained in this model, indicating that male birds from Pyramiden were paired with shyer partners. The model Akaike weights indicate that the probability of each of these two models being the best fitting model was roughly equal (Table 2). However the results of the permutation tests (see below) also demonstrate evidence of assortative mating at Grumant but not at Pyramiden, thereby strengthening this result.

3.2 | Boldness and breeding outcome

Following model selection from the global M2: boldness_breeding outcome (marginal $R^2 = .09$, conditional $R^2 = .65$), two models remained in the top model set. The absolute difference in boldness was retained in the best fitting model. This weak relationship indicated that pairs with a greater absolute difference were more likely to fail during breeding than pairs that were more similar in boldness (Table 2, Figure 3, Appendix S3d). The null model was retained as the second-best fitting model. Although the effect of absolute difference on breeding outcome was modest (Figure 3), the associated Akaike weights show that the model that included this parameter was twice as likely to be the most parsimonious model than the null model (Table 2).

3.3 | Breeding outcome and re-pairing

Breeding outcome was the only fixed effect retained in the single best fitting model derived from the global M3: breeding outcome_re-pairing outcome (marginal $R^2 = .07$, conditional $R^2 = .30$). Breeding failure in year t increased the probability of re-pairing in year $t+1$ (Table 2, Figure 4).

From the global M4: re-pairing outcome_ breeding outcome (marginal $R^2 = .35$, conditional $R^2 = .96$) (Table 2), only the null model was retained. Therefore, there was no evidence that the birds' recent re-pairing outcome (faithful or re-paired) impacted their reproductive success in year $t+1$.

3.4 | Boldness and re-pairing

The global M5: boldness_re-pairing outcome (marginal $R^2 = .14$, conditional $R^2 = .32$) produced a single best fitting model. The probability of re-pairing increased with number of missing seasons (Table 2), thus pairs that were not recorded every year were more likely to

TABLE 2 Parameter estimates, standard errors, and model information for the top-ranking models (the simplest version of models with Δ Akaike's information criterion$_c$ < 2) investigating the links between boldness, breeding outcome and re-pairing.

Global model number: predictor_response	Best fitting model rank	Retained fixed effects	Estimate	Standard error	AIC$_c$	Δ AIC	Deviance	Akaike weight
M1: female boldness_male boldness	1	Intercept	1.67	.05	24.08	.00	11.42	.43
		Colony-Pyramiden	−.19	.05				
		Female boldness	.09	.04				
		Colony × female boldness	−.11	.05				
	2	Intercept	1.71	.04	24.17	.09	15.86	.41
		Colony-Pyramiden	−.23	.05				
M2: boldness_ breeding outcome	1	Intercept	−.7	.78	230.95	.00	170.34	.18
		Absolute difference	−.35	.18				
	2	Intercept	−.66	.77	232.30	1.36	169.83	.09
M3: breeding outcome_re-pairing outcome	1	Intercept	−.15	.36	271.23	.00	201.4	.71
		Breeding outcome year *t*-success	−1.15	.43				
M4: re-pairing outcome_breeding outcome	1	Intercept	−3.79	3.3	233.92	.00	75.46	.35
M5: boldness_re-pairing outcome	1	Intercept	−1.76	.43	190.4	.00	130.53	.17
		Missing seasons	1.04	.44				

Note: The column 'Retained fixed effects' outlines those variables from the global model that were retained in each best fitting model, suggesting substantial support for an effect within the data. 'Akaike weight' represents the probability that the associated model is the most parsimonious model. The response variable in M1: female boldness_male boldness was continuous, while in all other models the response variable was binary (0/1). All continuous fixed effects were scaled (mean = 0 ± 1 SD). Female ID was fitted as a random intercept in M1: female boldness_male boldness. Year, pair ID, female ID and male ID were fitted as random intercepts in M2 boldness_ breeding outcome, M3: breeding outcome_re-pairing outcome and M5: boldness_re-pairing outcome, while year, pair ID and bird ID were fitted in M4: re-pairing outcome_ breeding outcome.
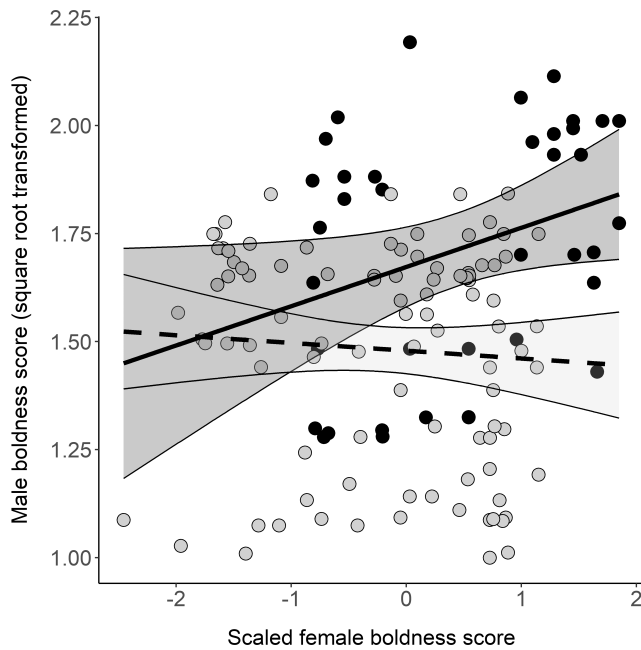
FIGURE 2 Relationship between male boldness score (square root transformed) and female boldness score (scaled, mean = 0 ± 1 SD) at Grumant (black points, solid line) and Pyramiden (grey points, dashed line). Points represent individual pairs, and lines represent colony trends. Shaded areas represent 95% confidence limits.
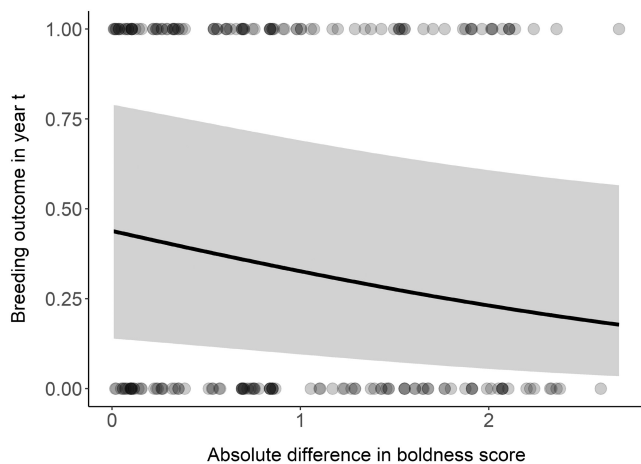
FIGURE 3 The relationships between the absolute difference in boldness between pair members and breeding outcome in year t. Grey points represent individual breeding attempts as either success (1) or failure (0). Individual breeding attempt points are translucent, so a darker shade represents a greater density of points in that location on the axes. The black line represents the predicted probability of reproductive success. Shaded areas represent the 95% confidence intervals. A higher absolute difference is indicative of greater dissimilarity in boldness between pair members.

re-pair. None of the boldness variables were retained in this top model set.

For focal birds that re-paired, the observed mean difference in boldness between their original partnership and their new partnership was slightly positive at both Grumant (.01) and Pyramiden (.15).
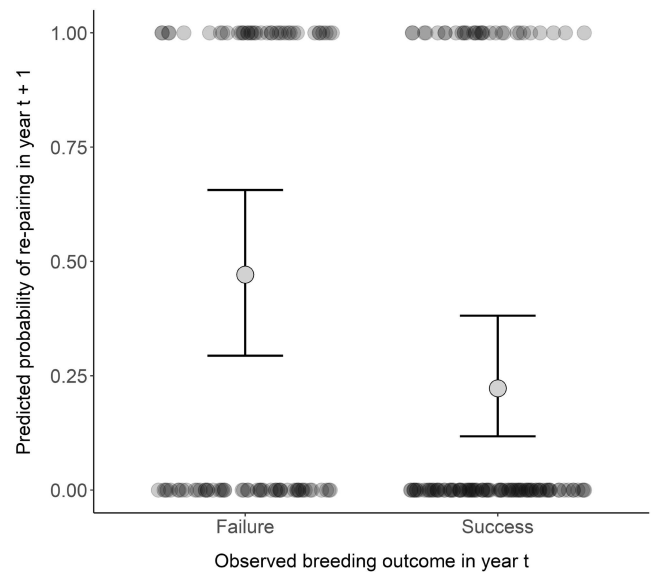

FIGURE 4 Comparing the probability of re-pairing in year $t+1$ following reproductive success or failure in year t. Smaller, dark points represent individual breeding attempts as either success or failure against re-pairing outcomes of either re-pair (1) or faithful (0) the following year. Individual breeding attempt points are translucent, so a darker shade represents a greater density of points in that location on the axes. Larger, whiter points represent the predicted probability of re-pairing following success or failure. Error bars represent the 95% confidence intervals.

This weak effect suggests that re-pairing birds displayed a general tendency to choose new partners that were only marginally more similar to themselves than their previous partner. When compared to the randomised mean difference scores generated by the permutation tests, this effect was significant at Grumant ($p=.031$) but not at Pyramiden ($p=.431$) (Figure 5). Thus, re-pairing birds at Grumant appeared to choose new partners whose boldness was statistically more similar to themselves than if they had chosen a partner at random. Overall, at Grumant, re-pairing birds chose new partners that were similar in boldness to their old partners and statistically more similar to one another than would be expected due to chance. This suggests that Grumant birds were already mated assortatively by boldness before re-pairing and that they did not dramatically increase similarity between partners by re-pairing. In contrast, although re-pairing Pyramiden birds made greater gains in terms of similarity with their new partner, these choices could have occurred by chance. These findings are in keeping with the results of M1: female boldness_male boldness (Table 2, Figure 2), which imply inter-colony differences in mating patterns.

4 | DISCUSSION

Our results describe an indirect pathway in kittiwakes whereby greater within-pair personality differences were associated with an increased risk of breeding failure, which in turn was associated with an increased probability of re-pairing. We found mixed evidence
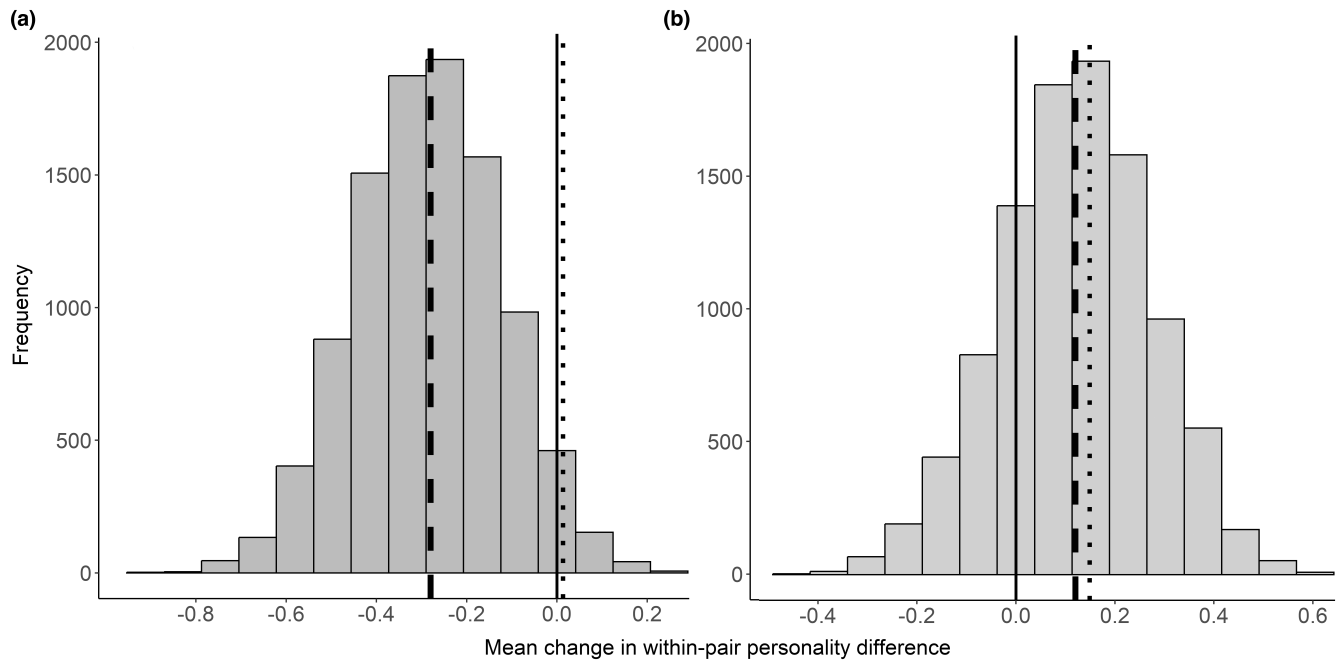
FIGURE 5 Distributions of the 10,000 randomised mean differences in pair members' boldness produced by the permutation tests for (a) Grumant and (b) Pyramiden. Comparing the observed mean difference for each colony (dotted vertical lines) to 0 (plain vertical lines) demonstrates to what degree re-pairing bird's new partners are more similar to them compared to their old partners. At both colonies, re-pairing birds chose partners that were slightly more similar to themselves than their previous partners. The mean of the randomised mean differences (dashed vertical line) represents the expected observed mean difference if the birds were paired at random. More than 95% of the randomised mean differences produced by the Grumant permutations were negative and therefore lower than this colony's observed difference, suggesting the birds were not re-pairing randomly at this colony.

of assortative mating by boldness and only weak evidence of the birds improving similarity following re-pairing. Birds at Grumant (the smaller colony), but not at Pyramiden, mated assortatively by boldness, and although birds at both colonies chose new partners that were more similar to themselves in boldness than their previous mates, this effect was extremely small. There was no evidence that re-pairing led to a reduction or increase in short-term reproductive output. Underrepresentation of shy individuals (caused by reduced trappability according to the STRANGE framework) is common in this field; however, visual inspection of the data confirmed our sample included birds from across the boldness spectrum, and thus we believe this to have had minimal impact on our results (Appendix S6).

As predicted, we found that pairs with similar boldness had greater reproductive success compared to more dissimilar partnerships. The effect was small (as demonstrated by the retention of the null model within the top model set); however, the evidence uncovered via our model selection criteria and associated Akaike weights suggests that this result has notable support within the data. This is not the first time that similarity between parents' personalities has been associated with fitness consequences in birds with biparental care. Schuett et al. (2011) found that parents with similar personalities produced healthier offspring, while Lou et al. (2021) reported higher provisioning rates within similar partnerships. In both cases, the authors postulate that similar personalities improve compatibility, leading to reduced sexual conflict by promoting balanced investment. Mechanisms for reducing sexual

conflict are common in long-lived, monogamous seabirds because the lifetime fitness of pair members overlaps so heavily. For example, several seabird species coordinate the length of their foraging trips within pairs, resulting in equal effort (McCully et al., 2022; Tyson et al., 2017).

Previous work on kittiwakes has highlighted the importance of efficient nest attendance coordination for reproductive success (Coulson & Thomas, 1983). Predation pressures mean that kittiwake nests are continuously occupied by an adult until at least 21 days post-hatching (Barrett & Runde, 1980). Coulson (1966) suggested that behavioural compatibility might improve coordination of nest attendance shifts in kittiwakes and reported that better synchrony within pairs resulted in both increased mate fidelity and fitness gains (Coulson & Thomas, 1983). Similar partners might be able to withstand a comparable length of time fasting when incubating (Visalli et al., 2023) or make similar decisions at sea, thereby allowing stronger nest attendance coordination to develop passively (Chaurand & Weimerskirch, 1994). Alternatively, having similar personalities might help individuals make more robust predictions regarding their partner's behaviour. Predictability should benefit coordinated behaviours and may allow individuals to adjust their behaviour to mitigate risk (Griffith, 2019; Wolf et al., 2011). For example, increased shyness appears to increase the willingness of great tits (*Parus major, Linnaeus*) to desert their nests (Cole & Quinn, 2014). Although the weak nature of this relationship suggests other, unmeasured factors are at play when determining kittiwake breeding

success, parents with comparable needs and limits might make more informed choices, resulting in higher quality parental care. Furthermore, individuals may use information on their partner's personality to adjust their foraging behaviour, as demonstrated in other seabird species (McCully et al., 2022).

The relationship we observed between within-pair personality differences and breeding success (in combination with empirical evidence reporting advantages to behavioural coordination) suggests that assortative mating should be adaptive in kittiwakes. Examining mate choice on a varying spatial scale is recommended if the relevant influences are to be fully unpicked (Rios Moura et al., 2021). This proved true for our study. Although assortative mating by boldness has been detected in previous work (Collins et al., 2019), two separate analysis techniques in our study detected assortative mating at only one of the two colonies in our sample. Mate choice at Grumant was assortative by boldness, which is particularly surprising given that Grumant is a smaller colony. Theory predicts that Grumant birds should experience limited options during mate choice that causes them to compromise on compatibility (Bried et al., 2021). The observed mating pattern may stem from local adaptation (Jiang et al., 2013). Grumant is a very small colony where predation pressure on chicks (from glaucous gulls, _Larus hyperboreus_, _Gunnerus_) may be higher than at Pyramiden. Under these circumstances, strong nest attendance coordination for defence may be particularly critical (Ihle et al., 2015). If personality influences behavioural compatibility and defence strategy, the more exposed birds at Grumant may face greater pressure than those at Pyramiden to choose a suitable mate. Certain personality traits have previously been tied to more active nest defence (for example, increased exploratory behaviour; Hollander et al., 2008), but a specific investigation is required to investigate if personality impacts anti-predator strategies in kittiwakes.

In contrast, mate choice was weakly disassortative at Pyramiden, which is harder to explain within the context of our other results. The social context within which mate choice occurs is complex. As it is impossible to account for all influences acting on mate choice, this can lead to decisions that appear imperfect to observers (Ryan et al., 2019). The Pyramiden kittiwakes may be more heavily influenced by other, unidentified mate choice criteria, for example, body size than boldness (Visalli et al., 2023). As the larger colony, Pyramiden may be more representative of broader kittiwake mating patterns than the much smaller population at Grumant; however, more colonies would need to be assessed to confirm this theory. Alternatively, assortative mating patterns may be diluted if birds are unable to forge optimal partnerships. It may be unrealistic to expect animals to make perfect decisions in a given scenario. Given that re-pairing birds at both colonies showed little improvement in terms of similarity when selecting a new partner, it is possible that poor-quality birds that are predisposed to divorce may also lack the capacity or knowledge to choose a more suitable partner, leading to imperfect choices (Choudhury, 1995; Ryan et al., 2019). This would weaken any population-level strategies whereby birds use re-pairing as an opportunity to improve on mate choice.

Coupled with our finding that similar personalities within pairs improve reproductive success, these results could potentially point to divorce as an adaptive strategy in some kittiwake populations. Re-pairing might allow individuals to improve their reproductive success or attempt to correct errors made during mate choice (Choudhury, 1995; Ens et al., 1993). This is reaffirmed by the finding that breeding failure was associated with an increased probability of re-pairing. When the unconfirmed divorces were removed, the link between breeding failure and divorce persisted (Appendix S3a). This relationship has been reported in kittiwakes (Naves et al., 2007) and elsewhere (Dubois & Cézilly, 2002), suggesting that breeding outcome is a key type of information that can influence pairing decisions (Naves et al., 2006).

Despite these findings, this study cannot confirm that re-pairing confers fitness benefits on kittiwakes. We observed that re-paired birds performed similarly to faithful birds the following season (Appendix S3a). Our results do not follow earlier studies on kittiwakes, which reported an initial decline in reproductive success after re-pairing (Coulson, 1966; Fairweather & Coulson, 1995); however, it has been reported that mate familiarity may not be as critical to success in this species as it is for others (Naves et al., 2007). We are not the first to report limited impacts of re-pairing on breeding success in long-lived birds. Previous studies indicate that re-pairing does not affect reproductive output in Eurasian oystercatchers (_Haematopus ostralegus_, _Linnaeus_) (Harris et al., 1987) or wandering albatrosses (Sun, Barbraud, et al., 2022) and that it has mixed effects (including no impact) on the breeding success of common guillemots (_Uria aalge_, _Pontoppidan_) (Jeschke et al., 2007). This suggests that divorce is not always adaptive, and in some cases, it may be a by-product of intrusion from extra-pair individuals or failure to reunite after the non-breeding season (Jeschke et al., 2007). Investigating this more thoroughly in kittiwakes requires a study into the implications of re-pairing on long-term reproductive output (such as looking beyond year $t+1$ to years $t+n$). Our sample contained only a small number of pairs where data was available across the entire study period, but a longitudinal study with a stronger sample size would establish whether any short-term costs of re-pairing are ultimately offset by an increase in reproductive success in years to come (McNamara & Forslund, 1996).

More information on how divorce is initiated in this species might allow for refinement of our analyses. Ens et al. (1993) predicted that in species where one partner decides to abandon the other, only the bird that triggered the divorce would benefit. The reluctant 'victim', which may have been benefiting from a high-quality mate, may struggle to recuperate the costs or find a new partner (Jeschke et al., 2007). The mechanism by which divorce occurs in kittiwakes is understudied. As we had no way of knowing which partner instigated each separation in our study, both 'initiators' and 'victims' may be included in M4: re-pairing outcome_ breeding outcome, complicating our results. Conversely, if divorce in kittiwakes is driven by some form of incompatibility, it may be mutual (Choudhury, 1995); however, more work is required on the dynamics of kittiwake divorce to address this uncertainty.

5 | CONCLUSIONS

Our results strengthen the links between personality and sexual selection by demonstrating that the intrinsic traits of both parents (and the interactions between them) have fitness consequences. This is particularly significant in long-lived monogamous animals because it improves our understanding of how sexual conflict might be resolved and coordination enhanced in these species. This study joins a growing body of work that concludes that behavioural compatibility may play a critical role in reproductive success, a concept that has implications for the study of biparental care in a range of taxa. In addition, our results further demonstrate that the effects of an animal's personality on its life-history characteristics are wide-reaching. In this case, personality may influence cooperation within mated pairs, which then has a cascading effect on breeding outcomes and finally re-pairing probabilities. The indirect effects of personality must be considered in future work, as must the possibility that these drivers vary between different populations of the same species. This is critical if we are to clarify how animals use information about themselves and their partner to help navigate through reproduction as part of a caring dyad.

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