



Boldness, mate choice and reproductive success in *Rissa tridactyla*

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As many long-lived seabirds are biparental and monogamous, individuals need to choose their mates wisely. While assortative mating based on physical traits is widely studied, mate choice in sexually monomorphic species based on behavioural traits remains poorly understood. We propose that personality is a possible factor on which mate choice is based and that certain personality traits within a behavioural syndrome confer a greater fitness. Here we measure boldness, a commonly explored behavioural syndrome, in black-legged kittiwakes, *Rissa tridactyla*, nesting at Middleton Island, Alaska, U.S.A. We measured boldness by presenting subjects with a novel object and recording the response. We considered the first principal component scores from the analysis of these responses to represent an individual's boldness. Some kittiwakes exhibited the strategy of assortative mating based on boldness, and bold birds that mated assortatively exhibited the greatest reproductive success. Within a breeding season, individuals became bolder as they reached the most critical point in the breeding season (chick hatching), which supports our finding that bolder individuals have greater reproductive success. We conclude that personality should be considered when investigating mate choice because individual personality may have an important influence on reproductive success.

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In many species, mate choice is based on physical attributes (e.g. Indykiewicz et al., 2017; Wiebe, 2000), but for sexually monomorphic species such as seabirds, the traits for which an individual chooses a mate are less apparent. Because differences in physical traits are not obvious, differences in behavioural traits among individuals should be considered as the basis for mate selection. The study of animal personality has revealed consistent differences in behaviour by individuals across various environmental, social or other differing contexts (review by Wolf & Weissing, 2012), and across taxa (e.g. review: Gosling & John, 1999; meta-analysis: Bell, Hankison, & Laskowski, 2009; rufous-collared sparrows, *Zonotrichia capensis*: van Dongen, Maldonado, Sabat, & Vásquez, 2010; sand-dwelling insects: Alcalay, Ovidia, & Scharf, 2014). Because personality is consistent and repeatable, individuals may be able to monitor distinct personality traits for the basis of mate selection.

Many studies have related personality traits, especially aggression or boldness, to measures of fitness (Alcalay et al., 2014; Ariyomo & Watt, 2013; Chira, 2014; Mulard et al., 2009; van

Dongen et al., 2010; Wolf, Van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2012). Specific traits may confer a greater level of fitness than others; for example, a relationship between boldness and foraging success, another measure of fitness, has been observed in albatross (Patrick & Weimerskirch, 2014). In their review of this concept, Smith and Blumstein (2008) suggested that specific, repeatable personality traits affect fitness differently based on external (such as environmental or social) conditions. For example, an aggressive individual may have an advantage in an environment of conspecifics because it can outcompete others for resources. In a predator–prey situation, however, an overly aggressive individual may demonstrate a lack of caution, which could risk individual health or diminish the chances of prey acquisition (Brick & Jakobsson, 2002). The fitness consequences of specific traits are therefore dependent upon the situation. Genetics account for much of the variation associated with individual personality (e.g. Dochtermann, Schwab, & Sih, 2015; Drent, van Oers, & van Noordwijk, 2003), and personality traits are often heritable (Edwards, Burke, & Dugdale, 2017), so it is likely that individuals consider optimal personality traits when selecting a mate. Because personality is consistent and heritable, and because it has fitness consequences, assortative mating towards a specific personality trait could occur.

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Many different species of seabirds exhibit biparental care when raising young (Bried, Pontier, & Jouventin, 2003; Hatch, Robertson, & Baird, 2009; Ismar, Daniel, Stephenson, & Hauber, 2010; Mulard et al., 2009). In biparental care, the traits exhibited by both parents are important to the reproductive success of the pair since both parents share the responsibilities of foraging, incubation and chick rearing (Leclaire et al., 2011, 2014). Because individuals who possess specific traits tend to be more successful, mate selection is often nonrandom (Bortolotti & Iko, 1992; Burley, 1983; Indykiewicz et al., 2017; Wiebe, 2000). The familiar phrases ‘opposites attract’ and ‘like favours like’ describe two possibilities of nonrandom mating. Traits on which mate selection is based differ across species and can include coloration and morphology (e.g. in barn swallows, *Hirundo rustica*: Saino et al., 2013), complexity of song (e.g. in song sparrows, *Melospiza melodia*: Pfaff, Zanette, MacDougall-Shackleton, & MacDougall-Shackleton, 2007), foraging ability (e.g. Förster’s terns, *Sterna forsteri*: Fraser, 1997), and how nurturing an individual is judged to be (pied kingfisher, *Ceryle rudis*: Reyer, 1986). In positive assortative mating, like favours like and individuals will choose mates that have phenotypic characteristics that are similar to their own (Allaby, 2012). In negative assortative mating, opposites attract; individuals will select mates with dissimilar phenotypic characteristics to their own (e.g. Hedrick, Smith, & Stahler, 2016; Hedrick, Tuttle, & Gonser, 2018; Rutz, 2012). Both strategies have advantages that vary depending on the situation. Negative assortative mating contributes to genetic variation within the population, which can influence the overall fitness and stability of a population (Burley, 1983; Karlin & Feldman, 1968; Rutz, 2012). Moreover, having two parents take different strategies can act as a hedge against environmental stochasticity, increasing both partner’s fitness (Elliott, Gaston, & Crump, 2010). Positive assortative mating, however, is the most commonly observed strategy across taxa (Burley, 1983; Hedrick et al., 2018; Ludwig & Becker, 2008). Positive assortative mating increases the likelihood that a specific characteristic is passed on to the offspring. Since the organism is selecting for this trait, it is likely that the selected trait leads to more fit individuals; the offspring will be more fit as a result of this mating strategy.

In terms of animal personality, mating pairs with similar personalities may be more likely to produce more fit offspring (Ariyomo & Watt, 2013; Chira, 2014; Schuett, Dall, & Royle, 2011). This may be because the trait itself causes an individual to be more fit, or it may be that behaviourally similar mates are more compatible than behaviourally dissimilar mates (Chira, 2014; Laubu, Dechaume-Moncharmont, Motreuil, & Schweitzer, 2016). Laubu et al. (2016) demonstrated that compatibility is so important within a mating pair that convict cichlids, *Amatitlania nigrofasciata*, adjust their own personality to be closer to that of their mates. In their cross-fostering experiment on zebra finches, *Taeniopygia guttata*, Schuett et al. (2011) found that foster parents with the most similar personalities raised the healthiest offspring, regardless of the personalities of the biological parents. This suggests that offspring fitness is more heavily influenced by the personalities of the parents than by its own, genetically based personality.

Here we investigate assortative mating based on boldness and the resultant fitness consequences. Boldness is a commonly tested behavioural syndrome (Sih, Bell, Johnson, & Ziemba, 2004) where traits lie along the shy–bold continuum (Wilson, Clark, Coleman, & Dearstyne, 1994). Boldness has been shown to be repeatable (Bell et al., 2009) and heritable (Brown, Burgess, & Braithwaite, 2007; Edwards et al., 2017; Patrick, Charmantier, & Weimerskirch, 2013) with various fitness consequences (e.g. Patrick & Weimerskirch, 2014). Black-legged kittiwakes, *Rissa tridactyla*, are gulls that nest on steep ocean cliffs of the northern hemisphere. Some of the largest breeding colonies of kittiwakes are found in the Gulf of

Alaska. Kittiwakes are monogamous and both parents are equally involved in rearing young, so mate choice is very important (Hatch et al., 2009). Kittiwakes exhibit no obvious sexual dimorphism (Jodice, Lanctot, Gill, Roby, & Hatch, 2000), and mate choice is mutual between the sexes rather than female-led (Hatch et al., 2009). Criteria upon which the kittiwakes choose their mates are currently unknown. Divorce rates of mating pairs are higher in years where resources are limited, probably because there is an imbalance in parental effort between the male and the female (Diamond, 2016). Because parental effort plays an important role in decisions relating to divorce, individual personality that relates to parental effort becomes a prime candidate for mate selection.

In this paper, we explore whether (1) boldness is repeatable within individuals across contexts, (2) boldness varies seasonally, (3) boldness is related to reproductive success and (4) pairs mate assortatively based on boldness traits. We begin first by establishing whether boldness is repeatable in black-legged kittiwakes and whether it is consistent across years. If being bold is costly, then we anticipated that population boldness would vary throughout the breeding season in association with the vulnerability of the chicks in the nest. We predicted that boldness of parent birds would be highest when they had young offspring, as young offspring are more vulnerable to predation and need more protection than older offspring. We hypothesized that boldness would play an important role in reproductive success via nest defence and predicted that reproductive success would increase with increased boldness. Because we expected bold individuals to have higher fitness, we predicted that bold birds would mate assortatively and that shy birds would mate with individuals that were bolder as a means of increasing ‘total nest boldness’. We therefore expected ‘total nest boldness’ to be related to reproductive success.

METHODS

Field Testing

The assessment of boldness levels took place on Middleton Island (59°26′9″N, 146°18′26″W) in the Gulf of Alaska in 2016 and 2017. In 2016, there was a severe El Niño event that significantly reduced fish populations in the Gulf of Alaska and therefore impacted the kittiwakes who were breeding there. The impacts of this event carried over to 2017. At Middleton Island, a modified radio tower provides sheltered nesting sites for the kittiwakes. This allows easy access to the birds by researchers. Each nest ledge has a window made of one-way glass, a slot underneath, and a hole for the feeding tube if the birds are part of a feeding study. All birds chosen for this study were unfed.

We monitored 24 mating pairs living on the tower three times daily to accurately record egg laying dates, hatch and death dates. Once hatched, chicks’ measurements and weights were taken every 5 days until they fledged. Mating pairs used in this study were randomly selected with a number generator, although a few windows were excluded from selection due to the lack of a feeding hole.

Boldness of individual kittiwakes was measured on a shy–boldness continuum in response to the introduction of a novel object. Because the boldness of an individual can be influenced by the presence of others (Kerman, Miller, & Sewall, 2018), tests were only conducted when one adult was present in the nest. The novel object was a ball made of tissue and bright green duct tape attached to a thick wire (Fig. 1b). We inserted the novel object through a small hole in each window panel (Fig. 1c) and placed it at the right edge of the nest, with some exceptions due to obstacles. We introduced the novel object to the nest for 5 min and videorecorded the individual’s response. A Nikon D3200 camera was mounted on

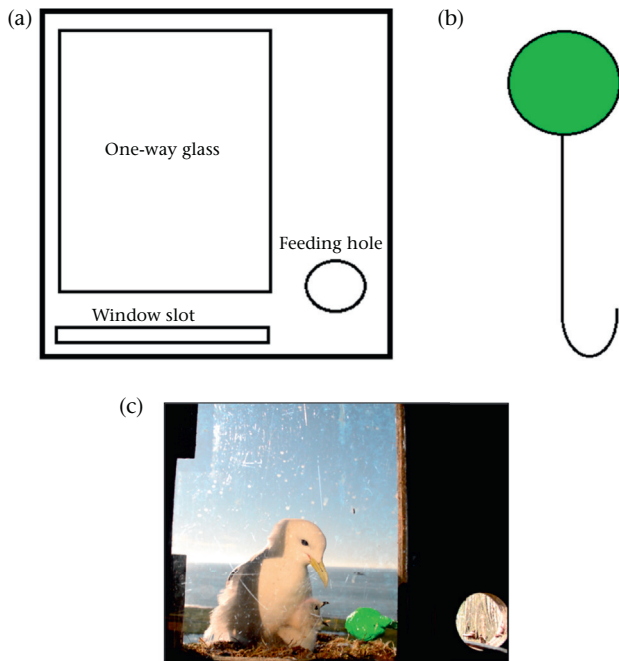


Figure 1. (a) Diagram of the window set-up as viewed from the interior of the Middleton Island Tower. The camera was placed about 0.3 m away from the one-way glass. (b) Diagram of the novel object. (c) Photograph of the nest set-up. All nests were set up in a similar fashion and the ball was held at the edge of the nest as illustrated.

a tripod and set 0.3 m away from the window. The novel object was held at the furthest end so that the researcher's hand was not visible through the feeding hole. It took 10 s to set up the camera and the bird was unable to see the set-up process. Insertion of the novel object lasted fewer than 3 s. This was done for 47 individuals in 2016 and 42 individuals in 2017. If the subject departed from the nest and had not yet returned by the end of the trial period, the novel object was removed at 5 min and the recording continued without the novel object in place until the individual returned. If the individual had not yet returned after 3 min following the removal of the novel object, the video was stopped. This was done for each individual five times throughout the breeding season or until the egg or chick was lost (Table 1). Exposure to a novel object is a common test for boldness that has been found to be a more accurate reflection of boldness than other methods (Carter, Marshall, Heinsohn, & Cowlishaw, 2012; Yuen, Schoepf, Schradin, & Pillay, 2017), yielding consistent, repeatable results in many different species (Dammhahn & Almeling, 2012; Patrick & Weimerskirch, 2014).

We determined five breeding phases (clutch completion, mid incubation, hatching, mid chick rearing, late chick rearing, phases A–E; see Table 1) before testing began. Pacific black-legged kittiwakes lay an average of two eggs (egg A, egg B) per clutch (Hatch et al., 2009), usually within 2–4 days of each other. Therefore, we began filming phase A (clutch completion) a maximum of 5 days

Table 1
The five phases of breeding black-legged kittiwakes during which the experimental protocol was carried out

Phase	Description	Time between phases (days)
A	1 day after clutch completion	14
B	Halfway through incubation (egg day 14)	8–15
C	1 day after all eggs hatched	20
D	Mid chick rearing (chick day 20)	8–20
E	Late chick rearing (chick day 35)	–

after laying the first egg. This wait period was chosen because egg B is rarely laid after a span of 4 days following the laying of egg A. Incubation lasts 24–32 days (Coulson & White, 1958), so the onset of phase B (mid incubation) was determined by the average median incubation period (14 days after the lay date) for consistency. The duration of phase B was determined by the hatch dates of the eggs. We began filming phase C (hatching) a maximum of 5 days after the hatch of the first egg. Chick rearing in black-legged kittiwakes takes 38–44 days (Coulson & White, 1958), so a median of 20 days from the hatch date was selected as the start of phase D (mid chick rearing) for consistency. Phase E (late chick rearing) was filmed at day 35, but kittiwakes bred relatively late in the season in 2016 and 2017 (Fig. 2), so phase E was filmed a few days early for some of the chicks because of logistical constraints (crew leaving at the end of the field season). Mating pairs were no longer tested after the eggs or chicks were lost, as they no longer had an attachment to the nest. If the window needed to be removed to be cleaned, the individual was given 15 min after reinsertion of the window to settle in before filming.

Ethical Note

This research was conducted in accordance with the Federal Tricouncil Funding Agencies of Canada, adopted by the University of Guelph where the protocol was subject to peer review and approved under the certification number AUP 3317. All efforts to minimize animal use in this research were made and the individuals used were part of a long-term study site where overlapping research programmes benefit from all findings.

Video Analysis

We recorded the time at which a response to the novel object occurred and classified responses into six different categories, in order of increasing boldness (Table 2).

We summed the total time spent by an individual displaying the behaviours in each category. The data were transformed to approximate normality with a fourth root transformation prior to running the principal component analysis. The first principal component (PC1) was taken as the representation of the individual's personality, called the boldness quotient (BQ). PC1 (accounting for 54% of the variation) was strongly correlated with extreme fear (68% correlated) and was also correlated with maximal complacency (62% correlated), and these were correlated in opposite directions, meaning that birds with high BQ scores were more bold and birds with low BQ scores were more shy (Table 3). BQ scores ranged from -3.78 to 3.03.

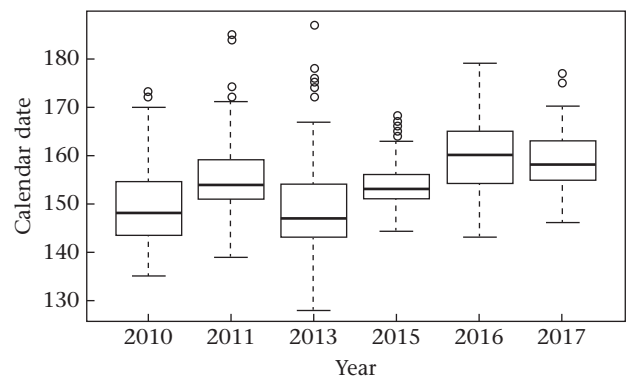


Figure 2. Comparison of dates that eggs were laid by black-legged kittiwakes over 6 years. Calendar date is days since 1 January of each year.

Table 2
Physical reactions of the individual to the novel object classified into six categories

Category	Description	Physical behaviour
F+	Extreme fear	Left the nest
F	Moderate fear	Flyby Hover
C	Complacency	Moves away from ball/eggs/chicks Stands at nest edge Adjusts eggs Returns to nest Stands up off eggs
C+	Maximal complacency	Sits on eggs/chicks Moves towards ball/eggs/chicks
A	Moderate aggression	Mid-air attack while flying past the nest
A+	Extreme aggression	Attack while in the nest

Table 3
Proportion of variance explained by the first two principal components (PC1, PC2) and the loadings associated with PC1 and PC2 for each behavioural category

Loadings and explained variance	PC1	PC2
Proportion of variance	0.54	0.23
Extreme fear	-0.69	0.20
Moderate fear	-0.18	–
Complacency	0.31	-0.71
Maximum complacency	0.62	0.64
Moderate aggression	–	–
Extreme aggression	0.17	-0.19

Behavioural categories that were not significantly correlated with the principal component have no associated loading. The total explained variation by PC1 and PC2 is 0.76.

Statistical Methods

All statistical analyses were run using RStudio v.1.1.442 (R Core Team, 2017). We ran a general linear mixed model for individuals who were tested in all five phases ($N_{2016} = 11$, $N_{2017} = 12$) to determine the effect that year, phase and sex had on individual BQ. The effect of interaction between year and sex and year and phase were also considered. A Tukey test (glht function from the multcomp package: Hothorn, Bretz, & Westfall, 2008) was run for phase to determine whether the mean BQs varied seasonally. Repeatability among individuals was calculated for the whole data set using the 'rptR' package (Stoffel, Nakagawa, & Schielzeth, 2017). To measure individual behavioural consistency within a population between years, we used a rank correlation, where maximum annual BQ scores regardless of phase were ranked in order of increasing neophobia, to assess interyear consistency of boldness. To test assortative mating and the fitness consequences of boldness, we determined the maximum BQ displayed by each individual for each year. We represented the personality of each bird with one BQ score per individual so that each bird had a single value per year that represented its maximum boldness for that year. A general linear mixed model (lme4 package: Bates, Maechler, Bolker, & Walker, 2015) explored the relationship between the maximum annual BQ of the shyest mate within a pair and the maximum annual BQ of the boldest mate in that pair, year of measurement and sex of the boldest mate. To investigate whether the personality of a mating pair is related to reproductive success, a general linear mixed model explored the relationship between offspring fitness and the maximum annual BQ of both the shyest and boldest parents. The year was included in the model to look for differences in offspring survival between years. The measure of reproductive success was represented by the total number of days survived by the offspring, from the lay date of the egg to the day the egg or chick was lost. A ceiling value of 70 days was assigned to chicks that fledged. Chicks that had not yet fledged but were still in the nest on the day of the

departure of the field crew were also assigned the ceiling value of 70, as they were all near fledging and were likely to do so. In all tests, P values of less than 0.05 were considered significant effects.

RESULTS

Neophobia of Individuals during the Breeding Season

Individual boldness scores were found to be repeatable ($R = 0.37$, $P < 0.001$). There were significant differences between the mean individual BQ scores between the phases, but BQ did not vary with year ($t_{106.84} = -1.29$, $P = 0.20$) or sex ($t_{106.65} = 0.17$, $P = 0.86$). In both years, population BQ increased from the time of egg laying up to when the chicks hatched, and it peaked during phase C, when the chicks had just hatched (see Table 4, Fig. 3). All significant differences found by the post hoc test related to phase C ($C - A$: $z = 4.88$, $P < 0.001$; $C - D$: $z = -3.36$, $P = 0.007$; $C - E$: $z = -5.33$, $P < 0.001$), with the exception of a difference between phase E and B ($B - E$: $z = -3.05$, $P = 0.02$). The population BQ decreased as the chicks progressed towards fledging. The variation of personality traits displayed within the population also decreased towards hatching; all birds became bolder, regardless of their original personalities. The variation then increased again as the chicks progressed towards fledging.

Relative Boldness within the Population Between Years

For a bird's maximum BQ rank, there was a significant linear relationship between the rank in 2016 and the rank in 2017 ($F_{1,35} = 18.49$, $R = 0.35$, $P < 0.001$); bold birds in 2016 were likely to be bold in 2017 (Fig. 4).

Personality and Reproductive Success

A general linear mixed model determined that offspring survival was most significantly correlated with the BQ of the shyest mate within the pair (shy: $t = 3.905$, $P < 0.001$, slope = 7.59; bold: $t = 1.62$, $P = 0.12$; year: $t = 1.21$, $P = 0.24$). The offspring survived 6.49 days longer for each one unit increase in the boldness of the shyest mate in the pair (Fig. 5).

Assortative Mating

There was no significant relationship between the maximum annual BQ of the shyest individual in a pair and its sex ($t_{23,31} = 2.04$, $P = 0.052$) and no relationship between the maximum annual BQ score of the shyest bird in the pair and the year ($t_{12,26} = 1.06$, $P = 0.31$). Because of this, we compared the boldest mate and the shyest mate in the pair for both years rather than comparing males and females in individual years. There was a significant linear relationship between the maximum annual BQ of the boldest and the shyest mated individuals ($t_{31,64} = 3.88$, $P < 0.001$, $r^2 = 0.41$; Fig. 6).

Table 4
The change in individual black-legged kittiwake personality through the breeding season in 2016 and 2017

Year	Phase	Mean	SD	Range	SE
2016	A	-0.31	2.45	5.79	0.74
	B	1.42	1.20	3.56	0.36
	C	2.40	0.53	1.76	0.16
	D	1.02	1.10	3.62	0.33
	E	0.64	2.11	6.00	0.64
2017	A	-0.23	2.57	6.67	0.74
	B	0.62	2.15	6.64	0.62
	C	1.86	1.16	3.55	0.33
	D	-0.03	1.99	6.21	0.58
	E	-1.52	1.99	4.65	0.57

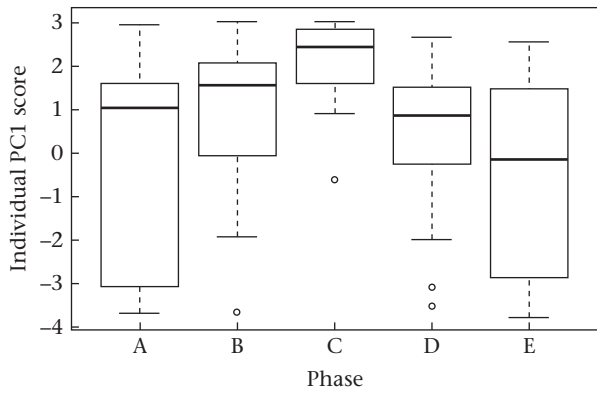


Figure 3. Box plots comparing the seasonal change in boldness over the breeding season. Fifteen unique birds in eight breeding pairs were filmed over all five phases, with eight of these birds filmed in both 2016 and 2017. Three birds were unique to 2016 and four birds were unique to 2017. The thick line in each box plot represents the mean individual boldness quotient (BQ) for that phase. Unfilled dots represent outliers within the phase.

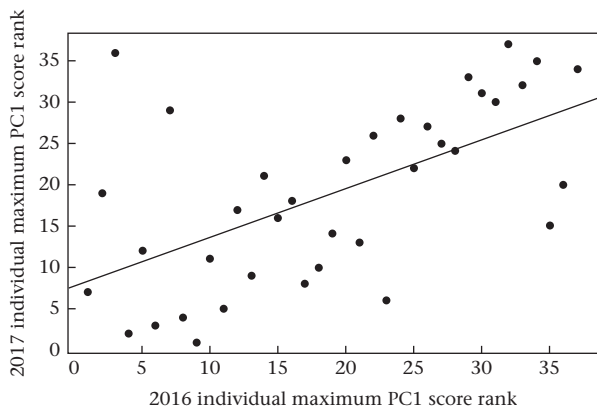


Figure 4. Rank of an individual's minimum 2016 score for the first principal component (PC1), regardless of phase, regressed with the rank of the same individual's minimum 2017 PC1 score, regardless of phase.

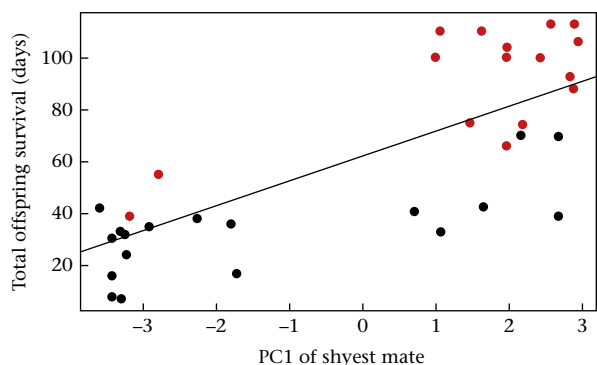


Figure 5. Relationship between the maximum parental score for the first principal component (PC1) within the breeding season exhibited by the shyest mate in the pair and the cumulative offspring survival in days, calculated from the date of egg laying to the date of the loss of the egg or chick. Red points represent pairs who laid two eggs; black points represent pairs who laid one egg.

DISCUSSION

An individual black-legged kittiwake's boldness rank was repeatable and consistent among years, and the seasonal shift of individual boldness within the breeding season was also consistent

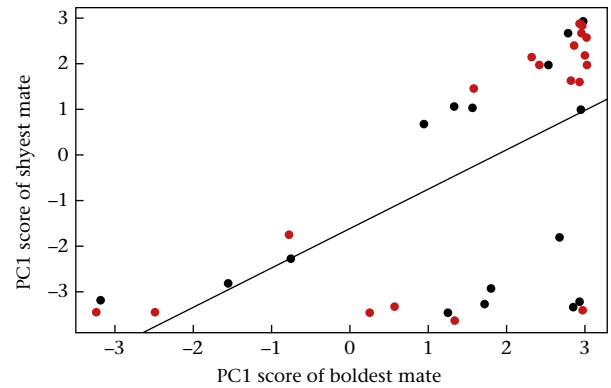


Figure 6. Relationship between boldness of the shyest mate and the boldest mate in a mating pair. Scores were calculated from the maximum score of the first principal component (PC1) for an individual within the year. Red points represent mating pairs for which the male was the boldest individual in the pair; black points represent mating pairs for which the female was the boldest individual in the pair.

among years. In their meta-analysis of the relationship between animal personality and metabolic rate, [Mathot, Dingemanse, and Nakagawa \(2019\)](#) determined that bolder individuals tend to exhibit a higher metabolic rate, and a review by [Careau, Thomas, Humphries, and Réale \(2008\)](#) discussed the higher daily energy expenditure by bold individuals due to a higher activity level and stress response in novel situations. There is therefore an energetic cost to being bold, so individuals should adjust their personalities in response to environmental conditions. The pattern of seasonal change in boldness that was found in the first half of the breeding season for the present study follows the well-established parental investment theory in which individuals increase investment as offspring age ([Redondo & Carranza, 1989](#); [Rytönen, 2002](#); [Shew, van der Merwe, Schaubert, Tallitsch, & Nielsen, 2016](#); [Trivers, 1972](#)). In this study, boldness was highest when chicks were young, and therefore most vulnerable, and so the changes observed in adult boldness throughout the breeding season may be in response to the vulnerability of the chick. When first laid, the egg is less vulnerable due to little development ([Hamdoun & Epel, 2007](#)), and it is less valuable to the parents, especially the male, because relatively little energy has been invested thus far. For the female, egg production represents a significant cost, yet if the gonads have not regressed, replacement egg production is easier ([Hipfner, Gaston, Herzberg, Brosnan, & Storey, 2003](#)). This is supported by the result that the population was, on average, less bold in the egg laying phase than during other phases. As the egg matures, organogenesis begins, and the fetus becomes more vulnerable to the environment. It is at this stage that the fetus is vulnerable to teratogens or dramatic changes in abiotic conditions, and so parental protection and an increase in boldness is observed. A chick is most vulnerable when it first hatches since it cannot thermoregulate, so it must be continually incubated and protected by the parents. It was at this stage (phase C) that the population was the most bold. Midway through the chick-rearing period, chicks gain the ability to thermoregulate and become more independent; the parents do not need to devote as much energy at the nest because the chicks are, once again, less vulnerable to predators. The increase in independence of the chicks corresponded to an increase in shyness by the parents. There was wide variation in individual BQ during phases A and E and less variation in phases B, C and D. Because chicks need the most care during the middle phases, we found evidence of parents prioritizing the needs of chicks at this time. During phases A and E, individual reactions followed more closely to the individual parent's baseline personality.

Parental boldness was highly correlated with chick survival, where pairs in which both individuals were bold were the most successful at raising young. Offspring survival was significantly correlated with the BQ of the shyest mate in the pair but was not significantly correlated with the BQ of the boldest mate in the pair, suggesting that the pair can only be as successful as its shyest member allows. One possible explanation for the elevated levels of fitness associated with high boldness is that bold individuals are more successful foragers than shy individuals (Short & Petren, 2008); it has even been suggested that boldness and foraging behaviour are part of the same behavioural syndrome (Patrick & Weimerskirch, 2014). Bold individuals tend to locate and approach a food source more quickly than shy individuals (Dammhahn & Almeling, 2012; Kurvers et al., 2009, 2012). Because they arrive earlier to the foraging grounds, bold individuals can monopolize resources. High boldness may also give individuals a competitive edge in that they may be more likely to compete with others (Cole & Quinn, 2012) and to take risks in the presence of predators (Dammhahn & Almeling, 2012). Greater resource access for bold individuals is supported by our result that bolder pairs tended to lay more eggs than shy pairs. On Middleton Island, pairs who receive supplementary food as part of a resource availability study laid more eggs, on average, than unfed birds (Hatch, 2016, 2017), suggesting that clutch size is related to food availability. Because bolder pairs tended to lay more eggs, it is possible that those pairs had greater foraging success.

Boldness is often associated with risk taking such as the willingness to approach a predator (Brick & Jakobsson, 2002) or to defend a nest against conspecifics (Traisnel & Pichegru, 2018). Generally, bold individuals tend to be more successful in territorial disputes (Taylor & Lattanzio, 2016), an issue that is quite prevalent in the close quarters of a kittiwake colony (Porter, 1990). Concurrent with our research, studies have shown that bold great tits, *Parus major*, are more reproductively successful and that they exhibit stronger defence responses in the presence of a predator (Hollander, Van Overveld, Tokka, & Matthysen, 2008; Vrublevska et al., 2015). In our study, birds with low BQ scores tended to abandon the nest during the test (Table 2), leaving their egg or chick vulnerable to attack by predators or conspecifics. Kittiwake chicks are altricial and highly vulnerable to predation when they are not being guarded by their parents, and those that fall from the nest or are blown out of it by the wind will not survive. Parents who will defend their chicks against predators rather than leave the nest in the face of danger are more likely to protect their chicks until they are independent enough to escape these dangers on their own.

Because fitness was limited by the boldness of the shyest mate in the pair, bold kittiwakes should mate assortatively to ensure maximum fitness, which aligns with our findings. Although bold birds are more favourable, they may be limited, which could explain why shy individuals also mated assortatively; those with the more favourable personality trait would not choose a mate with a less favourable personality trait, so shy individuals only have other shy individuals to choose from. We did, however, see a small subset of individuals who mated disassortatively based on boldness. This could also be due to a limited number of options for mates, but another potential explanation is that mate choice varies with age. It has been well established that reproductive success increases with age, and many studies support that this is due to experience (Cichoń, 2003; De Forest & Gaston, 1996; Elliott et al., 2014; Imlay, Steiner, & Bird, 2017). Younger birds may not have the experience to know which personality traits confer a greater level of fitness. Additionally, and alternatively, individuals may become increasingly bold over their lifetime. Studies have shown that although personality does not fluctuate rapidly in individuals (Ariyomo & Watt, 2013), personality changes throughout life. Elliott

et al. (2014) found variation in behavioural responses to stress with age, which they inferred was related to boldness. Thus, some of the variation in BQs we observed in individuals may have been related to the age of the individuals. Because kittiwakes are long-lived birds that reproduce every year of life, young kittiwakes may be shyer than individuals reaching the end of life, because they have more chances at reproduction in the future. Further research should be conducted to investigate the relationship between age of individuals, their boldness, their mating strategy and the rates of divorce based on mating strategy.

Pairs with dissimilar levels of boldness tended to have lower survival of one or more chicks than pairs where both individuals were bold, which is in accordance to a similar study performed on guppies by Ariyomo and Watt (2013); however, disassortative pairs tended to have higher fitness than assortatively mated shy pairs. This therefore suggests that assortative mating based on boldness is a better strategy for bold birds, but shy individuals should choose bold mates in order to maximize boldness of the pair.

Seabirds show a moderate degree of behavioural complexity with many evident behavioural syndromes such as exploration (Biondi, Bó, & Vassallo, 2010), sociability (Grace & Anderson, 2014), boldness (Patrick et al., 2013; Patrick & Weimerskirch, 2014), neophobia (Biondi et al., 2010; Grace & Anderson, 2014; Patrick & Weimerskirch, 2014) and aggression (Grace & Anderson, 2014; Kitaysky, Kitaiskaia, Piatt, & Wingfield, 2003; Viera, Viblanc, Filippi-Codaccioni, Côté, & Groscolas, 2011). It is therefore likely that adult black-legged kittiwakes exhibit other behavioural syndromes with various fitness consequences. While we have established a strong link between boldness and offspring survival, there may be other behavioural syndromes that play a part. Links between boldness and other behavioural syndromes have been established and suggest that many behavioural syndromes are not independent of one another (Biondi et al., 2010; Grace & Anderson, 2014; Greggor, Jolles, Thornton, & Clayton, 2016; Joyce, Demers, Chivers, Ferrari, & Brown, 2016), so studies linking mate choice to other behavioural syndromes should be conducted.

This study provides evidence for assortative mating based on boldness in a monogamous, biparental and long-lived seabird. We also show that boldness changes predictably with changing reproductive conditions and stressors, and that disassortative mating is probably more adaptive for those with low boldness levels. The interaction between these findings may explain the persistence of variation in boldness within the population, as boldness is costly but confers higher fitness to the mating pair.

For seabirds, the pair bond is critical to long-term reproductive success and survival, which relates directly to population parameters. Many seabirds are of conservation concern, including the black-legged kittiwake, which is listed as vulnerable on the ICUN Red List due to globally declining populations (BirdLife International, 2018). Because individuals with differing personalities react differently to novel or stressful situations, and because pairs with differing levels of boldness will have different rates of reproductive success, it is important to consider individual personality when looking into conservation tactics (Chira, 2014). Traditional methods of conservation assume that all individuals react similarly to stressors (Mace et al., 2008), and this study provides evidence that this is not the case. Future policies should consider individual personalities to best capture the processes that help populations to persist.

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Supplementary Data

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