Kin association during brood care in a facultatively social bird: active discrimination or by-product of partner choice and demography?

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Abstract

Intra-group relatedness does not necessarily imply kin selection, a leading explanation for social evolution. An overlooked mechanism for generating population genetic structure is variation in longevity and fecundity, referred to as individual quality, affecting kin structure and the potential for cooperation. Individual quality also affects choosiness in partner choice, a key process explaining cooperation through direct fitness benefits. Reproductive skew theory predicts that relatedness decreases with increasing group size, but this relationship could also arise because of quality-dependent demography and partner choice, without active kin association. We addressed whether brood-rearing eider (Somateria mollissima) females preferentially associated with kin using a 6-year data set with individuals genotyped at 19 microsatellite loci and tested whether relatedness decreased with increasing female group size. We also determined the relationship between local relatedness and indices of female age and body condition. We further examined whether the level of female intracoalition relatedness differed from background relatedness in any year. As predicted, median female intra-group relatedness decreased with increasing female group size. However, the proportion of related individuals increased with advancing female age, and older females prefer smaller brood-rearing coalitions, potentially producing a negative relationship between group size and relatedness. There were considerable annual fluctuations in the level of relatedness between coalition-forming females, and in 1 year this level exceeded that expected by random association. Thus, both passive and active mechanisms govern kin associations in brood-rearing eiders. Eiders apparently can discriminate between kin, but the benefits of doing so may vary over time.

Keywords: cooperation, fecundity, kin association, kin discrimination, longevity, partner choice, relatedness

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Introduction

The role of biotic interactions such as predation and disease as drivers of kin structuring has not been widely appreciated (e.g. Beckerman et al. 2011). This neglect is surprising given that these ecological processes are potent drivers of variance in longevity and fecundity, and mortality patterns in turn may affect kin structure and the potential for cooperation (Lehmann & Balloux 2007; Lehmann & Rousset 2010; Beckerman et al. 2011). Instead, the focus in understanding group formation and its evolution has been on kin selection theory (Hamilton 1964), which postulates that elevated relatedness among group members and the resulting inclusive fitness benefits could offset the costs associ-
lated with group living and thus maintain cooperative behaviour.

However, the mere presence of relatedness between group members does not necessarily imply that active kin association, let alone kin selection, is operating. First, kin groupings may develop simply through natal philopatry, and in line with this notion, the average relatedness among members of the more philopatric sex is often elevated (Queller & Goodnight 1989; de Ruiter & Geffen 1998; Tiedemann & Noer 1998; Surridge et al. 1999; Lawler et al. 2003). Second, large direct benefits of cooperation may be sufficient for the maintenance of cooperation, regardless of any inclusive fitness considerations (reviewed in Clutton-Brock 2009).

Individual variation in the costs and benefits of cooperation is important for understanding the evolution of cooperation through direct fitness benefits, and partner choice has been suggested as a widespread, but so far underrated, evolutionary mechanism underlying such cooperation (Noë 2001; Sachs et al. 2004). This has led to the development of biological market theory, which describes such social interactions as the trade of commodities between partners (Noë & Hammerstein 1995). Asymmetries in power and individual quality result in interindividual variation in these commodities, which may affect grouping decisions (e.g. Öst et al. 2003a; Jordan et al. 2010; Jaatinen & Öst 2011) and the social bonds within groups (McNamara & Leimar 2010). Individual quality attributes are often positively linked to longevity (e.g. Weladji et al. 2006; Lescroël et al. 2009) and fecundity (Weladji et al. 2006; Hamel et al. 2009), and these demographic parameters may be correlated (e.g. Yoccoz et al. 2002; Weladji et al. 2006; Hamel et al. 2009). We may therefore expect to find changes in local relatedness encountered by individuals depending on their quality or state (Johnstone & Cant 2010). Consequently, the availability of potential kin vs. non-kin cooperation partners in the population may vary as a function of correlates of individual quality such as age (e.g. Johnstone & Cant 2010; Beckerman et al. 2011).

Group size itself may influence kin structure within groups (e.g. Alvard 2003). Reproductive skew theory predicts that the size of cooperative groups declines with increasing relatedness (Reeve & Emlen 2000), and the same result was also obtained from modelling the effects of group size, reproductive skew and dispersal on average relatedness within groups (Łukas et al. 2005). In the model by Reeve & Emlen (2000), the negative relationship between relatedness and group size arises because reproductive output is assumed to be a decelerating function of group size, and thus, members of large groups will receive more inclusive fitness benefits from a relative reproducing on its own than joining the group. However, a relationship between relatedness and group size could also arise as a combination of demography and partner choice, without the need to invoke active kin discrimination. Individual quality may be connected with choosiness in partner choice, thereby directly influencing group size (e.g. Öst et al. 2003a; Riebel et al. 2010; Jaatinen & Öst 2011), and it may also determine the frequency of encountering relatives (Johnstone & Cant 2010). Because of this, a negative relationship between relatedness and group size could be explained simply by quality-assortative partner choice preferences. However, the possibility that the joint operation of demographic effects and partner choice could be sufficient for explaining the probability by which relatives engage in cooperative behaviours and the resulting group sizes has so far not been considered.

Waterfowl show female-biased natal philopatry that potentially elevates local relatedness, which may facilitate the evolution of kin-selected female cooperation (e.g. Andersson & Åhlund 2000; Roy Nielsen et al. 2006; Waldeck et al. 2008; Jaatinen et al. 2009; but see Pöysä 2004; Semel & Sherman 2001). The facultatively social, female-philopatric eider duck (Somateria mollissima) has emerged as a suitable model for testing this possibility, as it commonly forms cooperative brood-rearing coalitions. However, this species is also a good candidate for testing whether demography and partner choice could explain the kin structure in brood-rearing coalitions of variable sizes. The direct fitness benefits to coalition members are considerable (Öst et al. 2005), as the reproductive output of females in coalitions often exceeds that of solo parents (Öst et al. 2008a). Furthermore, older and better-condition females are more selective in their partner choice (Öst et al. 2003b, 2007), being found in groups with fewer brood-tending females (Öst et al. 2003a; Jaatinen & Öst 2011). Available evidence in this species also suggests selective disappearance of poor-condition individuals (Öst & Steele 2010; J. Ekroos, M. Öst, P. Karell, K. Jaatinen & M. Kilpi, submitted), and positive correlations between fecundity and survival (Yoccoz et al. 2002), and between hatching success and female age (Öst & Steele 2010) and body condition (Lehikoinen et al. 2010).

Our previous study suggested the absence of kin association of eider females during brood care (Öst et al. 2005). However, this study has later been criticized for drawing conclusions based on a limited sample size and a small number of microsatellite loci, which may have compromised the detection of relatedness among females (Csilléry et al. 2006). Following the call of Csilléry et al. (2006), we now revisit the question whether brood-rearing eider females preferentially associate with kin based on an extensive 6-year data set with individuals genotyped at 19 polymorphic
microsatellite loci and test the prediction that relatedness decreases with increasing female group size (Reeve & Emlen 2000). We then explore the possibility that demographic effects and partner choice, in concert, could produce a negative relationship between relatedness and group size, without active kin association. To this end, we tested for connections between female quality attributes and the relative frequencies of relatives in the population. Finally, to assess the role of active kin association and its temporal dynamics, we examined whether the level of relatedness exceeded that expected under random association of prospective coalition partners in the 6 years under study.

Methods

Field methods

This study was conducted at Tvärminne (59°50’ N, 23°15’ E), western Gulf of Finland, in 2005–2010. Female eiders were captured during nesting by using hand nets. Upon capture, females were weighed, measured for structural size (length of the radius-ulna), and ringed with a standard metal ring. We calculated the number of years since the bird was first ringed and used this as a minimum estimate of years of maternal experience (Öst et al. 2008a; Öst & Steele 2010). This is a reasonably accurate indicator of age because more than half of the successfully breeding females on our study islands are trapped annually (Jaatinen & Öst 2011), and annual trapping effort has been similar since 1996. Females were also equipped with a unique combination of one to three permanent colour rings (2003–), as well as with a wing flag (1996–) to ease recognition during brood care. Wing flags are shed each year during molting, whereas colour rings allow identification of females over years. Shortly after hatching their ducklings, females escort their broods to the water (Öst & Bäck 2003). In this population, females either tend their ducklings alone or form brood-rearing coalitions with typically one to four other females. We recorded coalition sizes by observing the brood care behaviour of colour-ringed individuals throughout the brood-rearing period (c. 40 days). Eider coalitions vary slightly in size over the season because of females that are transient in broods, mainly in the social interaction period spanning the first 2 weeks after hatch (Öst et al. 2003a). In the first few days after ducklings have hatched, broods using overlapping feeding areas may also temporarily merge. However, the females truly participating in the coalition can, based on our detailed observations typically lasting up to several hours per brood, be identified based on their brood care behaviour and social interactions (Öst et al. 2003b).

In this study, coalitions consisting of at least two individually known females and their ducklings were classified as enduring, transient or as brief associations. Females in enduring coalitions consistently associated over a period of at least 2 weeks after the estimated hatching date of their clutch (Öst et al. 2003a). Transient coalitions were observed together at least twice and subsequently broke up within 2 weeks after hatching of the young. Females from transient coalitions sometimes went on to join other groups, continued to care for their brood alone, or terminated brood care for the season, while leaving their ducklings behind in the broods of the other females (cf. Öst et al. 2003b). Brief associations represented groups which were observed only once during the brood-rearing season before breaking up or were never re-sighted again. We used the modal number of females present in coalitions over the entire brood-rearing season as the size of individual groups (Jaatinen et al. 2011).

Eider body condition exhibits considerable inter- and intra-annual variation. As a global condition index, we used the standardized residuals of a regression of log-transformed projected weight at hatching (response variable) on log-transformed radius-ulna length; indices were derived for the pooled data from all study years. A female’s weight at hatching was estimated by subtracting an estimate of the weight she would be expected to lose during the remaining incubation time from her measured incubation weight. Each female was weighed once, but because females do not feed during incubation and we captured females at different times in their incubation, we can estimate average weight loss rate during incubation as the slope of the regression of log(body weight; response variable) on log(incubation time) and projected hatching date (Öst et al. 2008b). The validity of using this index for estimating body condition has been examined elsewhere (Öst & Steele 2010).

Laboratory methods

Genomic DNA was extracted from 1 to 2 μL of blood or from the base of a feather. DNA was extracted by using 96-well glass fibre filtration plates (P2 [no. 5053], PALL; Ivanova et al. 2006). Extracted DNA was diluted 20× for further use in genotyping procedures. In total, 72 microsatellite loci known to be polymorphic in waterfowl were screened for cross-species amplification. 19 loci were found to be polymorphic in our study population (Table 1). Polymerase chain reaction (PCR) was carried out in volumes of 10 μL, containing 1 μL template DNA, 5 μL 2× Multiplex mastermix (HotStart Taq DNA polymerase, MgCl₂, dNTPs and buffer; Qiagen), 1 μL of Q solution (Qiagen), 2 μL MQ H₂O and 1 μL primer.
mix (2 μm of 5’ and 3’ primers each). Forward primers carried fluorescent labels (HEX, TET or FAM, DNA Technology A⁄S). Multiplex PCRs were performed by organizing microsatellite markers into 2–6 marker panels. We used MBS 0.2G ThermoHybaid (Pegasus Scientific Inc.) and BIO-RAD S1000 thermal cyclers with an initial denaturation step at 95 °C for 15 min, followed by 34 cycles at 95 °C for 30 s, the locus-specific annealing temperature (50–58 °C, see Table 1) for 90 s, elongation at 72 °C for 1 min and a final elongation step at 60 °C for 5 min. Amplification products were verified by 2% agarose gel electrophoresis. For determination of amplicon size, we used the MegaBACE1000 sequencer with MegaBACE ET400-R size standard (GE HealthCare Life Sciences), and the resulting peaks were analysed using the Fragment Profiler 2.2 software (GE HealthCare Life Sciences). Microsatellite allele scoring was performed by one person (K.N.) to avoid potential observer bias. Unclear genotypes were rerun on multiplexed marker panels to check for mismatches in loci other than the target locus.

Errors, which routinely occur during genotyping, can seriously bias further analyses and subsequent conclusions (Bonin et al. 2004; Hoffman & Amos 2005). For quality control purposes, we re-extracted and re-genotyped 14–15% (mean = 14.62%, ±0.24 SE) of randomly chosen samples for each microsatellite locus. For re-extraction, we used the Chelex-method introduced by Walsh et al. (1991). Samples were incubated at 56 °C overnight in 5% Chelex 100 (BIORAD) containing proteinase K (Thermo Fisher Scientific). Allelic diversity was very high, ranging from 2 to 35 (Table 1) with a mean of 8.95 (±1.84 SE). Our error rate was 1% (mean = 0.90%, ±0.22 SE), a remarkably low value in comparison with those obtained in previous studies (Hoffman & Amos 2005; McKinnon et al. 2006).

### Population genetic structuring and relatedness

The 529 unique female genotypes were checked for typographical errors using the Microsatellite Toolkit software (Park 2001) and standardized using automated binning in the FLEXIBIN software (Amos et al. 2007). All loci were tested for deviations from Hardy–Weinberg equilibrium using the software Cervus 3.0 (Kalinowski et al. 2007) and verified using GenePop 4.1 (Rousset 2008). No significant deviations from Hardy–Weinberg equilibrium were found.

Females show strong breeding philopatry and return to breed in close proximity to their previous breeding site (Öst et al. 2011). We therefore caught a considerable proportion of the females repeatedly during the study. Table 2 shows the total numbers of genotyped females in the years 2005–2010 as well as the number of females that were observed in brood-rearing coalitions. The group-wise relatedness coefficient r between coalition members was estimated using Kinship 1.2 (Queller & Goodnight 1989). This coefficient measures the genetic

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**Table 1** Microsatellite loci utilized for this study: annealing temperature ($T_a$), allele size range, number of alleles per locus ($N_A$), expected heterozygosity ($H_E$) and the source of primer sequences

<table>
<thead>
<tr>
<th>Locus</th>
<th>$T_a$</th>
<th>Allele size range*</th>
<th>$N_A$</th>
<th>$H_E$</th>
<th>Primer sequence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aalnl</td>
<td>50</td>
<td>72–91</td>
<td>8</td>
<td>0.565</td>
<td>Fields &amp; Scribner (1997)</td>
</tr>
<tr>
<td>APH2</td>
<td>50</td>
<td>88–110</td>
<td>5</td>
<td>0.091</td>
<td>Maak et al. (2003)</td>
</tr>
<tr>
<td>APH8</td>
<td>56</td>
<td>119–121</td>
<td>2</td>
<td>0.172</td>
<td>Maak et al. (2003)</td>
</tr>
<tr>
<td>APH9</td>
<td>50</td>
<td>90–106</td>
<td>9</td>
<td>0.670</td>
<td>Maak et al. (2003)</td>
</tr>
<tr>
<td>APH11</td>
<td>54</td>
<td>159–192</td>
<td>7</td>
<td>0.510</td>
<td>Maak et al. (2003)</td>
</tr>
<tr>
<td>APH20</td>
<td>58</td>
<td>142–148</td>
<td>5</td>
<td>0.412</td>
<td>Maak et al. (2003)</td>
</tr>
<tr>
<td>APH23</td>
<td>58</td>
<td>182–197</td>
<td>6</td>
<td>0.481</td>
<td>Maak et al. (2003)</td>
</tr>
<tr>
<td>Apl36</td>
<td>54</td>
<td>101–125</td>
<td>6</td>
<td>0.663</td>
<td>Denk et al. (2004)</td>
</tr>
<tr>
<td>Sfiu3</td>
<td>58</td>
<td>123–129</td>
<td>3</td>
<td>0.217</td>
<td>Fields &amp; Scribner (1997)</td>
</tr>
<tr>
<td>Sfiu4</td>
<td>58</td>
<td>161–189</td>
<td>12</td>
<td>0.640</td>
<td>Fields &amp; Scribner (1997)</td>
</tr>
<tr>
<td>Sfiu9</td>
<td>58</td>
<td>129–153</td>
<td>8</td>
<td>0.687</td>
<td>Öst et al. (2005)</td>
</tr>
<tr>
<td>Sfiu10</td>
<td>58</td>
<td>179–234</td>
<td>25</td>
<td>0.778</td>
<td>Öst et al. (2005)</td>
</tr>
<tr>
<td>Sfiu11</td>
<td>58</td>
<td>204–216</td>
<td>4</td>
<td>0.287</td>
<td>Öst et al. (2005)</td>
</tr>
<tr>
<td>Smo4</td>
<td>50</td>
<td>133–222</td>
<td>35</td>
<td>0.928</td>
<td>Paulus &amp; Tiedemann (2003)</td>
</tr>
<tr>
<td>Smo6</td>
<td>50</td>
<td>106–129</td>
<td>10</td>
<td>0.649</td>
<td>Paulus &amp; Tiedemann (2003)</td>
</tr>
<tr>
<td>Smo7</td>
<td>56</td>
<td>176–186</td>
<td>4</td>
<td>0.492</td>
<td>Paulus &amp; Tiedemann (2003)</td>
</tr>
<tr>
<td>Smo8</td>
<td>58</td>
<td>78–102</td>
<td>5</td>
<td>0.346</td>
<td>Paulus &amp; Tiedemann (2003)</td>
</tr>
<tr>
<td>Smo9</td>
<td>58</td>
<td>157–175</td>
<td>6</td>
<td>0.434</td>
<td>Paulus &amp; Tiedemann (2003)</td>
</tr>
<tr>
<td>Smo12</td>
<td>58</td>
<td>80–102</td>
<td>10</td>
<td>0.322</td>
<td>Paulus &amp; Tiedemann (2003)</td>
</tr>
</tbody>
</table>

*Base pairs.
similarity of individuals taking into account the mean similarity in the population. Here, the background allele frequencies were calculated based on all sampled females nesting in a particular year. The pairwise relatedness values between females in coalitions ranged from −0.71 to 0.58 with a mean of 0.026 (±0.023 SE). We used median relatedness as a proxy for in-tracollision relatedness. This measure was chosen because individual pairwise relatedness coefficients within coalitions are not statistically independent from each other. Medians, rather than means, were used to guard against possible skewness in the relatedness estimates. Furthermore, the likelihood of encountering extreme pairwise relatedness values may be expected to increase with female coalition size by chance alone, and medians are much less sensitive to such outliers than means. Mean median intra-group relatedness values observed in different years are reported in Table 2.

The individual frequency of relatives in the population was calculated as the sum of the estimated number of parent offspring, full-sib and half-sib relationships. These relationships were estimated using the maximum likelihood approach implemented in the software ML-Relate (Kalinowski et al. 2006). The annual individual frequencies of relatives were divided by the number of sampled females in each year to standardize the proportion and enable comparison over years.

Statistical methods
To assess the effect of group size on median relatedness in brood-rearing coalitions, we constructed a generalized linear model (GLM), where group size explained median relatedness between coalition partners. The type of group (enduring coalition, transient coalition and brief association) was included to correct for potential bias in relatedness arising from different effects of group size on relatedness in different types of associations between eider females. Because the type of group was entered in the model as a factor, we conducted a post hoc test (Tukey’s all-pair comparisons) between the different types of groups (Hothorn et al. 2008), using the ‘glht’ function in the ‘multcomp’ package in the software R 2.8.1 (R Development Core Team 2008). Also year was added to the model to control for potential differences in median in-tracollision relatedness between years and to correct for potential bias arising from variables not measured.

To assess how an individual’s quality affected the annual frequency of relatives in the population, we constructed a linear mixed effects model (LMM), which was fitted using restricted maximum likelihood (REML) estimation. In this model, the individual frequency of relatives in the population was explained by female minimum breeding experience and body condition at hatching of her brood. Female identity was used as a random factor to correct for the fact that the same females appeared in the data in several years. The residuals of both the GLM and the LMM models adhered to the assumption of normality.

We conducted a randomization test to examine whether the level of relatedness among females in brood-rearing coalitions differed from the random expectation and fluctuated over years. For this purpose, we calculated the pairwise relatedness coefficients for all females observed in brood-rearing coalitions (column ‘GT ♀ in coal.’ in Table 2), and this was performed separately for each year. For example, there were 39 genotyped females in coalitions in 2005, and we therefore calculated all pairwise relatedness values for these females (39 × 38/2 = 741 values). The analysis was then run in a two-step process, where first, a number of relatedness values, equal to the number of coalitions containing at least two genotyped females in the same coalition in each respective year (column ‘Coal. with r’ in Table 2), were picked at random (without replacement) from the annual distributions of relatedness values (‘GT ♀ in coal.’ in Table 2). Second, the mean

Table 2. Annual sample sizes for all types of coalitions (enduring, transient coalitions and brief associations) where Ni is the total number of genotyped females nesting in a focal year; ♀ in coal, the number of females that engaged in coalitions, whether genotyped or not; Coal., the number of coalitions observed in the focal year (the values are elevated by brief associations breaking up and becoming e.g. enduring coalitions); GT ♀ in coal., the number of genotyped females in coalitions; Coal. with r, the number of coalitions containing at least two genotyped females, allowing for relatedness values to be calculated; Mean median r, the mean median in-tracollision relatedness for the focal year (calculated based on Coal. with r; ±SE)

<table>
<thead>
<tr>
<th>Year</th>
<th>Ni</th>
<th>♀ in coal.</th>
<th>Coal.</th>
<th>GT ♀ in coal.</th>
<th>Coal. with r</th>
<th>Mean median r</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>124</td>
<td>60</td>
<td>37</td>
<td>39</td>
<td>11</td>
<td>−0.09 ± 0.08</td>
</tr>
<tr>
<td>2006</td>
<td>125</td>
<td>62</td>
<td>37</td>
<td>36</td>
<td>13</td>
<td>0.04 ± 0.03</td>
</tr>
<tr>
<td>2007</td>
<td>163</td>
<td>88</td>
<td>49</td>
<td>64</td>
<td>24</td>
<td>0.04 ± 0.04</td>
</tr>
<tr>
<td>2008</td>
<td>169</td>
<td>79</td>
<td>46</td>
<td>51</td>
<td>25</td>
<td>0.008 ± 0.06</td>
</tr>
<tr>
<td>2009</td>
<td>194</td>
<td>62</td>
<td>31</td>
<td>44</td>
<td>29</td>
<td>0.007 ± 0.05</td>
</tr>
<tr>
<td>2010</td>
<td>174</td>
<td>32</td>
<td>19</td>
<td>28</td>
<td>13</td>
<td>0.16 ± 0.08</td>
</tr>
</tbody>
</table>
relatedness based on these randomly drawn values was calculated. These values correspond to the mean median relatedness of two-female coalitions in the field and the mean (±SD) number of genotyped females in coalitions for which mean median relatedness values were obtained was 2.32 (±0.62) females. These two steps were then iterated 100 000 times for each year to generate the annual expected relatedness values. The number of times that the simulated relatedness was greater than the observed mean median relatedness for each year was recorded and used to calculate a P-value, defined as the proportion of the total number of iterations (Fisher 1935).

Results

Median relatedness decreased with increasing female group size in brood-rearing coalitions (GLM: \( b = -0.04, F_{1,113} = 6.72, P = 0.01 \); Fig. 1). There were also differences in median relatedness between strategies (GLM: \( F_{2,111} = 4.05, P = 0.02 \)). Tukey’s all-pair comparisons revealed that enduring coalitions did not differ from transient coalitions (\( b = 0.03, z = 0.52, P = 0.86 \)), but that brief associations exhibited lower relatedness than both transient (\( b = -0.25, z = -2.78, P < 0.02 \)) and enduring coalitions (\( b = -0.22, z = -2.73, P < 0.02 \)). We detected no significant year effects in intracoalition relatedness (\( b = 0.02, F_{1,110} = 2.52, P = 0.12 \)).

The annual frequency of relatives in the population was unaffected by female body condition (LMM: \( b = 0.0001, t = 0.12, \text{d.f.} = 369, P = 0.90 \)) and the term was thereafter removed from further modelling. In contrast, female minimum breeding experience affected the frequency of relatives: the proportion of relatives in the population increased significantly with increasing experience (LMM: \( b = 0.0011, t = 2.30, \text{d.f.} = 370, P = 0.02 \); Fig. 2).

The observed mean median relatedness values between coalition-forming females showed marked annual fluctuations (Table 2). Our randomization test verified that in 1 of 6 years (2010), these values differed significantly from those expected under random assortment of females, while a marginally significant trend was detected in another year (2007; Fig. 3).

Discussion

The most salient finding of this study was that median intra-group relatedness was elevated in small eider brood-rearing coalitions and decreasing with increasing female group size. Such an effect was not detected in our earlier study from the same population (Öst et al. 2005), perhaps in part because this earlier study did not specifically separate co-tending genotyped females according to female group size. However, the apparent discrepancy between these studies may also reflect the fact that only a relatively large number of microsatellite
loci and a reasonably large sample size may facilitate the detection of the typically rather weak relatedness patterns observed in the wild, a fact duly pointed out by Csilléry et al. (2006). Our results also showed that female quality, as measured by our proxy for age, but not by body condition, was positively correlated with the availability of related coalition partners, an important finding when taken in context with age-dependent partner choice preferences (see below). We also found that the level of relatedness between coalition-forming females in some years exceeded that expected by chance alone. This finding is robust and not dependent on, for example, female age-specific hatching success (cf. Öst & Steele 2010), because our randomization procedure was based on sampling only the females successfully hatching a brood and subsequently entering brood-rearing coalitions. Our study also revealed considerable annual fluctuations in the level of relatedness between coalition-forming females. This result adds to the recently emerging evidence that fine-scale genetic structure may be temporally labile (e.g. Busch et al. 2009), for reasons that are still inadequately understood.

Our finding of elevated intra-group relatedness in small brood-rearing coalitions may be viewed as a confirmation of reproductive skew theory, where relatedness is expected to decline with group size because of diminishing reproductive returns with increasing group size, rendering the acceptance of additional related group members increasingly less attractive as groups increase in size (Reeve & Emlen 2000). This theory implicitly assumes the presence of kin recognition, but there are at least two lines of evidence arguing against a prominent role of selective kin association in explaining the genetic structure observed in eider brood-rearing coalitions. First, the mean median relatedness between cooperating females is at its highest in two-female coalitions, yet only reaching a level of 0.065, and declining in larger coalitions (Fig. 1). If relatives indeed do associate actively, then the mechanism either does not seem very accurate or the benefits of active kin association do not outweigh the costs of finding closely related individuals. For example, there are obvious costs associated with prolonged searching for suitable coalition partners, as predation on eider duckling peaks in the first few days after hatching (Öst et al. 2008a) and prospective coalition partners need to hatch their broods within approximately the same time window of about 1 week in order for successful cooperation to

![diagram](image-url)
emerge (Öst et al. 2003b). Second, in the light of the substantial direct fitness benefits accruing to coalition-forming females, such as dilution of predation risk on offspring (Monro & Bédard 1977; Öst et al. 2008a), predator detection (Öst & Tierala 2011) and shared parental care duties (Öst et al. 2002), the inclusive fitness benefits arising from cooperating with such distant relatives seem diminutive (Sharp et al. 2005; Nam et al. 2010).

Our results indicated that in most years (at least 4 of 6), the observed patterns of relatedness in brood-rearing coalitions could be explained by a simple null hypothesis of random association of females, and we also identified a possible passive pathway explaining the elevated relatedness in the smallest coalitions. Thus, we found that the availability of consanguineous cooperation partners increased with female age. While this effect was relatively weak, it may signify a more general phenomenon not solely restricted to eiders. The survival and fecundity of high-quality individuals are often positively correlated (e.g. Hamel et al. 2009), and this probably also applies to eiders (Yoccoz et al. 2002). Thereby, eider females that are successful at reproduction and that live long enough for their offspring to accumulate in the population will experience a rise in the proportion of close relatives in the population. This effect may be further enhanced by the tendency of offspring of high-quality individuals to likewise show greater fecundity (e.g. Messina 1993). While we did not find any direct relationship between female body condition and the proportion of relatives in the population, female body condition may still be a factor contributing to a selective disappearance of poor-quality breeders. Thus, available evidence suggests that female body condition at the first verified breeding attempt (i.e., after controlling for female breeding experience) is positively correlated with subsequent survival (J. Ekroos, M. Öst, P. Karell, K. Jaatinen & M. Kilpi, submitted). Considering that older females prefer small brood-rearing coalitions (Jaatinen & Öst 2011) and that they have a greater availability of potential kin cooperation partners in the population, it is plausible that the increased relatedness in small coalitions may arise as the product of age-dependent partner choice preferences and demographic patterns. This conclusion underlines the often overlooked fact that mortality and fecundity may shape population relatedness structure (Beckerman et al. 2011), although we do not rule out the possibility of active kin discrimination processes taking place.

In contrast to our findings, Beckerman et al. (2011) showed that the proportion of relatives decreased with adult longevity. The reason for this discrepancy stems from two features of the model employed by Beckerman et al. (2011). First, the negative effect of longevity on the proportion of relatives may be due to immigrants being over-represented among the longest living individuals, and these immigrants are by definition non-relatives to most other individuals in the ‘kin neighbourhood’ (sensu Beckerman et al. 2011). Second, Beckerman et al. (2011) note that the negative effect of longevity on the proportion of close kin is weak in comparison with the negative effect of immigration. This contrasts with the life history of eider ducks, where females exhibit strong breeding philopatry (Öst et al. 2011) and are also reasonably philopatric to their natal sites (Swennen 1990; Goudie et al. 2000). Perhaps even more pertinent is the fact that breeding dispersal decreases with advancing age in female eiders (Öst et al. 2011), and so younger breeders may more often be immigrants, contrasting with the situation described by Beckerman et al. (2011). To conclude, these life history characteristics probably reduce the role of immigration in affecting changes in local relatedness with female age, allowing the gradual build-up of local relatedness over the reproductive lifespan of a female.

When scrutinizing the previous studies on eider social genetics, it becomes apparent that no conclusive evidence exists at present for kin-selected social organization. The level of relatedness between eider females in arriving and departing groups and in neighbouring nests in a colony in the Canadian Arctic (0.069, 0.055 and 0.055, respectively; McKinnon et al. 2006), as well as between neighbouring breeding females in Finland (0.09: Waldeck et al. 2008), is similar to that found between females in two-female coalitions in our study \(r = 0.065\). Interestingly, McKinnon et al. (2006) discuss the potential for such relatedness to arise through natal philopatry, but nonetheless argue that the operation of kin recognition and kin selection is a more plausible hypothesis to explain the social structuring observed. While this may admittedly be true, Waldeck et al. (2008) infer, based on the slightly higher level of relatedness observed by them, that such relatedness patterns between close neighbours are expected under strong natal philopatry. In the light of the fact that close neighbours are related in both previous studies and that our results indicate that similar levels of relatedness may arise in brood-rearing groups as a consequence of partner choice and demography, the possibility that passive mechanisms may play a substantial role in explaining the social structure in this species cannot be discarded.

However, our study also provides support for active kin association, as previously suggested by McKinnon et al. (2006) and Sonsthagen et al. (2010). In 1 of 6 years (2010), females formed coalitions with more closely related partners than expected by chance \(r = 0.16; \) Fig. 3) and tended to do so also in another year (2007; \(r = 0.04; \) Fig. 3). Because the expected values shown in Fig. 3 were drawn at random from the pool of females

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that did form coalitions, and not from the population at large (e.g. McKinnon et al. 2006), this result strongly suggests that kin may actively associate in some years. The question immediately arises as to which conditions favoured kin cooperation in those years? While we cannot provide a definitive answer to this question, it is noteworthy, and perhaps not coincidental, that the ranking of predation rates on incubating adult females in 2005–2010 appears to mirror the degree of kin association in eider brood-rearing coalitions. The sum total of females found killed at their nests divided by the total number of censused nests can be used as an annual index of predation pressure on females (e.g. Jaatinen et al. 2011). To reduce the age heterogeneity in our sample, we here only calculated the predation index for unringed killed females (cf. J. Ekroos, M. Öst, P. Karell, K. Jaatinen & M. Kilpi, submitted). This comparison revealed that predation pressure was by far the highest in the year 2010 (0.15), followed by the year 2007 (0.051), and the remaining 4 years had indices ranging from 0.036 to 0.049. Following this argument further, we may speculate that teaming up with related individuals may only pay for females when ecological constraints such as predation risk are severe enough. However, correlation by no means implies causality, and so the conditions favouring preferential kin interactions still await discovery.

Taken together, our study identified several mechanisms governing kin association and cooperation in breeding eiders. In most years, the elevated relatedness in small brood-rearing coalitions may arise as a byproduct of demography and partner choice, driven by the preference for small coalitions by older high-quality females, having more relatives in the population. However, our observation that females in some years associated with kin more than expected by random suggests that there may be additional factors, beside demography and age-related group-size preferences, steering kin association in brood-tending eiders. Our data therefore suggest that eiders are indeed capable of discriminating between kin, but that the benefits of doing so may vary over time, for reasons that are still unknown. We encourage studies assessing the generality of biotic processes such as predation and disease in determining population relatedness structure, and research efforts aimed at pinpointing the specific conditions needed for kin cooperation to be favoured in species gaining substantial direct benefits of cooperation.

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**Data accessibility**

Data files deposited at DRYAD: doi:10.5061/dryad.11312674