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JOURNAL OF AVIAN BIOLOGY

Research

Nest defence behaviour is similar between pair members but only male behaviour predicts nest survival in barnacle geese

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Behavioural patterns often differ consistently across individuals and are linked to fitness. In species with biparental care, the defence behaviour of both parents can affect reproductive success through offspring survival. In addition to the intensity of defence behaviour by both pair members, the similarity in this behaviour among parents may affect offspring survival. However, few studies have investigated the relative impact of both the intensity and similarity of defence behaviour. Here, we examined nest defence behaviour of males and females during the incubation stage in an Arctic population of barnacle geese *Branta leucopsis*. We calculated the repeatability of defence behaviour to test whether this behaviour is consistent within individuals and investigated how it is associated with age. In addition, we investigated how daily survival rate (DSR) of the nests until hatching is associated with nest defence behaviour and age of the parents, as well as the effect of parent similarity in nest defence behaviour as an emergent trait of the pair bond. Both male and female defence behaviour were highly repeatable. The ages of both partners within breeding pairs were positively related, but age was only significantly associated with defence behaviour in females. Further, we found high similarity in defence behaviour within breeding pairs, but the similarity and intensity of defence behaviour within breeding pairs did not predict DSR. Finally, male defence behaviour positively predicted DSR, but female defence behaviour and male and female age did not. Our results suggest that nest protection is adaptive in males but behavioural similarity of pair members does not enhance nest survival, indicating behavioural similarity itself is not adaptive but rather a by-product of different effects.

Keywords: assortment, barnacle goose, *Branta leucopsis*, nest protection, nest survival model, reproductive success

Introduction

Individuals often display consistency in behaviour across time and/or across contexts (Sih et al. 2004, Réale et al. 2007). These patterns include different behavioural types, such as boldness, aggressiveness and activity, and are often adaptive (Biro and Stamps



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2008). For example, a study examining boldness in great tits *Parus major* revealed that differences in exploration behaviour are associated with differences in both reproductive success and adult survival (Dingemanse et al. 2004, Both et al. 2005). However, this raises the question how variation in systematic behavioural patterns within populations is maintained when there are associated fitness differences. Possible causes include spatiotemporal variation in the environment consistently favouring different behavioural patterns (Dingemanse et al. 2004, Nicolaus et al. 2016). Other causes may be life-history trade-offs (Wolf et al. 2007, Biro and Stamps 2008), and the physiological and environmental state of individuals (Wolf and Weissing 2010, Dingemanse and Wolf 2013), as they are known to contribute to differences across individuals. Finally, the social environment of an individual including their social breeding partner can affect an individuals' behaviour, which may allow for the variation of behavioural patterns to exist (Schuett and Dall 2009, Rudin et al. 2018).

Although behavioural differences are highly variable within populations, there can be an association of similar behavioural patterns within pair bonds (Madsen et al. 2009, Jiang et al. 2013, Clermont et al. 2019a). This correlation between phenotypes is often adaptive; phenotypically similar mates often have increased fitness compared to dissimilar ones (Groothuis and Carere 2005, Schuett et al. 2011, Jiang et al. 2013). Moreover, mate similarity may result in reduced sexual conflict, which in turn may enhance reproductive success (Schuett et al. 2011). Increased fitness through mate similarity would help maintain behavioural variation in a population (Groothuis and Carere 2005, Schuett et al. 2011). Different behavioural patterns can achieve equal fitness as long as individuals have partners with the same behavioural pattern, thus allowing for different behavioural patterns to coexist in a population (Brommer and Class 2017). We propose that coordination of behaviour as an emergent trait of the pair bond and its fitness benefits can be an underlying mechanism for the coexistence of different behaviours in a population.

One type of behaviour clearly associated with offspring recruitment is the protection of eggs and offspring (Osiejuk and Kuczyński 2007, Clermont et al. 2019b, Szípl et al. 2019). Defensive behaviour to protect a clutch against predation will enhance the likelihood that the clutch survives, hence increase reproductive success. This association between high defensiveness and reproductive success can be explained through the parental investment theory (Wallin 1987). It predicts that individuals with clutches of higher reproductive value, i.e. with a higher chance of yielding more offspring, will invest more in their clutch (Quillfeldt et al. 2005, Osiejuk and Kuczyński 2007). However, in species where both partners invest in a clutch, not only individual behaviour, but also the behaviour of the partner and the emergent traits of the pair bond can affect reproductive success. Thus, the similarity of defensive behaviour between partners may affect reproductive success, since the coordination of behaviour between partners within a breeding pair may be more important for clutch survival than the overall investment in clutch defence (Coulson 1966, Spoon et al. 2006, Schuett et al. 2011, Burtka

and Grindstaff 2015). If behavioural similarity exists in a species, it could have evolved as a result of selective advantages in reproductive success. However, whether this may be the case is not yet known, as only few studies have investigated the importance of the similarity of defensive behaviour between the parents for reproductive success, and these studies have found mixed results. For example, in the eastern bluebird (*Sialia sialis*, Burtka and Grindstaff 2015) and convict cichlid (*Amatitlania siquia*, Laubu et al. 2016), behavioural similarity between pair members in nest defence behaviour increases reproductive success. Contrarily, similarity did not affect reproductive success in the Kentish plover (*Charadrius alexandrinus*, Gómez-Serrano and López-López 2017) and Canada goose (*Branta canadensis*, Clermont et al. 2019a) – both long lived species. Clearly, more studies are needed to understand the importance of behavioural similarity on fitness.

In this study we investigated whether defensive behaviour is similar within pairs of wild-living barnacle geese *Branta leucopsis*, and how the intensity and similarity of defence behaviour relates to the survival rate of their clutches. Barnacle geese are monogamous biparental waterfowl that nest in colonies on the Arctic tundra. During incubation, the female stays on the nest almost continuously, while the male stays close-by the nest. In an earlier study on the same population, it was found that a proxy for nest defence behaviour (flight initiation distance (FID) from a human disturber), was strongly repeatable within and across seasons in females (de Jong et al. 2021). However, females showed plastic adjustments of this behaviour as they decreased their FID both over the season and across years (de Jong et al. 2021). Barnacle geese mate assortatively with regard to life-history traits, such as age and size (Choudhury et al. 1992, 1996, Black and Owen 1995), and social display during mate choice (Hausberger and Black 1990). Additionally, barnacle geese form pair bonds with familiar individuals from the same breeding area more often than with unfamiliar individuals (Choudhury and Black 1994), and choose their mate by sampling each individual and comparing it to the previously sampled mate (Choudhury and Black 1993). There is still a lack of information regarding how breeding pairs are assorted with respect to behaviour, how it relates to the age of individuals, and how these factors combined influence reproductive success in barnacle geese. For example, older barnacle geese are more experienced and usually more aggressive, and therefore will be more successful in their breeding attempts (Black and Owen 1989, 1995, Van Der Jeugd 2001). This combined with a higher reproductive success due to pair similarity in behaviour and age provides insights on how behavioural similarity evolved.

Here, we investigated nestdefence behaviour in both males and females; the response of parents when their nest is approached by a human intruder. First, we tested if defence behaviour is consistent within individuals, and whether there is a correlation between male and female defensive scores. We also tested whether defence behaviour correlates with age. Thereby, we can explore whether a similarity in defence behaviour between pair members could be a by-product of assortment in age of breeding pair members. For instance, if defence behaviour positively increases with age in both sexes and there

is assortment in age within breeding pairs, this could lead to the emergence of assortment in defence behaviour. Second, we investigated how behavioural intensity and similarity explain daily survival rate (DSR) of the nest during the incubation period (Dinsmore et al. 2002, Jehle et al. 2004, Rotella et al. 2004, Laake 2013). Unattended nests are vulnerable to egg predation (Samelius and Alisauskas 2001), making nests of highly defensive individuals that do not flee from their nest in response to disturbance to be more likely to survive. Here, we test four hypotheses: 1) the female intensity hypothesis, where the daily nest survival depends on the intensity of the female defensive behaviour only. The better the female defends the nest, the higher the DSR. In the barnacle goose, only females incubate. As females have to incubate on the nest almost constantly for the eggs to hatch (Prop et al. 1984), females that are less likely to leave the nest in response of disturbance will have higher hatching success. 2) The male intensity hypothesis, where the hatching success of the nest depends on the intensity of the male defensive behaviour only. Male barnacle geese stay close to the nest and usually respond to potential threats before females do. According to this hypothesis, DSR will be higher when males are more defensive while protecting the nest. 3) The pair intensity hypothesis, where pairs that have the highest combined intensity of defence behaviour are predicted to have the highest DSR. 4) The pair similarity hypothesis, where the pairs which have the highest similarity in behaviour will have highest DSR. Here, pairs with the smallest difference in defence behaviour intensity, thus with highest similarity in nest defence behaviour, are expected yield higher DSR for their nests. Pairs that behave similarly may improve offspring survival through increased efficiency, synchrony and coordination of parental effort, and reduced conflict (Spoon et al. 2006, Mariette and Griffith 2012, 2015, Mutzel et al. 2013, van Rooij and Griffith 2013).

Methods

Study species and population

The study population is located on the islands Storholmen (ca 30 ha) and Prins Heinrichøya (ca 3 ha) in Kongsfjorden, Svalbard (Spitsbergen), near the settlement Ny-Ålesund (78°55'N, 11°56'S). This population established in the 1980s and since increased considerably (Loonen et al. 1998, Layton-Matthews et al. 2019). Population numbers have been monitored since 1990. Some geese (39%) in the study population are ringed with unique alphanumeric rings and thus recognizable on the individual and usually also the pair level. For a number of these ringed geese the exact ages are known since they were ringed as goslings or juveniles (3.5% of males, 12.1% of females). For individuals that were not first ringed as a gosling or juvenile, a minimal age was assigned based on the year of ringing as an adult plus one year (30% of males, 41% of females). We included measures of minimal age since the sample size of geese with exact age data is very limited. During the summer season from May to September, barnacle geese breed in monogamous

pairs. The first eggs are laid in June and clutches usually contain between four and six eggs. The incubation period takes around 24 d and geese produce one clutch per season (Dalhaug et al. 1996, Tombre and Erikstad 1996). When clutches get predated, barnacle geese rarely produce replacement clutches within the short breeding season (Mitchell et al. 1988), the only exception being during the egg laying phase following egg predation by polar bears *Ursus maritimus* (de Jong et al. 2021). Nests on the islands can be predated by arctic skuas *Stercorarius parasiticus* who target one egg by picking it open and by glaucous gulls *Larus hyperboreus*, who approach nests in flocks and swallow entire eggs. During our study, there was no ice linking the breeding islands with the mainland, so arctic foxes *Vulpes lagopus* were unable to reach the islands. In recent years, polar bears visit the islands frequently and forage on barnacle goose eggs (Drent and Prop 2008, Prop et al. 2015).

Data collection

The study was conducted in 2019 from 21 June to 7 July, until all nests hatched or were predated. Most nests (n = 286, 91%, Supporting information) already contained eggs from the start of the observation period, and therefore initiation dates of most nests were unavailable. Our first visit to the breeding site was during the egg laying and incubation phase, and most nests already contained more than one egg (n = 268, Supporting information), and only a few nests increased in clutch size after the first observation (n = 23, Supporting information). We could not infer nest initiation date using the number of eggs in the nest, since barnacle geese already started laying a couple days before the nest visit, and eggs could have been subject to predation before a nest was found. The exact nest number in the breeding colonies were unknown, since an unknown number of nests could have disappeared before data collection started. However, we expect this number to be low, since the overall nest loss rate during the study period was 15.6%. We gathered GPS coordinates of all nest locations and read rings of individuals for identification upon later visits. All nests were separated from one another by more than 10 m. During the observation period, the breeding islands were visited every other day (a total of seven times) to check all the nests present at the breeding sites for signs of predation or hatched eggs and score the behavioural response to human approach during the incubation period as a proxy for nest defence towards potential predators (Cossa et al. 2018). We decided on this interval to minimize nest disturbance while ensuring accuracy of nest survival rates. All nests were approached calmly on foot (approximately 3 km h⁻¹) by one person (FS) in a straight line towards the nest from at least 20 m distance. The researcher always wore the same clothing and same pace during nest approaches, and varied the initiation point and direction of the approaches towards the nest. Barnacle geese that were not present or fled before the nest was approached were not used in the analyses as we could not collect nest defence scores for these individuals (see similar methodology: de Jong et al. 2021). Since we were highly dependent on weather conditions, the time of day at which

the observations were conducted varied over the observation period. However, since there is constant daylight in the Arctic summer and barnacle geese incubate and forage throughout the whole 24-h period (Prop et al. 1984), we assume time of day does not affect their behavioural response to human approach. During these approaches, nest defence behaviour was noted for both male and female using a score between 0 (no defensive response to approacher) and 4 (strong defensive response to approacher, see Table 1. We assumed that a short fleeing distance and aggressive behavioural response to the approacher equals a high nest defence intensity and high risk-taking, whereas long fleeing distance and no aggressive behaviour equals low nest defence intensity and risk-taking (Blumstein et al. 2016, Clermont et al. 2019a, de Jong et al. 2021). Nest defence behaviour is a risk assessment in response to potential predation events; individuals have to decide whether to flee from the nest to ensure survival, but risk nest predation. Fleeing distances were assessed visually by the approacher as the geese fled from the nest. The categorisation of defence behaviour was used to account for the difficulty of judging distances visually with high accuracy, and these categories were already used during routine nest checks for this population. The observer was trained at judging distances between the different behaviour scores before nest approaches were conducted. We did not observe any distraction displays (e.g. simulations of barnacle geese being injured) in response to nest approaches, with the exception of some geese (often with defence score 1 or 2) making sounds throughout the approach ('honking'). At the start of the approaches, females were on the nest with the male close-by within 5 m of the nest. Clutch size was defined as the maximum observed number of eggs. Clutches were considered hatched if newly hatched goslings were present, or eggshells with egg membranes when the nest was found empty (Davis et al. 1998). If at least one egg hatched, the nest was considered successful. Hatch dates were determined by signs of hatching using two methods. First, the exact hatch date was known for nests that were found on the day of hatching (when at least one egg just hatched or was about to hatch as indicated by pipping sounds and/or cracks in the eggs). Second, when at least one of the eggs had already hatched, the hatch date was estimated between the current and previous visit at 40% of the interval (to decrease biases of the midpoint assumption as date estimate; Miller and Johnson 1978, Johnson 1979). Nests that were predated by polar bears were excluded from the nest survival analysis as barnacle geese cannot protect their nest against this predator and we were interested in nest survival in relation to defence behaviour towards humans and small egg predators. These nests were identified based on records of polar bear visits to the islands

and the condition of the nest: nests predated by a polar bear were completely destroyed. An individual polar bear always predaes a limited number of nests (Prop et al. 2015).

Ethics statement

The Governor of Svalbard approved the study (RiS-ID 11281, 21 June 2019) and all fieldwork complied with local ethical guidelines and regulations. No animals were handled or captured, and disturbance was kept to a minimum. Barnacle geese were chased away from the nest not more than once per visit of the breeding island. Observational data of nests were collected as quickly as possible to minimize disturbance time.

Statistical analyses

Analysis of nest defence behaviour

We used R for statistical analyses (<www.r-project.org>). We estimated the intensity of defence behaviour for each individual by calculating the mean defence score over the observation period; the higher the defence score, the more intense an individual's behavioural response. To justify this, we measured repeatability to evaluate the temporal consistency of defence behaviour within individuals across both sexes. As defence behaviour was measured on an ordinal scale, we calculated the intraclass correlation coefficient (ICC) for both sexes using the R package *irr* (Gamer et al. 2019) as an assessment of repeatability (Nakagawa and Schielzeth 2010).

The similarity between male and female behaviour was analysed using the association between the mean defence scores per pair with a Spearman rank correlation test. For further analyses, we calculated the summed mean ranked defence behaviour per nest as a measure of pair defence intensity. Pair defence similarity was calculated as the difference between mean male and female ranked behaviour. We examined the relationship between maximum clutch size and nest defence score (male, female, summed defence score and pair similarity in defence scores) for all nests with a Kruskal–Wallis test, to test whether there is an effect of defence behaviour on partial clutch loss rather than full clutch loss. To investigate if there were differences within pairs between male and female defence scores, we performed a Wilcoxon signed-rank test. We tested for similarity in age between males and females within breeding pairs, as well as an association between defence behaviour and age, using a Spearman rank correlation test. We ran a binomial generalised linear model (GLM) to model hatching success as a function of mean male and female defence scores. Means are presented with standard error of the mean (SE) and results are considered significant when $p < 0.05$.

Table 1. Ranked nest defence intensity scores and frequencies of all observations (n).

Score	Defensive behaviour	n
0	Flee at > 10 m, no other behavioural response	494
1	Flee at > 10 m, call from distance	696
2	Flee at 10–5 m	242
3	Flee at 5–1 m	188
4	Flee at < 1 m or not at all, possibly attack observer	181

Nest survival model

As a measure for hatching success, we estimated daily survival rate (DSR) of nests. For this, we performed generalized linear models with a binomial error distribution and logit link function using the R package *RMark* (Laake 2013) to construct daily nest survival models for the program MARK (White and Burnham 1999). The probability of a nest surviving over the entire incubation period, or hatching success (H), can be calculated as DSR to the power of 24 (DSR^{24}) since the incubation period of barnacle geese is circa 24 d. We considered DSR of the entire nest rather than individual eggs, since nest DSR values are independent from one another, whereas DSR per egg is not (if one egg in the nest is predated, it is likely that other eggs in the nest are or will be predated as well) (Beintema 1992). We focused on pairs rather than individuals, as each pair takes care of one nest and therefore yields one DSR. We used a hierarchical modelling approach to identify the best-fitting model predicting DSR (Rotella et al. 2004). Location, date and age of each pair member were added as candidate parameters to estimate DSR, as they have been found to affect reproductive success in barnacle geese (Black and Owen 1995, Dalhaug et al. 1996, Lameris et al. 2018). At each modelling stage, we identified the model fitting the data best and proceeded with this model to the next stage (Table 2; Sexson and Farley 2012). We used Akaike's information criterion for small sample sizes AICc (Akaike 1973) and normalized Akaike weights w_i (Burnham and Anderson 2002, Anderson 2008) to compare models. The best fitting model has the lowest AICc value. In the first stage, we built models assuming a constant DSR over time and tested for differences between both breeding islands (Storholmen and Prins Heinrichøya). Second, we added the effect day of the nesting season. Third, we assessed male and female age separately and as an additive combination. In the fourth and last stage, we added the different measures of defence behaviour (Table 2). We did not use the incubation day as a predictor in the model, since dates at which the first eggs are laid were unavailable and incubation days could only be inferred for successful nests using the hatch date. Using observation date as a proxy for incubation day allowed us to take the entire dataset into account rather than solely successful nests. Barnacle geese can adjust their

behaviour closer to hatching, since the survival probability of the goslings increases. However, since we used average defence score variables and calculated their repeatability, we account for this temporal variation. We excluded any combination of defence score covariates in a single model, as we found these covariates have strong collinearity (variance inflation factor $VIF > 3$), which may result in misleading parameter estimates (Cade 2015). All models including age were kept at the same sample size ($n=240$) to allow for adequate model comparison. Missing datapoints in the age variables were substituted in the model using the average sex-specific age. We calculated the parameter estimates β and 95% confidence interval (CI) for each variable in the best-fitting model.

Results

Defence scores and behavioural strategies

We monitored a total of 314 Barnacle goose nests on two breeding islands (Storholmen ($n=279$) and Prins Heinrichøya ($n=35$)). For 69 nests, no defence scores were recorded due to the absence of the pair during every nest visit. Polar bears depredated 8 nests during the observation period. This left a total of 240 nests with nest defence scores. On average, defence scores were recorded 2.46 ± 0.09 (mean \pm SE) times per nest with a range of 1–6 (1x=70, 2x=71, 3x=51, 4x=21, 5x=20, 6x=7).

We found high repeatability of nest defence scores for both males ($ICC=0.77$, $CI=0.69-0.83$, $p < 0.001$) and females ($ICC=0.71$, $CI=0.63-0.79$, $p < 0.001$). The mean ranked defence behaviour (\pm SE) of males (1.37 ± 0.08) was significantly higher than that of females (1.05 ± 0.07), with males defending the nest more intensively than their female partner at the same nest ($Z=-5.106$, $n=240$, $p < 0.001$). We found a strong and positive association between male and female defence scores within nests ($r_s=0.67$, $n=240$, $p < 0.001$; Fig. 1). In only 10% ($n=25$) of all pairs, males and females differed in their mean defence score by ≥ 2 . We found no association between maximum clutch size and male defence score ($H_4=3.13$, $n=240$, $p=0.537$), female defence score

Table 2. Description of the covariates used in the nest survival models of barnacle geese including the hierarchical modelling stage in which they were introduced to the models

Modelling stage	Covariate	Description
1	Location	Storholmen or Prins Heinrichøya
2	Date	Date of the observation period: 21 June to 7 July
3	MaleAge	Age of the male
3	FemaleAge	Age of the female
4	MaleDef	Mean male ranked defence behaviour (range 0–4)
4	FemaleDef	Mean female ranked defence behaviour (range 0–4)
4	SummedDef	Summed mean ranked defence behaviour of all nest visits (range 0–8)
4	DifDef	The difference between male and female mean ranked defence behaviour (range –4 to 4)
4	NestDef	Mean of the highest value of ranked defence behaviour of either male or female during each visit (range 0–4)
4	MaleMax	Maximum male ranked defence behaviour over all nest visits (range 0–4)
4	FemaleMax	Maximum female ranked defence behaviour over all nest visits (range 0–4)
4	NestMax	Maximum ranked defence behaviour of either male or female over all nest visits (range 0–4)

($H_4=5.98$, $n=240$, $p=0.201$), summed defence scores ($H_4=4.24$, $n=240$, $p=0.375$) or pair similarity in defence scores ($H_4=5.69$, $n=240$, $p=0.224$). While age-assortment was high within pairs ($r_s=0.47$, $n=74$, $p < 0.001$; Fig. 2), age was only significantly positively associated with defence behaviour in females ($r_s=0.25$, $n=107$, $p=0.009$; Fig. 3a). In males, this association was also positive, but it was not statistically significant ($r_s=0.13$, $n=77$, $p=0.268$; Fig. 3b) although the sample size for males was lower. Hatching success was not significantly associated with mean male and female defence score (Supporting information).

Individual and pair defence behaviour and nest survival

We created a total of 14 candidate models over the four modelling stages using all covariates for 240 nests. For 69 of these nests, male age was known and for 98 nests female age was known. The highest-ranking model for nest survival contained observation date and mean male defence, and had a model weight of 0.517 (Table 3), whereas the second-ranking model that contained date and summed pair defence had a model weight of only 0.128 with $\Delta AIC_C > 2$. The model containing mean female defence was less well supported by the data than a model containing no behavioural measure. Moreover, the model containing location received less support than the null model (i.e. assuming a constant DSR). While the model containing male age ranked higher than the model containing female age, models containing male and/or female age were poorly supported by the data.

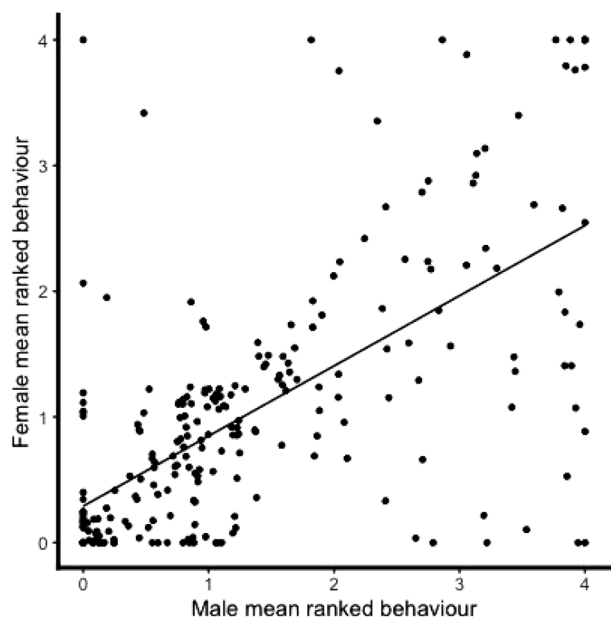


Figure 1. Male mean ranked defence behaviour in relation to female mean ranked defence behaviour. Each datapoint represents one barnacle goose pair ($n=240$). A linear regression line is shown to portray the direction of the correlation. Datapoints are jittered to give an overview of the spread of data.

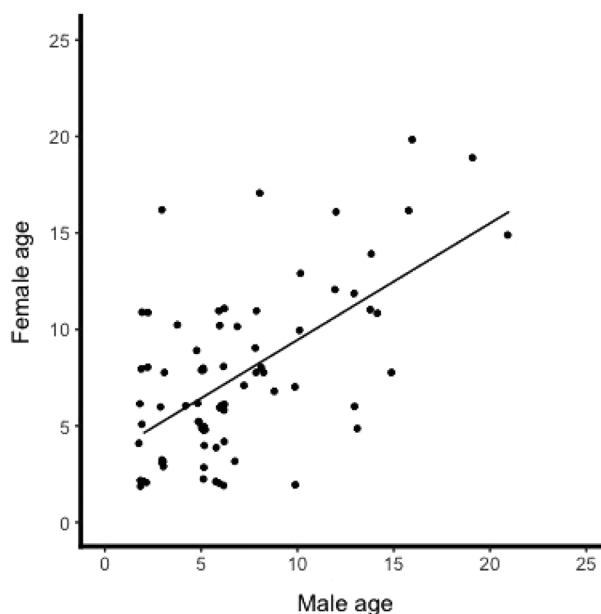


Figure 2. Male age in relation to female age. Each datapoint represents one goose pair ($n=74$). A linear regression line is shown to portray the direction of the correlation.

The coefficients from the highest-ranking model indicated a strong positive relationship between male mean defence scores and DSR ($\beta \pm SE=0.55 \pm 0.25$, $CI=0.07-1.04$, Fig. 4b). When the mean male ranked behaviour is equal to 0, the nest has a predicted DSR of 0.985 ($H=0.693$), whereas when mean male ranked behaviour is equal to 4, the nest has a predicted DSR of 0.998 ($H=0.960$). Predicted DSR decreases over the observation period (Date) from a predicted DSR of 0.996 on 21 June to 0.913 on 7 July ($\beta \pm SE=-0.21 \pm 0.06$, $CI=-0.33$ to -0.09 , Fig. 4a). There was no effect of any defence score variable on partial clutch loss (all NS). Thus, while male defence is a predictor for the survival of at least one egg (which is considered as a successful nest in the nest survival model), the fraction of eggs lost over the observation period appears independent of male defence.

Discussion

In species with monogamous pair bonding and biparental care, paired individuals may have similar behavioural patterns, and thereby increase their reproductive success through increased coordination and reduced conflict (Spoon et al. 2006, Mariette and Griffith 2012, Mutzel et al. 2013, van Rooij and Griffith 2013, Mariette and Griffith 2015). While overall males defend their nests more intensively than their female partners, we found barnacle geese pair members show high similarity in nest defence behaviour. We also found that defence behaviour is highly repeatable in both males and females. These results indicate that individuals within pairs of barnacle geese often behave similarly with regard to offspring protection. There was strong positive similarity in age within pairs, but the relationship between defence behaviour and age

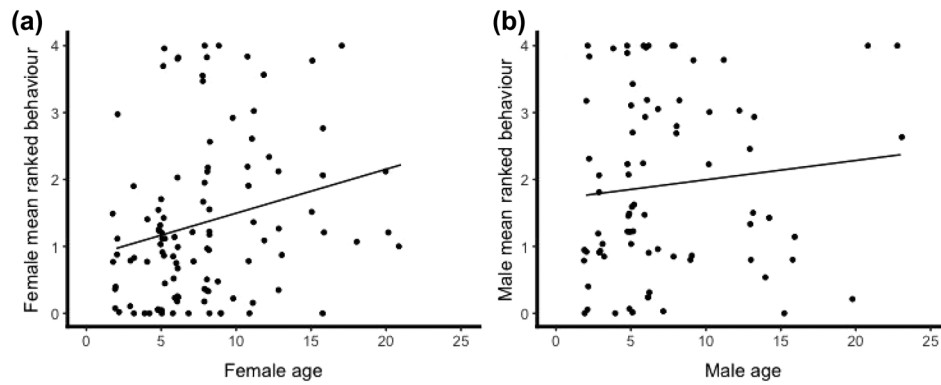


Figure 3. Age in relation to mean ranked defence behaviour in (A) females ($n=107$) and in (B) males ($n=77$). Linear regression lines are shown to portray the direction of the correlation. The correlation is significant in females, and nonsignificant in males.

was only statistically significant for females. Observation date and mean male defence behaviour best explained variation in daily nest survival, whereas measures of female defence behaviour, pair similarity in defence behaviour, location and age were much less important.

Defence behaviour on the individual and pair level

The existence of pair similarity in life-history traits such as age and size (Choudhury et al. 1992, 1996, Black and Owen 1995) and reaction when approached by a human (Madsen et al. 2009) has been identified before in barnacle geese. However, to our knowledge, this is the first study that quantified behavioural similarities and the implications on reproductive success in this species. Examples of behavioural assortment in pairs positively affecting reproductive success do exist in other bird species, including great tits *Parus major* (Both et al. 2005), zebra finches *Taeniopygia guttata* (Schuett et al. 2011) and eastern bluebirds (Burtka and Grindstaff 2015). A recent study by Clermont et al. (2019a)

Table 3. Model selection results with all candidate models of daily survival rate (DSR) of 240 barnacle goose nests at Kongsfjorden, Svalbard (Spitsbergen) in 2019. Candidate models are ordered based on difference in AIC_c (ΔAIC_c) compared to the lowest AIC_c (160.24) and model weight (w_i). The number of parameters (K) is presented for each model.

Modelling stage	Model	K	ΔAIC_c	w_i
4	Date+MaleDef	3	0.00	0.5172
4	Date+SummedDef	3	2.80	0.1278
3	Date+MaleAge	3	4.04	0.0685
2	Date	2	4.35	0.0587
3	Date+MaleAge+FemaleAge	4	5.23	0.0378
4	Date+FemaleDef	3	5.50	0.0331
4	Date+FemaleMax	3	5.76	0.0290
4	Date+MaleMax	3	5.83	0.0280
4	Date+DifDef	3	6.01	0.0256
4	Date+NestMax	3	6.03	0.0253
4	Date+NestDef	3	6.16	0.0238
3	Date+FemaleAge	3	6.25	0.0228
1	Constant	1	11.79	0.0014
2	Location	2	12.74	0.0009

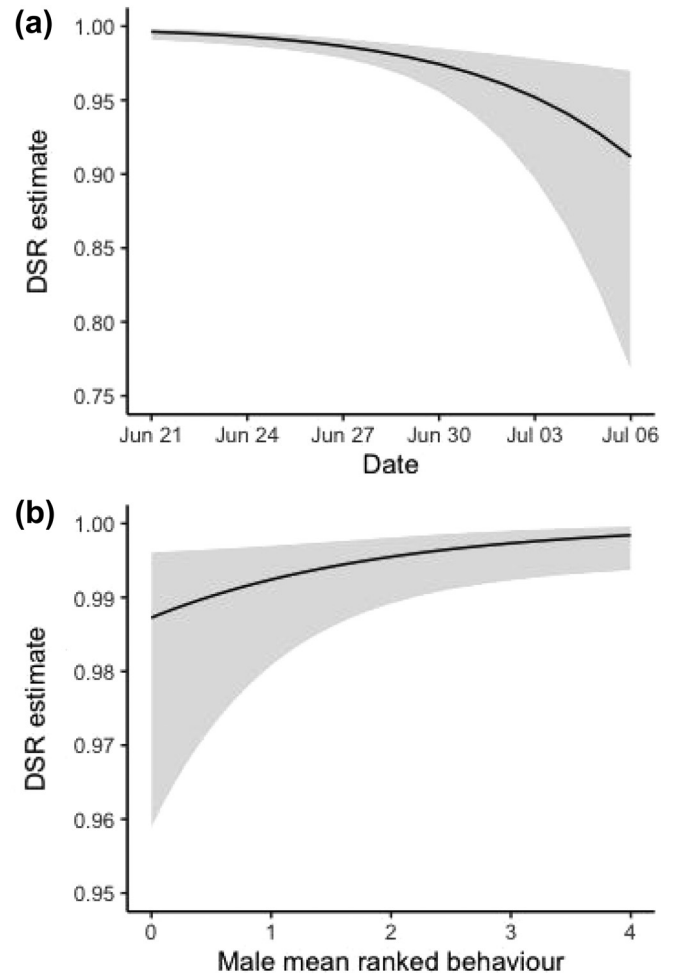


Figure 4. Daily survival rate (DSR) estimates of barnacle goose nests at Kongsfjorden, Svalbard (Spitsbergen) in 2019 in relation to (A) day of the season and (B) mean male ranked defence behaviour. 95% confidence intervals are included.

examined similarity in nest defence behaviour of the long-lived biparental Canada goose. They found a strong relationship between male and female defence scores. However, pairs with similar defence behaviour did not acquire higher reproductive success compared to pairs with non-similar defence behaviour, which is consistent with our findings.

Behavioural similarity in barnacle geese could arise through assortative pairing, in which individuals choose their partners actively based on their likeness in various traits (Groothuis and Carere 2005, Réale et al. 2007, Schuett et al. 2010, Jiang et al. 2013). Defence behaviour could be a signal of high partner quality; highly defensive partners may be 'good parents' since they may increase reproductive success through offspring protection. If highly defensive individuals are favoured in a population through mate choice, individuals will pair assortatively. Alternatively, different behavioural types might be correlated and selected with different life history strategies (Stamps 2007), for example investment in current versus future reproductive success. When the nest defence score is high, this may indicate individuals invest more in their current clutch, and less in their own survival. On the other hand, a low nest defence score indicates an individual flees from a potential predation event at larger distances, which can increase individual survival and therefore potential future reproductive success. If there are different life history strategies linked to defensive behaviour in barnacle geese, pairing up with a similar partner may increase fitness, since their life history strategies (i.e. investment in current reproductive success versus future reproductive success) will match with their partner. Barnacle geese have age-related mate access and high mate fidelity, and have been found to pair assortatively for age (Black and Owen 1995) and even social display (Hausberger and Black 1990). Our findings show strong assortment in behaviour, although it is unclear whether this effect emerges through mate choice. Whereas defence intensity increases significantly with age in females, this increase was not significant for males. This may indicate that males generally have strong defence responses, whereas in females mainly the older birds increase their defence response. Thus, although both defence behaviour and age were highly similar between partners, the age-assortment alone likely does not explain the emergence of behavioural assortment. However, it is important to note the correlation coefficients were similar for males and females, indicating the discrepancy between the sexes could also be due to differences in sample sizes, as for females we had more age data available than males, thereby increasing the power to detect significant effects. Furthermore, the nest approaches were subject to variability with regard to weather conditions, time of day, exact starting distance and exact starting location. These factors could have affected the behavioural response of barnacle geese to human intrusion, and could potentially account for (part of) the within- and between-individual variation we observed in nest defence scores throughout the observation period. Finally, the usage of categories during assessment of nest defence behaviour reduced the resolution of the behavioural response data. This could have reduced our ability to detect significant effects in our analyses.

Alternatively, behavioural similarity can arise through individuals tuning their behavioural patterns post-pairing to their partner (Dingemanse and Araya-Ajoy 2015). Here, focal individuals can adjust their behaviour to be more alike the behaviour of their partner in order to more effectively coordinate and cooperate within a partnership (Laubu et al. 2016). Similarly, shared environmental effects may shape the behaviour of paired individuals in an analogous way (Class et al. 2017). Hence, an individual's environment is expected to affect behavioural similarity, including the sites of pair formation and breeding. Nonetheless, we assume it is unlikely that the environment alone shapes the observed similarity in defence behaviour. Barnacle goose pairs breed in highly homogeneous breeding colonies, but we still observed large differences in behaviour between geese in relatively similar nesting sites. Finally, similarity of the trait under study could be a by-product of mate preference or restricted mate access. Hausberger and Black (1990) found the display duration of male barnacle geese during pair formation to be longer when the reaction of the females was more intense. A correspondence between social display and defence behaviour could perhaps explain the similarity of defence intensity in barnacle goose pairs, but this is yet to be explored. Thus, although we did find similar defence patterns in barnacle goose pairs, whether this similarity arises from active mate choice, another mechanism or a combination of the two is still to be determined.

Implications of defence behaviour on clutch survival

Between-individual differences in the intensity of defence behaviour may have fitness consequences. In most studies investigating the effect of behaviour on fitness, the intensity of behaviour is often the main focus, sometimes even of solely one sex (Réale et al. 2007). In species with biparental care, both individuals contribute to offspring survival, so it is crucial to consider behaviour of both sexes and emergent effects of the pair bond. Some studies have found an effect of behavioural similarity between partners on reproductive success (Both et al. 2005, Burtka and Grindstaff 2015), although it is unclear what exact mechanisms cause reproductive success to be higher in pairs with similar behavioural traits (Kralj-Fišer et al. 2013). Using different models for nest survival to estimate DSR (Dinsmore et al. 2002, Jehle et al. 2004, Rotella et al. 2004, Laake 2013), we found that the averaged defence intensity of the males, along with date in the season, predicted DSR most accurately. We found no association between DSR and female defence intensity, total defence intensity and similarity in defence intensity. Observation date is negatively correlated with DSR. Barnacle geese very rarely replace their clutch if it fails within the short breeding season, making the clutch highly valuable immediately from laying date. It is likely that nests face more predation towards the end of the season as predation pressure increases. The breeding islands are populated by barnacle geese and common eiders *Somateria mollissima* that share the same predators. Over time, a declining number of nests of both species are exposed to a constant number of predators, which may lead to an increase in predation pressure. Moreover, it could be that barnacle geese that breed later

during the season invest less in their clutch (Dalhaug et al. 1996). Thereby, the reduced DSR over time could be due to the limited reproductive success of individuals breeding later in the season (Forsslund and Larsson 1992). Our study has some restrictions regarding the validity of DSR estimates over time, since we had no access to exact laying dates in the nest survival analyses, and some nests in the population may have been depredated before the observation period started. Thus, we cannot infer the exact causes underlying the negative relationship between observation date and DSR.

There is also a positive relationship between male defence score and DSR, which is in line with the male intensity hypothesis (i.e. only defence behaviour of the male affects nest survival). During the breeding season, males stay close to the nest and are very attentive of their surroundings while doing so. Males and females likely occupy different roles with respect to parental care: the male is safeguarding the nest from most avian predators found on the breeding islands while the female remains stationary on the nest while incubating. If so, highly defensive males may allow the female to remain and incubate on the nest for longer. Subsequently, nests with highly defensive males may face less predation and may therefore retain a higher DSR. Finally, male barnacle geese are larger on average than their female counterparts (Choudhury et al. 1996), potentially allowing them to defend the nest more effectively than females, since large male barnacle geese are more successful at aggressive interactions with conspecifics than small males (Van Der Jeugd 2001).

We found no support for the pair similarity hypothesis (pair similarity in defence behaviour affects nest survival), while the observed similarity of defence behaviour in pairs is high in barnacle geese. Thus, we found no direct evidence of a selective advantage of behavioural similarity in pairs in relation to enhanced reproductive success. A fitness advantage for similar defence behaviour in pairs could still exist, but we failed to detect it. For example, since we found a very high prevalence of similar behaviour, it could be the sample size for dissimilar pairs was too small (in only 10% of pairs, male and female mean defence score differed with ≥ 2) to detect differences in breeding success. This would possibly explain why we did observe an effect of male defence and not of female defence. Male defence score is relatively more variable than female defence score between individuals, which makes it more likely to detect effects of intensity of male defence behaviour on DSR. The strong effect of male behaviour on DSR may even mask the effect of a correlated variable (i.e. female defence behaviour). Additionally, it may be that a fitness advantage of behavioural similarity exists for a trait other than nest survival. For example, gosling survival is highly variable across pairs and is strongly determined by predation pressure. Loonen et al. (1999) found that the number of goslings is related to parental vigilance behaviour and fitness, with parents with large broods being more attentive of their surroundings. Large brood size also enhanced the fitness of both the parents and the offspring, likely through enhanced dominance and increased access to food sources. Whether behavioural similarity is related to gosling survival and brood size remains to be determined. Another

explanation for the absence of enhanced fitness due to behavioural similarity is that similarity in defence behaviour may have a long-term effect on reproductive success, which is not visible in one breeding season. Barnacle geese form multiyear pair bonds which allow for long-term effects to arise, although divorces do take place (Black et al. 2007). Additionally, there could be different sex roles in behavioural defence of the offspring. Defence behaviour can be adaptive through different mechanisms in both sexes. For example, behaviour in males may be important for fitness during a different time of year than female behaviour. Here, it would indicate male defence affects reproductive success during the incubation period by protecting the nest, which is in agreement with our results, while female defence affects reproductive success in a different way or stage of offspring development. However, outside the breeding season in wintering flocks, males are overall more vigilant than females (Carbone et al. 2003) and direct fitness benefits of defence behaviour in female barnacle geese remain unidentified. Finally, similarly behaving pairs may enjoy an adaptive advantage that is not directly related to reproductive success, but rather benefits their own survival, for example through enhanced dominance and access to better resources (Loonen et al. 1999, Stahl et al. 2001).

Conclusion

We have shown that barnacle goose pairs exhibit high similarity in the intensity of defence behaviour during the breeding season. However, a higher level of behavioural similarity was not associated with increased nest survival. Instead, there was a positive association between male defence intensity and the daily survival rate of a nest, which suggests protective behaviour of the male affects reproductive success during nest incubation. The mechanisms behind high behavioural similarity remain to be identified. We recommend future studies to investigate multiple aspects of fitness and consider non-adaptive routes that lead to the evolution of behavioural similarity.

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Data availability statement

Data are available from the Dataverse: <<https://doi.org/10.34894/QTRW9D>> (Speelman et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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