Original Article

Female sociality and kin discrimination in brood parasitism: unrelated females fight over egg laying

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In conspecific brood parasitism, some females ("parasites") lay eggs in nests of other females of the same species ("hosts"). This reproductive tactic is particularly common in waterfowl, in which studies suggest that parasites are often related to the host. Here, we test the hypothesis that hosts may discriminate and reject unrelated parasites. Based on observations and >4100 h of digital video film, we analyze behavioral interactions at 65 nests of High Arctic common eiders during the laying sequence. We also estimate parasitism and host–parasite relatedness by albumen fingerprinting of 975 eggs from 232 nests. Among the video-filmed nests in which interactions were recorded during the egg-laying period, 11 had eggs from 2 females. At 8 of these 11 nests, there was overt female aggression and significantly lower host–parasite relatedness (mean coefficient of relationship $r = -0.40$) than in the nests with tolerant or no interactions ($r = 0.91$). The results demonstrate active female kin discrimination in common eiders, used against nonrelatives that try to lay eggs in the nest. Other females trying to access the nest were often prevented from doing so: in 65% of 34 such attempts, the sitting female rejected the intruder. Brood "parasitism" in eiders and other waterfowl is complex, ranging from violent female conflict and parasitic exploitation of the host's parental care to nest takeover and potential kin selection favoring acceptance of related parasites. These and other aspects of female sociality in eiders are discussed; in some respects, they may resemble certain long-lived matriarchal mammals.

Key words: **aggression, common eider, conflict, cooperation, inclusive fitness, kin recognition, matriarchal mammals, parental care, relatedness, reproductive strategy, social insects, waterfowl**.

INTRODUCTION

Hamilton's (1964) inclusive fitness theory 50 years ago predicted that altruistic behavior and cooperation are biased toward close genetic relatives and that selection can favor behavioral discrimination leading to such bias. Subsequent research has shown that kin discrimination is common in social animals, particularly in cooperatively breeding vertebrates (Griffin and West 2003; Komdeur et al. 2008; Cornwallis et al. 2009), but less so in eusocial insects, where variation in recognition cues is often insufficient (reviewed by Boomsma and d'Ettore 2013, but see Leadbeater et al. 2013).

It is not known whether kin discrimination occurs also in another situation that interested Hamilton (1971): parasitic "tendencies to dump eggs in other nests of the same species." Parasites avoid or reduce costs of parental care if host females raise the parasitic offspring together with their own. Such conspecific brood parasitism (CBP) is a common alternative reproductive tactic among females in egg-tending animals. It occurs in insects, fish, amphibia, and more than 200 bird species (e.g., Yom-Tov 2001; Tallamy 2005; Harris 2008; Taborsky 2008). Some females combine brood parasitism with subsequent care for a clutch of their own, greatly increasing reproductive success (e.g., Sorenson 1991; Lyon 1993; Brown and Brown 1998; Åhlund and Andersson 2001; Loeb 2003; Reichart et al. 2010; Andersson and Åhlund 2012).

CBP is most common in species with precocial, self-feeding young, in which additional offspring cost less to raise than in species where parents feed young. It is particularly common in waterfowl Anatidae, for debated reasons (reviewed by Lyon and Eadie 2000; Eadie and Lyon 2011). Parasites reduce own cost of reproduction, but in hosts a larger clutch requires more energy for incubation and other parental care (Erikstad and Tveraa 1995; Kilpi and Lindström 1997; Hanssen et al. 2003, 2005; Milonoff et al. 2004). Parasitism can also cause a

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host to lay fewer eggs (e.g., Andersson and Eriksson 1982; Erikstad and Bustnes 1994; Waldeck et al. 2011a, 2011b). Given that parasitism can be costly to hosts, why do they accept foreign eggs?

In many cases, a host may simply be unable to prevent parasitism, for instance, if she is away from the nest when a parasitic egg is laid and cannot detect it. But there is an additional interesting possibility in waterfowl, which in contrast with other birds have female philopatry, females tending to nest near their birthplace. Most waterfowl form pairs in the wintering area and the male follows his mate to her breeding site (e.g., Anderson et al. 1992; Tiedemann et al. 1999). Local females hence are often related (e.g., Andersson and Åhlund 2000; Van der Jeugd et al. 2002; Fowler 2005; McKinnon et al. 2006; Waldeck et al. 2008; Jaatinen et al. 2009, 2012; Sonsthagen et al. 2010; Tiedemann et al. 2011; Hario et al. 2012; Moore et al. 2012). It has therefore been suggested that female kinship structure and host–parasite relatedness, found in several waterfowl, may facilitate evolution of CBP by kin selection (Andersson and Eriksson 1982; Andersson 1984, 2001; McRae and Burke 1996; Lyon and Eadie 2000; Lopez-Sepulcre and Kokko 2002; Roy-Nielsen et al. 2006; Eadie and Lyon 2011; Jaatinen et al. 2011a; Tiedemann et al. 2011; Moore et al. 2012; but see Zink 2000; Semel and Sherman 2001; Pöysä 2004; Anderholm et al. 2009b).

Local kinship can lead to host–parasite relatedness without kin recognition, but active discrimination favoring relatives might also be involved (Andersson 1984, 2001; Lyon and Eadie 2000; Lopez-Sepulcre and Kokko 2002; Jaatinen et al. 2011b, 2012). Suggestive evidence comes from cases where relatedness is higher between host and parasite than between neighbors (Andersson and Åhlund 2000; Roy-Nielsen et al. 2006; Andersson and Waldeck 2007; Waldeck et al. 2008; Jaatinen et al. 2009, 2011b; Tiedemann et al. 2011). Spatial kin structure then is not a sufficient explanation. Another possibility is similar timing of breeding or choice of nest site in relatives, making parasitism more likely among kin than unrelated females (Andersson and Waldeck 2007; Waldeck et al. 2008; Eadie and Lyon 2011). Demography and social partner choice may also contribute to kin association (Johnstone and Cant 2010; Jaatinen et al. 2012). Here, we test for the first time the role of active kin discrimination as a cause of host–parasite relatedness.

Most studies of host–parasite relatedness have been based on molecular genetic analyses, but direct observations of behavioral interactions between females are also needed to clarify the role of kinship (Dickinson 2007; Eadie and Lyon 2011). Observations that hosts are less tolerant of unrelated than of related females trying to lay eggs in their nest would constitute evidence that there is active kin discrimination in waterfowl. This could have important implications for their sociality and for selection and evolution of brood parasitism and alloparental care.

Brood parasitism is frequent in common eiders (*Somateria mollissima*) (e.g., Bjørn and Erikstad 1994; Robertson 1998; Waldeck et al. 2004, 2008, 2011a; Waldeck and Andersson 2006; Lusignan et al. 2010; Tiedemann et al. 2011; Hario et al. 2012). Here, we combine estimates of host–parasite genetic relatedness with data from video-filmed interactions between females at nests of High Arctic common eiders (*S. m. borealis*). Aggressive interactions are rare among eider females, and a previous study observed none during 160 h at nests, some of which were parasitized (Robertson 1998). We therefore video recorded female behavior at many nests during the egg-laying sequence and estimated female relatedness by albumen fingerprinting of eggs (see Andersson and Åhlund 2000, 2001). Our main aims were to test whether females discriminate kin and reject unrelated females that try to access the nest.

METHODS
Study area and population

We studied behavioral interactions among eiders at Prince Heinrich Island, a 400 × 150 m low, barren moraine island near Ny-Ålesund, Kongsfjorden, West Spitsbergen (79°N, 12°E). Old nest bowls are common, offering many suitable nest sites, usually in low moss or gravel (Bjørn and Erikstad 1994; Waldeck et al. 2011a, 2011b). Owing to flat topography and low or no vegetation, nests and sitting females are visible from a considerable distance. About 170 eider females breed on the island, with numbers varying between years depending on ice conditions and weather (Hanssen et al. 2013), which also influence the start of egg laying, taking place from mid-May to early June. Eiders usually lay 3–6 eggs at intervals of 24 h or more, starting continuous incubation after the second or third egg (Swennen et al. 1993; Hanssen et al. 2002; Andersson and Waldeck 2006). Glaucous gulls (*Larus hyperboreus*) and arctic skuas (*Stercorarius parasiticus*) take a high proportion of first and second eggs, before incubation starts (e.g., Bjørn and Erikstad 1994; Robertson 1998; Andersson and Waldeck 2006; Waldeck et al. 2011a, 2011b). The clutch is incubated for 22–26 days, during which females seldom leave the nest (Hanssen et al. 2002).

Egg sampling and albumen fingerprinting

We searched the island for active nests twice a day in late May to late June 2007–2009, recording nest positions with GPS (Garmin GPS Map 76) and sampling new eggs for albumen. We marked eggs individually with a nontoxic felt pen and measured their length and width with callipers. To detect parasitism, we used electrophoretic fingerprinting of egg albumen, which can reveal parasitism with high accuracy, as shown by video-recorded egg-laying sequences of marked females (Andersson and Åhlund 2001) and by comparison with microsatellites (Anderholm et al. 2009a). From each egg, we took a nondestructive sample of 0.3 mL albumen, which is produced by the female and reflects her genotype only, not that of her mate (e.g., White 1991). We drilled a 1 mm hole 5–10 mm from the pointed end of the egg and extracted albumen with a syringe, sealed the hole with cyanoacrylat glue (Loctite Superattack), and added a drop of activator to accelerate hardening (Loctite TAK PAK 7452). Samples were stored at −20 °C until electrophoresis by isoelectric focusing. This method separates the albumen proteins, which come to rest in the gel's fixed pH gradient at their respective isoelectric points, producing individual-specific, reproducible band patterns that reflect genetic differences and allow discrimination between females (for details, see Andersson and Åhlund 2001).

To resolve an adequate number of albumen proteins, we ran samples on 4 precast gel types (GE Healthcare, Immobiline DryPlates pH 4.7 code no. 80-1128-28, pH 4.2–4.9 code no. 80-1128-29, and pH 4.5–5.4 code no. 80-1128-30 [run with 2 recipes]). Gels were rehydrated for 2–4 h using recipes modified from Andersson and Åhlund (2001) and Waldeck et al. (2004). Electrophoresis was performed with an Amersham Pharmacia Biotech Multiphor II System and power supply EPS 3501. Based on the albumen band patterns, we determined the number and order of females contributing eggs to a clutch.

Band scoring and parasitism analysis

In eggs sampled 2007 and 2008, we scored presence/absence of 48 nonredundant "standard bands." We also scored 15 fainter bands, useful for separation of individuals with identical patterns of standard bands (Waldeck et al. 2011a). Because of reduced resolution

in gels obtained in 2009, only 30 standard bands and on average 13 fainter bands could be used consistently in all gels. Among these 30 standard bands, a female had on average 7.14 ± 0.15 (standard error [SE]) bands (2007–2009). Mean frequency of occurrence in the 30 bands was 0.24 ± 06.

An egg was here regarded as laid by another female if it differed in 2 or more bands from other eggs in the nest. The reliability of this criterion was tested and verified in previous studies (Andersson and Åhlund 2001); even a difference in only one band produced the same result as a difference in 3 bands or more (Anderholm et al. 2009a). In 2 cases, a parasitic egg had exactly the same band pattern and similar length and width as the eggs in another nest. These may be cases where females laid parasitically before starting nests of their own (e.g., Andersson and Åhlund 2012). A nest is here labeled "parasitized" if it simultaneously contained eggs from more than one female, and the female with most eggs in the nest is labeled "host."

We found 6 nests where the eggs had the same standard band patterns as those in one or more other nests. At least 2 eggs from each of these nests were then run beside each other on the same gel. They differed in 2 or more nonstandard bands and therefore came from different females.

Relatedness analysis

Relatedness between individuals can be estimated from their albumen band patterns (Andersson and Åhlund 2000; Andersson and Waldeck 2007; Anderholm et al. 2009b), similar to multilocus DNA fingerprinting (Bruford et al. 1998; Hardy 2003). Albumen fingerprinting, like other genetic marker methods, cannot determine relatedness between 2 individuals with high precision (e.g., Csillery et al. 2006), but it is useful for comparison of group means (Hardy 2003), as verified by results from individuals with known pedigree relationships (Andersson and Åhlund 2000; Anderholm et al. 2009b).

Here, we tested whether aggression between females during the laying sequence at parasitized nests depends on their relatedness. We used the 30 standard bands scored all 3 years to estimate relatedness with the SPAGeDi 1.3 software, which can handle dominant genetic markers such as protein fingerprint data (Hardy and Vekemans 2002; Hardy 2003). Like other relatedness coefficients, Hardy's (2003) coefficient of relationship, r, measures relatedness relative to the mean genetic similarity between individuals in a reference population. As reference population for a host–parasite pair we use all $n(n-1)/2$ pairs that can be formed among the n females albumen-sampled with a full clutch in the same year as the host–parasite pair ($n = 117$, 83, and 76 in 2007–2009, respectively). The coefficient for a pair of individuals is expected to be positive if they are more closely related than average individuals in the population, negative if less related. Hardy's (2003) coefficient of relationship corresponds to, for example, that of Queller and Goodnight (1989) and to Hamilton's r (see Hardy 2003 and the SPAGeDi manual, available at http://ebe.ulb.ac.be/ebe/SPAGeDi.html).

Pairwise nest distances calculated in SPAGeDi also let us explore spatial trends in relatedness (e.g., Waldeck et al. 2008). For this purpose, we combine results from the 3 years, using 5 classes of distances (≤10 m, with 407 pairwise distances; 11–50 m, 3115; 50–100 m, 3042; 100–170 m, 3130; >170 m, 3301). To allow estimation of relatedness between close neighbors, the shortest class was limited to ≤10 m.

For dominant genetic markers, an inbreeding coefficient must be entered in SPAGeDi. Estimated relatedness is usually robust to variation in the level of inbreeding (Hardy 2003), and varying the coefficient from 0 to 1 had only minor effects on individual estimates of r (<0.02).

Behavioral interactions

Interactions (described below) between females at nests in 2007 were studied from a hide at Prince Heinrich Island, or using a 60x Zeiss spotting scope from ~300 m distance, taking notes of behavior and interactions. Observation periods lasted 1–4 h, in total about 330 h. To increase the chances of observing interactions between females, we focused on nests near which several females were observed.

In 2008–2009, we used digital SD video cameras (Panasonic SDR-SW20 with ×10 optical zoom), running for long periods at 25 frames/s, powered by 60–80 Ah car batteries. We placed a camera 10–20 m from the nest after its first egg was laid and ran the camera until the female started permanent incubation and there were no interactions, no new eggs appeared in the nest for 2–3 days, or the nest was depredated. Cameras could be run continuously for up to 15 h with 16 GB memory cards. We changed cards twice per day and downloaded their contents to external hard disk drives. For recording, we favored nests near which several females were seen, which probably resulted in over-representation of nests with conspicuous aggressive interactions, desirable in order to obtain a sufficiently large sample of such events, which are rare (see Introduction). We could not see in the video film when a female laid an egg; this was determined at nest inspection, usually when changing memory cards. Film sequences were analyzed with the Video Redo Plus software, scanning in fast forward mode. When an event was detected (e.g., a female arriving at or leaving the nest, or an interaction between females), we reduced the speed to normal or slow motion and recorded details of the event.

Each video-filmed nest was scored as belonging in 1 of 3 interaction categories for statistical analyses: Overt aggression, Tolerant interaction, or No interaction (for clarity, the initial letters of these categories are capitalized in the following).

1) In Overt aggression, behavior took 2 easily identified main forms: *rush* and *fight*. In a *rush*, the sitting female left the nest and ran with neck stretched forward toward the intruder, trying to bite and chase her away. We scored such aggressive interactions up to a distance of about 5 m between females when it was obvious at whom the rush was aimed (usually only 2 females were present). If the intruder did not flee but stood her ground, the 2 females usually engaged in a bill-clash or biting *fight* (e.g., see movies in the Supplementary Material). Fighting sometimes also resulted if the female at the nest refused to leave when the intruder tried to take her place. One of the 2 females eventually left in such cases.

2) In Tolerant interactions, there was no Overt aggression between the female at the nest and a visiting female that came closer than about 1 m and stayed there for 2 min or more. The female at the nest usually remained sitting, sometimes responding with "chin lifting" and/or "bill pointing" displays toward the approaching female (for eider displays, see e.g., Cramp and Simmons 1977).

3) When neither of behavioral categories 1 or 2 occurred in the entire video data from the nest, it was scored as having No interaction. If one or more rushes or fights occurred, the nest was scored as having Overt aggression (also if there were

additional episodes of Tolerant interactions). A nest was scored in category 2 if there were only Tolerant interactions (which in some cases involved display), but no Overt aggression.

Relatedness was not normally distributed. We therefore used 2-tailed exact randomization tests (Pitman permutation tests, calculated in StatXact 6), which have high power and assume no particular statistical distribution (e.g., Edgington and Onghena 2007).

RESULTS

Parasitism

Among full-laid clutches, we albumen-sampled 367 eggs from 93 nests in 2007, 303 eggs from 73 nests in 2008, and 257 eggs from 66 nests in 2009. In 2007–2009 combined, parasitism occurred in 42 (18.1%) of 232 nests surviving until incubation, involving 56 (6.0%) of 927 eggs (see Table 1: A–C, G). Two of these nests contained eggs from 3 females. In 10 of the nests, 1 female started laying, then another female took over and continued laying the remainder of the clutch. In 9 cases, takeover occurred after the first egg of the initial female, and in 1 case, it occurred after her second egg.

Behavioral interactions

We used video cameras at 65 nests in 2008–2009 for in total 4122 h, on average 63.4 h/nest (±39.4 standard deviation [SD]). Recording times for the different categories of nests are shown in Table 1. Female interactions occurred at 39 of the video-filmed nests (Table 1: B, C, E, F). Among 31 other nests (Table 1: G), one was monitored from a hide in 2007 for 20 h, as Overt aggression was repeatedly observed there. Protein fingerprinting detected parasitism in 11 of 65 video-filmed nests (Table 1: A–C). Overt aggression between females was recorded at 8 of these 11 nests (Table 1: B). Parasitism usually occurred on the same or adjacent days as interaction, the mean time between nearest interaction and parasitism being about 29 (±13 SE) h (using halftime between nest checks as an approximation of the time when a new egg was laid; see Methods).

Overt aggression also occurred at 24 video-filmed nests that were not parasitized (Table 1: E). In 34 aggressive interaction episodes, the sitting female rejected the intruder in 22 cases and continued sitting; in 11 episodes, the approaching female drove away the sitting female; one outcome was uncertain.

Females were often accompanied by their mate, and in one other case, the male rejected the intruding female. At another nest, both mates together drew her away. Usually, however, males directed their aggression toward other males. At 7 of the 65 video-filmed nests, there were only Tolerant interactions (sometimes involving chin-lifting and bill-pointing displays) (Table 1: C, F).

Relatedness

In the reference population of $n(n-1)/2$ female pairs that can be formed among the n different females (including parasites) albumen-sampled a particular year, mean pairwise relatedness (estimated by the coefficient of relationship r in SPAGeDi) as expected was ≈0 each year (2007: $n = 117$, $r = -0.0022$; 2008: $n = 83$, $r = -0.0037$; 2009: $n = 76$, $r = -0.0034$).

Mean pairwise relatedness among all 44 host–parasite pairs (Table 1: A–C, G) was $r = 0.040 \pm$ SE 0.11. In the 8 video-recorded parasitized nests with Overt aggression (B), mean host–parasite relatedness was -0.40 ± 0.16 (Figure 1). Mean relatedness was significantly higher in the 3 video-recorded parasitized nests without Overt aggression (Table 1: A, C) ($r = 0.91 \pm 0.28$, $P < 0.0061$). The difference remains significant also if the nest without observed interactions (A) is excluded ($r = 1.03 \pm .44$, $P < 0.022$). Relatedness in each of the 2 Tolerant cases (C) was higher than in the nests with Overt aggression (Figure 1). These Tolerant cases clearly were not "false positives" but represented 2 different females in each nest. The albumen patterns of their eggs differed in 3 and 4 bands, respectively, and already a difference in only 2 bands reliably distinguishes 2 females (see Methods). There were 2 episodes of Tolerant interactions at each of these 2 nests, 2 and 3 min and 2 and 7 min long, respectively. The females remained calm, lying less than 1 m from each other (for a video example, see Supplementary Material).

Data from the 31 parasitized nests that were not video filmed (2 of which had 2 parasites; Table 1: G, footnote) also suggest aggression bias toward unrelated females (Figure 1). The nest with repeated aggression observed from a hide had the second lowest relatedness in this group of 33 host–parasite pairs (Figure 1). Female relatedness in the other 32 host–parasite pairs ($r = 0.099$) also tended to be higher than in the video-filmed nests with Overt aggression ($r = -0.40$), but being based on different methods these results are not strictly comparable (Figure 1).

In the 10 nests where another female took over after the first female started laying, the mean relatedness coefficient between the 2 females was 0.40 ± 0.28, whereas in the other 34 host–parasite pairs, it was -0.0067 ± 0.11 (difference not significant; $P = 0.074$). Among the video-filmed parasitized nests, the 2 with Tolerant interactions (above) were among the 10 taken-over nests, as was one of those with Overt aggression.

Spatial relatedness analysis gave no evidence of consistent decline with distance at the only 400-m long island. The linear regression of pairwise female relatedness versus nest distance x is

Table 1

Eider nests used in tests of female behavior, parasitism, and relatedness

Nest category	65 video-filmed nests						G. Other parasitized nests
	Parasitized			Not parasitized			
		Interactions			Interactions		
Type of interaction	A. No interactions	B. Aggressive	C. Tolerant	D. No interactions	E. Aggressive	F. Tolerant	
Number of nests	1	8	2	25	24	5	31[a]
Recording[b] time (h), mean (SD)	12	97 (24)	58 (34)	44 (36)	71 (35)	82 (49)	—

[a]Two of these nests had 2 parasites each. At 1 of the 31 nests many Overt aggressive interactions were observed from a hide during 20 h.
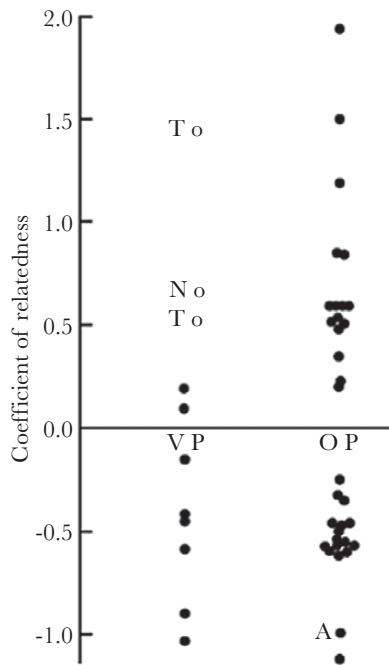[b]Video recording time.

Figure 1

Host–parasite coefficient of relatedness in common eider nests at Prins Heinrich Island, Svalbard. VP: 11 video-recorded parasitized nests, 8 with Overt aggression between females (black points, mean $r = -0.40$), 2 with only Tolerant interactions (open points, T, mean $r = 1.03$), and 1 (N) with no recorded interaction ($r = 0.68$). OP: 33 host–parasite pairs at nests that were not video recorded. One nest (A) observed from a hide for 20 h had Overt aggression between females ($r = -0.98$). For the other 32 OP pairs, mean $r = 0.099$. (See main text for statistical analyses.)

$r = -0.0058 + 0.000025\ x$ ($P = 0.74$). Host–parasite relatedness (mean $r = 0.040$) tended to be higher than that among close neighbors (<10 m, $r = -0.029$), but not significantly so ($P = 0.46$, $n = 44$ and 407, respectively).

DISCUSSION

Behavior and relatedness among common eiders in the High Arctic study colony provide evidence of active kin discrimination, used by females against nonrelatives that try to lay eggs in their nest. Among video-filmed parasitized nests, host and parasite were significantly less related in the 8 nests with aggressive female interactions than in those with Tolerant or No interactions. Host–parasite relatedness also tended to be lower in nests with recorded Overt aggression than in 32 other host–parasite pairs with unknown interaction status (Figure 1). In contrast, host–parasite relatedness was high in the video-filmed nests with Tolerant interactions, in the range most likely for mother–daughter or sisters.

Females were not individually marked, and egg laying could not be directly observed in the video film (see Methods). However, egg addition by an unrelated female near in time to aggressive female interactions strongly suggests that nonrelatives trying to access the nest are met by host aggression. It is not always effective in preventing parasitism, as 9 nests with observed aggression were parasitized (Table 1: B, G). However, 24 such nests were not parasitized, and in 22 of 34 episodes of aggression, the sitting female rejected the intruder and prevented her from accessing the nest. Aggressive host defense hence is often effective in rejecting a parasite (see also Sorenson 1997).

Host–parasite relatedness in eiders therefore is probably not just a passive side effect of other aspects such as strong natal philopatry and population kin structure (e.g., McRae and Burke 1996; Hatchwell 2010), similar nest-site preferences or timing of egg laying in close relatives (Andersson and Waldeck 2007; Waldeck et al. 2008; Eadie and Lyon 2011), or social partner choice and demography (Jaatinen et al. 2012). The results suggest that average host–parasite relatedness in eiders is increased by active kin discrimination and resistance against unrelated females, tending to bias parasitism toward relatives (see also Andersson and Waldeck 2007; Waldeck et al. 2008; Tiedemann et al. 2011).

In spite of kin discrimination and aggressive host defense, brood parasitism was fairly common in the eider colony at Prince Heinrich Island, and average host–parasite relatedness was low compared with other eider studies (Andersson and Waldeck 2007; Waldeck et al. 2008). High nest visibility is a likely reason. Lusignan et al. (2010) found that the risk of being parasitized is highest for the most visible eider nests. As nests and females are easy to see from a distance at the flat, barren gravel ground of Prince Heinrich Island, finding and accessing a nest is easy for parasites when a female leaves for drinking or feeding, as she does early during the egg-laying sequence (Swennen et al. 1993).

A nest that contained eggs from more than one female for simplicity was here labeled "parasitized," but females may lay eggs in the same nest for several reasons (e.g., Eadie et al. 1988; Lyon and Eadie 2008). In some cases, another female can take over the nest from the one who started egg laying (above), and females may also compete over the same nest site (Semel and Sherman 2001; Åhlund 2005). However, competition is not the only reason even in cavity-nesting species such as goldeneyes or wood ducks (Åhlund 2005; Roy-Nielsen et al. 2006). Among the common eiders studied here, many suitable nest sites and old nest bowls were unoccupied, and parasitism in common eiders is probably not mainly a consequence of nest site scarcity (Robertson 1998; Waldeck et al. 2011a). But even if competition over the same nest were the reason for some female fights, the association between fights and low relatedness remains evidence of active behavioral kin discrimination.

Whether parasites are expected to lay eggs in the nests of related or unrelated females is debated (e.g., Andersson 1984, 2001; Lyon and Eadie 2000; Zink 2000; Semel and Sherman 2001; Lopez-Sepulcre and Kokko 2002; Pöysä 2004; Eadie and Lyon 2011; Jaatinen et al. 2009, 2011a, 2011b). If there is a cost of being parasitized and nothing to hinder a parasite from laying successful eggs in the nests of unrelated females, parasites may gain inclusive fitness by targeting nests of nonrelatives (Andersson 2001). But the situation is usually more complex. When hosts can resist being parasitized, for instance, by aggressive discrimination of unrelated females, or by rejection of their eggs, hosts as well as accepted parasites may gain inclusive fitness benefits if they are sufficiently closely related and the cost of being parasitized is not too large (Andersson 1984, 2001; Lopez-Sepulcre and Kokko 2002; Jaatinen et al. 2011a).

Nepotistic kin discrimination by females may occur also in nests of other animals than birds. It is rare in eusocial hymenoptera, but workers in ant nests with several reproductive queens may favor those with which they are most closely related (Hannonen and Sundström 2003; Boomsma et al. 2014).

Our results corroborate the hypothesis of behavioral kin discrimination against unrelated females in brood parasitism among waterfowl (Andersson 1984, 2001; Lopez-Sepulcre and Kokko 2002; Jaatinen et al. 2011a). Kin discrimination occurs in many

cooperative vertebrates, including birds (Griffin and West 2003; Komdeur et al. 2008; Cornwallis et al. 2009). Recognition of relatives seems to be achieved mostly by learning phenotypes during a period of close association. For instance, in long-tailed tits (*Aegithalos caudatus*), it is based on vocal cues learned during the nestling period (Sharp et al. 2005). In waterfowl, long-term kin associations have been found in, for example, goldeneye ducks (*Bucephala clangula*), barnacle geese (*Branta leucopsis*), and common eiders, perhaps based on learned recognition of brood mates (Andersson and Åhlund 2000; Van der Jeugd et al. 2002; McKinnon et al. 2006).

In many cases, parasitized clutches may reflect exploitation, adaptive for the parasite but negative for the host, but in some cases, there may be inclusive fitness benefits for host as well as parasite if they are closely related (Andersson 1984, 2001; Lopez-Sepulcre and Kokko 2002; Jaatinen et al. 2011a). Such benefits, however, remain to be demonstrated in the wild. Are some females cooperating in a joint laying system (Vehrencamp and Quinn 2004)? In 10 cases, 1 eider female began laying eggs, then another female took over and continued laying the remainder of the clutch. The females involved in these cases tended to have higher pairwise relatedness than other parasitized nests. Nest takeover has also been found in other eider populations (Robertson 1998; Hario et al. 2012), and where relatedness was studied it tended to be higher in taken-over nests (Waldeck and Andersson 2006; Andersson and Waldeck 2007). Some groups of female eiders raising ducklings together are also closer relatives than expected by chance (Jaatinen et al. 2012).

We do not know which female incubated the clutch in taken-over nests. The female taking over egg laying may seem the most likely candidate, but Tiedemann et al. (2011) reported that some females incubated more foreign than own eggs, and 3 over 15-year-old females had no eggs of their own, incubating only eggs from close relatives. If this is a regular pattern, it suggests remarkable age-dependent kin relations in eider females, some of which are old (in a long-term study, the oldest incubating female was at least 33 years; Coulson 2010). This possibility deserves further behavioral and genetic study, as does relatedness between eider females involved in nest takeovers. Behavioral observations of marked individuals of known age and relatedness are desirable for further analysis of sociality in this fascinating species. A combination of female philopatry, local relatedness, active kin discrimination, long life, reproductive senescence, and parental care for offspring of relatives may suggest a social system in female eiders that in some respects resembles that of long-lived matriarchal mammals such as elephants (Moss 2001), killer whales (Foote 2008), and perhaps our own species (e.g., Lahdenperä et al. 2004; Johnstone and Cant 2010; Hawkes and Coxworth 2013). Exploring and testing this possibility is an interesting challenge for the future.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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