The spatial structure of relatedness among individuals in a population can have important consequences for competition, reproductive tactics, sociality, inbreeding, dispersal, and other aspects of population biology. Here we analyze a female alternative reproductive tactic, conspecific brood parasitism, in relation to spatial relatedness among females in a Baltic Sea population of the common eider Somateria mollissima. The role of relatedness in brood parasitism is a candidate mechanism for further study. Key words: joint nesting, kinship, local genetic structure, protein fingerprinting, spatial trend analysis. [Behav Ecol 19:67–73 (2008)]

The spatial structure of relatedness between individuals in a population can be crucial for social selection and evolution. Here we analyze a female alternative reproductive tactic, conspecific brood parasitism, in relation to spatial relatedness among females in a Baltic Sea population of the common eider Somateria mollissima. The role of relatedness in brood parasitism is debated: some models predict parasite avoidance of related hosts, others predict host–parasite relatedness. We estimate pairwise relatedness from protein fingerprinting of egg albumen in 156 nests, with pairwise nest distances ranging from 1 m to 6 km. Relatedness increases significantly from the longest distances to an average of $r \approx 0.09$ below 20 m. Brood parasitism is common, and average pairwise relatedness between host and parasite is estimated at 0.18–0.21. Parasites thus do not avoid relatives, and combined with the findings of a similar study in another eider population, the results show that mean host–parasite relatedness is higher than that among close neighbors. High host–parasite relatedness is therefore not an effect of natal philopatry alone; some other form of kin bias is also involved. Recognition and association between birth nest mates is a candidate mechanism for further study.

Spatial trends in relatedness for these and other reasons are increasingly being explored in animals and plants (e.g., Lynch and Riland 1999; Hardy and Vekemans 2002; Ratnayeke et al. 2005). Here we analyze a female alternative reproductive tactic, conspecific brood parasitism (CBP), in relation to spatial relatedness.

Most mammals have male-biased dispersal and female natal philopatry (Greenwood 1980), and their social groups tend to be matrilines, with high levels of female relatedness (Colman et al. 2003 and references therein). Most birds on the other hand are male philopatric, and in some species, there is strong kin structuring of male groups or neighborhoods, for instance, in red grouse (Lagopus lagopus scoticus) (Hołguland et al. 1999; Petrie et al. 2002; Colman et al. 2003; Fowler et al. 2004; Double et al. 2005). Here we analyze a female alternative reproductive tactic, conspecific brood parasitism (CBP), in relation to spatial relatedness.

In contrast to other birds, waterfowl (Anatidae) have female-biased natal philopatry, and the male usually follows his mate to her birth area for breeding (reviewed by Anderson et al. 1992). This leads to male-biased gene flow and a matriarchal population structure (Chesser 1991; Avise et al. 1992; Tiedemann et al. 1999; Rumsila et al. 2000; Scrihner et al. 2001). Most previous research on spatial population genetic structure in waterfowl concerns large-scale patterns (e.g., Avise et al. 1992; Tiedemann and Noer 1998; Pearce et al. 2004). Here we explore the fine-scale pattern of female relatedness, which is of interest owing to its potential effects on sociality among female neighbors (see also McNinnon et al. 2006). Proximity to kin can lead to inclusive fitness benefits (e.g., Hamilton 1964; Frank 1998; Rousett 2004; but see e.g., West et al. 2002), for instance, through helping (Brown 1987; Emlen 1994; Lessells et al. 1994) or decreased aggression between relatives (Greenwood et al. 1979; Brown and Brown 1993). Philopatry and familiarity with the breeding area can also enhance fitness traits such as competitive ability (Anderson et al. 1992) and brood-rearing success (Lessells 1985).

CBP, where more than one female contributes eggs to a clutch that is cared for by a single female, the “host,” is common in many animals with parental care of the eggs (e.g., reviewed by Field 1992; Wisenden 1999; Yom-Tov 2001; Vehrencamp and Quinn 2004; Tallamy 2005). Among birds, CBP is especially common in waterfowl (e.g., Sayler 1992; Yom-Tov 2001), for reasons that are debated. Much of the debate concerns the role of relatedness. One hypothesis suggests that inclusive fitness benefits favor host–parasite relatedness (Anderson 1984, 2001; López-Sepulcre and Kokko 2002) and another hypothesis suggests that parasites avoid parasitizing close relatives (Zink 2000; Semel and Sherman 2001; Pöysä 2004). We test these 2 alternative hypotheses in common eiders, a female-philopatric sea duck with frequent brood parasitism (e.g., Robertson et al. 1992; Björn and Erikstad 1994; Robertson 1998; Waldeck et al. 2004; Waldeck and Andersson 2006, Andersson and Waldeck 2007).

Eiders often nest in colonies, and females show strong breeding philopatry as well as natal philopatry, in many cases returning to their birth area for nesting (e.g., Franzmann 1983; Coulson 1984; Baillie and Milne 1989; Swennen 1990).
Genetic differentiation between eider populations is probably caused by the high female natal philopatry (Tiedemann and Noer 1998; Scribner et al. 2001), but fine-scale genetic consequences have rarely been studied (but see Öst et al. 2005; McKinnon et al. 2006).

Natal philopatry is expected to generate spatial genetic structuring in the adult female population, leading to declining pairwise relatedness with increasing distance between the individuals compared. This aspect is tested here among female eiders nesting on islands in the Tvarminne archipelago, SW Finland (Figure 1). We use protein fingerprinting of egg albumen to estimate female relatedness in relation to nest distance and brood parasitism. Like DNA multilocus fingerprint bands (Reeve et al. 1992), albumen bands reflect the degree of genetic similarity between females (Andersson and Ahlund 2000). Protein fingerprinting allows the advantage of sampling directly after laying, thus producing larger sample sizes than DNA methods if there is high nest predation (as is the case in eiders, e.g., Andersson and Waldeck 2006), or differences in hatching success between host and parasite eggs (e.g., Roy Nielsen et al. 2006). Furthermore, egg albumen is of strictly maternal origin, which simplifies relatedness analyses. Pairwise genetic relatedness can be estimated through protein fingerprinting and band sharing analysis (Andersson and Ahlund 2000, 2001). By exploring patterns of relatedness among conspecific brood parasites and their hosts, while controlling for spatial trends in relatedness arising from natal philopatry, we can test the 2 alternative hypotheses (above) on the role of relatedness in CBP.

MATERIALS AND METHODS

Study area and population

About 1000 pairs of eiders breed in the archipelago near Tvarminne Zoological Station in the Baltic Sea, SW Finland (60°N, 23°E). Eiders nest on most of the many islands in the archipelago (Figure 1), making the population relatively continuous in distribution, although limited to islands for nesting. No nests are known from the nearby mainland, probably because of higher risk of predation by mammals there. The nesting islands range from rocky open islets to larger (often >100 m across) wooded islands (Kilpi and Lindström 1997; Öst and Kilpi 2000). In 2001 and 2002, we studied 8 locations in total, 3 wooded and 5 groups of smaller islands within 5 km of the station and 1–2 km apart (Figure 1). An island was sampled in only one of the 2 years, with exception of one large island that was sampled both years but at opposite sides, largely without overlap. The risk that a female is included both years is therefore low. With one exception (probably relaying by a female after her first clutch was lost, see Waldeck et al. 2004), we found no case were 2 nests had the same albumen band pattern, verifying that we did not sample the same female twice. Band pattern has proved to be fully repeatable between years for another sea duck where this has been tested (Andersson and Ahlund 2001). This is also supported by our ongoing work on eiders.

The sites were visited at 2- to 5-day-intervals throughout the laying season, and about 50% of all new nests were randomly selected and sampled at each visit. All eggs in selected nests were sampled. After hatching, the positions of all nests were estimated. Within each island, the position relative to a suitable reference point was estimated for each nest. Distance from the reference point was paced out, and the direction was estimated using a compass (on the larger islands, several reference points where used). These data were transferred to a GPS software (OziExplorer GPS Mapping Software) containing a map of all sampled islands, with reference points. The position of each nest was transferred to the software using these reference points, and the internest distance was calculated for each pair of nests. This study includes 156 nests for which we have the GPS position.

Albumen sampling and isoelectric focusing electrophoresis

Albumen was sampled from all eggs in a nest by drilling a 1-mm hole in the shell and extracting about 0.3 ml of albumen with a syringe and sealing the hole with cyanoacyrlid glue. Sampled eggs hatched as normal (see Andersson and Ahlund 2001; Waldeck et al. 2004). Samples were stored at −20 °C until electrophoresis, when they were analyzed with isoelectric focusing (IEF) in precast gels. With this technique, proteins that differ in charge are separated in an electric field applied over the fixed pH gradient of the gel. A protein comes to rest as a narrow band at the gel site corresponding to its fixed isoelectric point (Rhitgetti 1990). IEF with immobilized pH gradients therefore provides high resolution of protein bands, and the results are reproducible and comparable between gels (Andersson and Ahlund 2001). Egg albumen is of strictly maternal origin, secreted by specific cells in the oviduct, and it contains many genetically polymorphic proteins (e.g., Burley and Vadhera 1989; Palmer and Guilette 1991). Individual albumen band patterns obtained by IEF electrophoresis are highly repeatable and represent part of the genotype expressed as proteins in the female. Protein fingerprinting does not have enough resolution for reliably estimating genealogical relationship between specific individuals, but it is suitable for comparisons between categories of individuals (Andersson and Ahlund 2001) and for estimating relatedness trends.

To resolve a sufficient number of protein variants, we ran the samples on 5 gel types: Immobiline DryPlates pH 4–7 code no. 80-1128-28, pH 4.2–5.4 code no. 80-1128-29, pH 4.5–5.4 code no. 80-1128-30 (run with 2 recipes), and pH 5–6 code no. 80-1128-32 (Amersham Biosciences, Upsalsa, Sweden). Electrophoresis was done with Amersham Pharmacia Biotech Multiphor II System and power supply EPS 3501. Five microlitres of each sample was applied with a pipette onto IEF sample application pieces placed along the cathode. Gels were run for 8–12 h. After electrophoresis, the gels were fixed in a solution of trichloracetic acid and 5-sulphosalicylic-di-hydrat acid, rinsed in destaining solution, and then stained with...
Estimation of relatedness

We analyzed the relationship between relatedness and geographical distance for all possible pairs that can be formed among the host females in 156 nests (156 \times 155/2 = 12,090 pairs). The distance between the 2 nests in a pair ranged from about 1 m to 6 km (2.7 ± 1.6 km, mean ± standard deviation [SD]).

To check the consistency of relatedness estimates (Hardy and Vekemans 2002), we used 2 different methods: (a) band sharing analysis (Andersson and A˚hlund 2000) and (b) calculation of relationship coefficients using the SPAGeDi software (Hardy and Vekemans 2002). The rationale for using these 2 methods is outlined below.

(a) Band sharing analysis of albumen bands based on IEF electrophoresis like DNA fingerprint analysis (e.g., Birkhead et al. 1990; Reeve et al. 1992; McRae and Burke 1996) can be used for estimating differences in mean relatedness between categories of individuals (Andersson and A˚hlund 2000). For each egg, presence/absence of each band is recorded in a matrix. Band sharing between 2 individuals x and y is calculated as $r = (w - b)/(1 - b)$

\[
Nxy / (N_x + N_y),
\]

where

\[
w = 2N_y / (N_x + N_y),
\]

and

\[
b = \bar{N}_x / (N_x + N_y),
\]

are the mean band sharing in the reference population, relative to which the estimate of relatedness is calculated (Reeve et al. 1992, see also Hardy 2003).

(b) We also estimated pairwise relatedness with program SPAGeDi version 1.2 (Hardy and Vekemans 2002), computing a relationship coefficient (corresponding to Hamilton’s r) for dominant markers (Hardy 2003). The level of inbreeding can influence this estimate; we assume no inbreeding, as a previous study of the same population found no significant inbreeding (Ost et al. 2005). The program option used here computes genetic relatedness between individuals in each possible pair and regresses relatedness on pairwise spatial distances. A multilocus estimate is computed by first averaging pairwise coefficients over loci, then averaging these multilocus pairwise coefficients over all pairs. The program can also in a similar way test between groups of pairs in specified distance intervals (Hardy and Vekemans 2002, see below).

Both methods are useful for testing whether the average relatedness in host–parasite pairs differs from that of a relevant reference population (see Reeve et al. 1992; Andersson and A˚hlund 2000; Hardy 2003). What is an appropriate reference depends on the question being asked. We ask 2 main questions: about host–parasite relatedness compared with that among close neighbors and about female relatedness in relation to spatial distance. For hosts and parasites, we aim to find out whether they tend to be less or more closely related than expected from natal philopatry alone. We therefore compare host–parasite relatedness with that among pairs of close neighbor females, nesting <20 km from each other. We estimate relatedness in both these categories (host–parasite pairs and pairs of close neighbors), relative to the same reference population: all 12,090 pairs that can be formed in the entire sample of 156 females (see above). Both measures are therefore estimated relative to the same reference population, making them comparable. As regards the other question, about spatial relatedness, it requires a large enough area to discover and estimate the slope of a relatedness trend, if there is one. In another eider population, we found no trend over a distance of 3 km (Andersson and Waldeck 2007). We therefore use the data from the entire study area (distances up to 6 km) to explore spatial relatedness.

Spatial analyses

To test for a spatial trend in relatedness with method (a) above, we use a simple robust approach based on the 156 nesting females as statistical sampling units. For each female, we calculate her band sharing similarity and distance relative to each of the other 155 females. We then use the results to calculate the Spearman rank correlation $r_s$ between her band sharings and distances. Under the null hypothesis of no spatial trend in relatedness, a positive value of $r_s$ is as likely as a negative one. A sign test then shows whether the observed $r_s$ values for all 156 females taken together reject the null hypothesis of no spatial relatedness trend in the population. With method (b) above, we test for a trend in relatedness with the permutation test (e.g., Mainly 1997) in the SPAGeDi software (equivalent to a Mantel test permuting locations; Hardy and Vekemans 2002).

Scoring of parasitism

We identify parasitism mainly by protein fingerprint differences between the eggs in a nest. All eggs were scored by 1 person, and cases of suspected parasitism were scored by 2 persons independently. In a method test with female golden-eye ducks of known identity, protein fingerprinting identified parasites with high accuracy, also in nests where only 1 band differed between the eggs of host and parasite (Andersson and A˚hlund 2001). In another eider population, occurrence of several new eggs in the nest on the same day confirmed the detection of parasitism by protein fingerprinting (Andersson and Waldeck 2007). To avoid false positives and keep our estimate of host–parasite relatedness conservative, we only scored an egg as foreign when it differed from other eggs in the nest in at least 3 bands. These bands sometimes included others than the set of 37 bands used in calculating relatedness (see below). Compared with our study of parasitism rate in the same population (Waldeck et al. 2004), this approach excludes 5 cases with a difference in 1 band and 3 cases with a difference in 2 bands. These excluded cases may be real host–parasite pairs with very similar band patterns, hence, likely to be relatives. For this reason, and because of inherent downward bias in estimates obtained by Equation 1 (see Reeve...
et al. 1992 and below), our results are likely to underestimate host–parasite relatedness.

Unless otherwise stated, numerical estimates below are means ± sample SDs.

RESULTS

Scoring of bands

Mean clutch size, parasitic eggs included, was 4.56 ± 1.23. Among the 156 nests, there were eggs from more than 1 female in 25 nests, of which contained eggs from 3 females. Among these 182 females, we scored in total 71 bands that were variable, that is, not present in all females. Twenty of these bands showed identical occurrence with one or more other bands on the same or other gel types. These 20 redundant bands were omitted from analysis. Among the 51 remaining bands, the number of bands per individual was on average 15.2 ± 3.32. The relative frequency of a specific band is the number of individuals that have the band, divided by the total number of individuals. The mean of this relative band frequency for the 51 bands was 0.30 ± 0.30. After deletion of bands with high population frequency (see Materials and Methods), 37 bands remained. Among these, the number of bands per individual was 5.26 ± 2.61, with mean band frequency 0.14 ± 0.17.

Distance trend in pairwise relatedness

Among the 156 rank correlation values of pairwise band sharing versus distance, 96 were negative and 60 positive (P < 0.01, 2-tailed sign test). The null hypothesis is therefore refuted: band sharing decreased with increasing distance between females.

There was also a significant negative relationship between spatial distance and relatedness as calculated by the SPAGeDi software: r = 0.039 − 1.5 × 10−5 × distance (n = 12 090, P < 0.001) (Figure 2; distance intervals were chosen so as to comply with the software recommendations on sample sizes and variances).

We also carried out the corresponding analysis using r values calculated from Equation 1 (method (a) above). Mean band sharing similarity among the 156 individuals, b in Equation 1, was 0.33 ± 0.24 (n = 12 090). Regression of r on pairwise nest distance gave r = 0.034 − 1.3 × 10−5 × distance, similar to the relationship estimated by the SPAGeDi software.

Host–parasite relatedness

We found no parasitic female that also had a nest of her own, but the proportion of sampled nests was low, and there may have been unnoticed cases.

Mean host–parasite relatedness was estimated at r = 0.18 ± 0.05 with the SPAGeDi software (mean ± jackknifed standard error [SE]; Figure 2). Compared with pairwise relatedness in the entire population, the difference was highly significant (P = 0.004, permutation test, 10 000 permutations, see e.g., Manly 1997). To test the null hypothesis (Introduction), however, we must compare host–parasite relatedness with that among close neighbor females, nesting <20 from each other (Figure 2). We can do so, estimating host–parasite relatedness with Equation 1. Mean host–parasite band sharing is w = 0.47 ± 0.28 (n = 26). With background band sharing b = 0.33, this gives host–parasite relatedness r = 0.21 ± 0.08 (mean ± SE).

We test host–parasite relatedness against the pairwise relatedness of other females breeding within 20 m of each other, estimated at 0.09 ± 0.03 (n = 166, mean ± SE). The difference is not statistically significant (P = 0.14, permutation test, 10 000 permutations, power = 0.17, calculated using normal approximation [Lenth 2006]). The pairwise estimates range from 1 to negative values, indicating that host and parasite in some cases are probably close relatives, in other cases unrelated. (Expected relatedness coefficients for mother–daughter and for siblings is 0.5, for half-sibs 0.25, and for first-order cousins 0.125.)

We used a conservative approach for identifying parasites (see Materials and Methods). If the 3 possible parasites are included that differ from the host in only 2 albumen bands, host–parasite relatedness is significantly higher (0.26 ± 0.43, n = 29) than that of the close neighbors (P = 0.012, permutation test, 10 000 permutations).

There is no indication that relatedness among neighbors increases sharply at very short distances. Among close neighbors (1–20 m), pairwise relatedness even tended to decrease slightly at the shortest distances (d), whether analyzed with linear regression (r = 0.052 ± 0.0040 d) or quadratic regression (r = 0.037 ± 0.023 d − 0.008 d²). The estimated host–parasite relatedness of r = 0.18–0.21 is therefore considerably higher than these regressions extrapolated down to distance 0 (0.052 and 0.037, respectively).

Host–parasite relatedness tended to be higher in nests where the foreign female had laid more than 1 egg (up to 3 eggs) (r = 0.34 ± 0.46, n = 8) than in nests with only 1 foreign egg (r = 0.15 ± 0.39, n = 18; P = 0.28, permutation test, 10 000 permutations, power = 0.15, calculated using normal approximation [Lenth 2006]).

DISCUSSION

We found that female relatedness decreased with increasing nest distance, as expected from strong natal philopatry. Host–parasite relatedness was higher than for close neighbors, but not significantly so. Several aspects, however, suggest that host–parasite relatedness cannot be explained by philopatry and spatial relatedness trends alone.

Spatial trends in relatedness

Breeding philopatry is often strong among eider females (e.g., Cooch 1965; Swennen 1990; Bustnes and Erikstad 1993), as in

Figure 2

Pairwise relatedness between nesting females in relation to the distance between their nests (see main text for explanation). h-p represents host–parasite pairs. The trend of increasing relatedness at shorter distances is statistically significant, also if host–parasite pairs are omitted. Host and parasite are significantly more closely related than other pairs in the population (see main text). Error bars are approximate SEs obtained by jackknifing over loci.
this population, where the nest cup from the previous year is often reused by the same female (Öst M and Kilpi M, unpublished data). There is also natal philopatry in eider females, for which return to breed near the place where they were born (e.g., Franzman 1983; Baillie and Milne 1989). In these respects, eiders conform to the general pattern of philopatry in waterfowl (Anderson et al. 1992). Strong natal philopatry provides scope for kin-based female sociality, and a recent molecular genetic study found social groups of related eider females arriving at the colony, selecting nest sites, and departing with broods from the colony (McKinnon et al. 2006). Kin-based female sociality therefore occurs in a range of circumstances in common eiders.

As expected from female philopatry, pairwise relatedness in this study increased with decreasing pairwise nest distance (Figure 2). In a Canadian study, McKinnon et al. (2006) found that nearest neighbors were more closely related than the population average. In a previous study in our population, and partly on the same islands (Öst et al. 2005), relatedness between females nesting on the same island was not significantly different from that of females nesting on different islands. The study by Öst et al. (2005) was, however, primarily focused on other aspects than the linear distance dealt with here, so the studies are not directly comparable. Sample size here (156 females, parasites excluded) is >60% larger than in the previous study, providing higher statistical power of detecting a trend in relatedness.

In contrast with this study, there was no distance trend in relatedness among common eiders at La Perouse Bay, Canada (Anderson and Waldeck 2007). Different environmental conditions, such as a short nesting season and large between-year variation in snow cover, may constrain fine-scale breeding philopatry in that population. Eiders at Tvärminne breed in a more benign climate which, although variable and influencing eider breeding success (Leikoinen et al. 2006), offers a longer breeding season and probably less constrained choice of nest site.

Several benefits of natal and breeding philopatry have been proposed, for example, increased competitive ability through familiarity with the breeding area (Anderson et al. 1992) and proximity to kin (Hamilton 1964; Frank 1998; Rousset 2004) (see Introduction). Some waterfowl studies have found population kin structuring (e.g., Avise et al. 1992; Tiedemann and Noer 1998; Fowler et al. 2004; Pearce et al. 2004), but few studies have analyzed the benefits and costs of nesting close to kin. There is a negative correlation between relatedness and nest distance in greater white-fronted geese (Anser albifrons frontalis) (Fowler et al. 2004), and relatedness to neighbors in Canada goose (Branta canadensis minima) appears to have a small but significant positive effect on nesting success (Fowler 2005). In Barnacle geese (Branta leucopsis), related individuals tend to nest closer to each other than expected by chance, but no effect was found on nesting success (van der Jeugd et al. 2002). If the benefit of nesting close to kin is less aggression, however, the fitness consequences may be substantial in the long term but difficult to estimate during the breeding period (Brown and Brown 1993).

In eiders, abundant food is important for duckling growth and survival (e.g., Christensen 1999). Knowledge of posthatch feeding grounds may be one important benefit of natal and breeding philopatry (Bustnes and Erikkstad 1993; Robertson 1995). Females in this population usually spend up to 2 months feeding with their ducklings around the nesting islands, before gradually dispersing to the outer archipelago (Öst 1999). Feeding grounds are relatively segregated also for broods hatched on islands near each other (Öst and Kilpi 2000). The up to 8 weeks spent together feeding in the natal area (Öst 1999) may enable ducklings to learn to recognize their brood mates and social mother and to associate as adults, with potential consequences for host-parasite interactions and relatedness (see below, Andersson and Åhlund 2000; McKinnon et al. 2006).

### Host–parasite relatedness

Tested against the entire population, pairwise relatedness was significantly higher among host-parasite pairs than among random pairs of nesting females (Figure 2). Mean relatedness was also higher in host-parasite pairs ($r = 0.18–0.21$) than among close neighbors ($r = 0.09$), but not significantly so. Is high host-parasite relatedness in this population therefore simply a consequence of the distance trend in relatedness arising from strong female philopatry? Several aspects suggest that this is not the full explanation. First, host-parasite relatedness seems considerably higher than the relatedness regression extrapolated down to nest distance 0 (see Results and Figure 2). Second, we used a conservative approach in identifying parasitism (see Materials and Methods), reducing the chance of detecting parasitism by the most closely related females and, therefore, biasing down the estimate of host-parasite relatedness. If the 3 possible parasites are included that differ from the host in only 2 albumen bands, host-parasite relatedness is significantly higher than that of close neighbors (see Results).

There is significantly higher pairwise relatedness between hosts and parasites than between close neighbors in Hudson Bay eiders studied by Andersson and Waldeck (2007). Natal philopatry alone therefore does not explain the high host-parasite relatedness in that population. Results from that study and this one also support each other: they both address the same scientific hypothesis and can be tested together using Fisher’s method (e.g., Sokal and Rohlf 1995). Their combined probability under the null hypothesis of no relatedness among host-parasite pairs, based on values from method (a) above, is $P < 0.02$. Mean host-parasite relatedness in eiders represented by these 2 populations is therefore higher than that among close neighbor females. This result is not fully explained by random parasitism among females that are related just because of natal philopatry; some additional kin-biasing mechanism is also at work.

Among goldeneye ducks analyzed with molecular methods, there is evidence for kin discrimination and association as adults between female birth nest mates, in addition to host-parasite relatedness (Andersson and Åhlund 2000). In wood ducks (Aix sponsa), nests with high host-parasite relatedness hatched more young, suggesting beneficial kin bias (Roy Nielsen et al. 2006), and there was a similar tendency in the goldeneye study by Andersson and Åhlund (2000). In this eider population, there was a nonsignificant tendency for host-parasite relatedness to be higher in nests where the parasite laid more than 1 egg.

Our estimate of host-parasite relatedness provides a test between 2 alternative hypotheses on the role of relatedness in CBP among waterfowl. Higher average relatedness in host-parasite pairs than in pairs of close neighbor females is evidence against the hypothesis that parasites in general avoid close relatives. Instead, it supports the alternative hypothesis that relatedness makes host-parasite association between 2 females more likely, perhaps being favored by kin selection (Andersson 1984, 2001; Andersson and Åhlund 2000; also see López-Sepulcre and Kokko 2002). This result strengthens the conclusions from a similar study of another eider population (Andersson and Waldeck 2007, see above).

Does the occurrence of some pairs where host and parasite are apparently unrelated imply that some parasites avoid relatives? Possibly, but a simpler explanation may be that...
variation in host–parasite relatedness is to be expected for other reasons. In some cases, there may be no related egg-laying host available in the neighborhood when the parasite is about to lay its eggs. The occurrence of some unrelated host–parasite pairs, among many other pairs of related hosts and parasites, therefore, need not imply that some parasites avoid related hosts.

An additional (nonsignificant) indication of possible kin bias is that females laying several parasitic eggs in the nest tended to have higher relatedness to the host than had other parasites. Statistically significant similar results have been found in goldeneyes and wood ducks (Andersson and Åhlund 2000; Roy Nielsen et al. 2006).

In contrast with host–parasite relatedness, females in coalitions raising young together (créches) were not found to be more closely related than expected by chance in this population (Öst et al. 2005). Females attending brood-rearing coalitions, which are established during a few days after females arrive at sea with their recently hatched broods (Öst and Kilpi 2000), instead, seem to use body condition as a partner choice criterion (Öst et al. 2003).

Additional work is needed to test in eiders and other sea ducks whether host–parasite relatedness and kin discrimination is widespread in this group and, perhaps, in female-philopatric waterfowl more generally. If so, there are likely consequences for the inclusive fitness of hosts and parasites (e.g., Andersson 1984, 2001; Lyon and Eadie 2000; Zink 2000; López-Sepulcre and Kokko 2002; McKinnon et al. 2006; Roy Nielsen et al. 2006; Andersson and Waldeck 2007; Dickinson 2007). A combination of behavioral and molecular studies may clarify the mechanism leading to kin bias in CBP in these and other female-philopatric species.

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