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Egg adoption can explain joint egg-laying in common eiders

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Abstract Hypotheses regarding the evolution and maintenance of intraspecific nest parasitism were tested with data collected during a 3-year study of common eiders (*Somateria mollissima*) breeding near Churchill, Manitoba. The nest parasitism rate was highest (42.4% of nests) during the year with the highest nest density and the best environmental conditions, and lowest (20.2% of nests) in the year with the lowest nest density and the poorest environmental conditions. Over the nesting season, parasitic eggs were laid at the same time as normally laid eggs. Most parasitic eggs (> 75%) were laid before the host female laid her third egg. The majority of the parasitic eggs were the first or second egg produced by the parasitic female. When a parasitic egg was laid before or on the same day as the host female initiated her clutch, the probability of her first egg being depredated before incubation was significantly lowered. First- and second-laid eggs suffered a high rate of predation probably because nesting females do not attend their clutch until their second or third egg is laid. Hypotheses that some females use intraspecific nest parasitism to parasitize the parental care of other females were inconsistent with these data. Egg adoption is a likely explanation for the prevalence of females incubating parasitic eggs in this population.

Key words Common eider · *Somateria mollissima* · Intraspecific nest parasitism · Brood amalgamation · Alternative reproductive behaviours

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Introduction

By laying their eggs in the nest of others, birds use brood parasitism to avoid costs of parental care (Andersson 1984; Yom-Tov 1980). The parasite is thus freed from the constraints of incubating or raising young and can potentially increase her reproductive output (Lyon 1991). Mechanisms to avoid being parasitized will also evolve, as parasitized birds are providing care to non-kin young (Møller 1987).

Altricial and precocial species display a dichotomy in the nature of nest parasitism. Generally, altricial species show low rates of conspecific nest parasitism and higher levels of interspecific nest parasitism, while precocial species tend to exhibit more conspecific nest parasitism (Lyon and Eadie 1991). This difference has been attributed to the relative costs and benefits of accepting parasitic eggs in these groups (Rohwer and Freeman 1989; but see Sorenson 1992). In precocial birds, clutch size is limited primarily by the number of eggs females can lay (Alisauskas and Ankney 1992) and the costs of raising extra precocial young are small. In fact, raising extra precocial young may have no costs at all (Lazarus and Inglis 1986; Sandercock 1994).

There are four hypotheses that are favoured in studies that address the evolution of intraspecific nest parasitism (Eadie et al. 1988). Nest parasitism in geese and some ducks appears to be a salvage strategy (or the best of a bad job, Dawkins 1980), where young or birds in poor condition salvage reproductive effort by laying eggs in the nests of conspecifics (Forslund and Larsson 1995; Lank et al. 1990; Sorenson 1993; Weigmann and Lamprecht 1991). In other species, high-quality individuals are able to nest parasitically and subsequently nest normally as well, enjoying an enhanced reproductive output (Gibbons 1986; Jackson 1993; Lyon 1993; Sorenson 1991). These are side-payment or enhancement strategies (Dunbar 1982; Kendra et al. 1988). Nest parasitism may have evolved as an evolutionary stable strategy (ESS; Maynard Smith 1982), whereby when a certain proportion of the population uses a parasitic strategy, normal nesting and parasitic laying have equal reproductive payoffs (Eadie 1989). Finally, when nest sites are limited in number or vary in quality, nest parastism may be an artifact of more than one female attempting to initiate their clutches in the same nest site (Erskine 1990; Semel et al. 1988).

The objective of this study is to evaluate these hypotheses on how intraspecific nest parasitism has evolved and is maintained in the common eider (*Somateria mollissima*). Common eiders nesting at La Pérouse Bay, Manitoba, exhibit relatively high levels of intraspecific nest parasitism with parasitic eggs found in 42.4% of nests studied in 1991 (Robertson et al. 1992). We found no evidence of a reduction in hatching success of the host's clutch or the parasitic eggs. We suggested that intraspecific nest parasitism in the common eider may be a mixed ESS (Maynard Smith 1982). However, Bjørn and Erikstad (1994) found a different pattern of parasitic egg-laying for eiders breeding in the high Arctic. Their data suggested that immature birds or birds in poor body condition were laying their eggs parasitically, data consistent with a salvage strategy. Eadie and Fryxell (1992) point out that at different densities of nesting birds, different conclusions can be drawn about how nest parasitism evolved. In this paper I report new data from La Pérouse Bay collected under different environmental conditions and nesting densities and use these new data to re-evaluate the hypotheses proposed to explain the evolution of nest parasitism in common eiders. Finally, I propose another hypothesis that is equally consistent with the observed patterns of nest parasitism seen in common eiders: nest parasitism may be active egg adoption by the host female.

Methods

Field work was carried out between April and August of 1991–1993 at the La Pérouse Bay Tundra Biology Station, 30 km east of Churchill, Manitoba. The study site was a complex of small islands and mainland shorelines in the Mast River Delta. Islands ranged in size from 2 to 2500 m^2, and were dominated by low-lying willows (*Salix* spp.), dwarf birch (*Betula glandulosa*), *Potentilla palustris*, and freshwater/estuarine grasses and sedges (Schmutz et al. 1983). The entire study area was searched daily (three times daily in 1991; Watson et al. 1993) for nests, and all previously discovered nests were visited daily until incubation began. At each visit to a nest, its contents were recorded and new eggs were measured and numbered with a permanent marker. In 1991–1993, length, breadth (with vernier calipers), mass (with a spring balance) and an estimate of the colour of the eggs (assessed by visually matching the egg with a collection of paint colour chips) were recorded as described in Robertson et al. (1992). In 1993, a layer of oviducal residue was noted on some eggs. The amount of residue on each egg was scored as: 1 thick, 2 thin or 3 none. Nests were visited daily around the expected hatching date and the fate of all eggs was determined.

All nests in which two or more new eggs were found on the same day were identified as parasitized (see Robertson et al. 1992 for details). The variance in the three measurements of the eggs (length, breadth, colour) were calculated for each clutch, including only one of the putative parasitic eggs. The variance in these measurements was then recalculated including the other putative parasitic egg(s). The egg which increased the variance in the measurements the most was identified as parasitic. If the results were ambiguous, the egg which increased the variance the most in colour was identified as parasitic because colour is the most reliable trait for identifying parasitic eggs (Robertson et al. 1992), and does not vary within a clutch as do length and breadth (Robertson 1995a; Robertson and Cooke 1993). This method cannot identify parasitic eggs if they are laid the day immediately before or after the host's clutch. Therefore, clutches with unusually high variances (outside the distribution of variances for normal clutches) in the three measures when including the last or first egg were examined. If the variance was substantially reduced when the first or last egg was removed then they were identified as parasitic.

With the data obtained in 1993 it was possible to create a discriminant function with eggs of known sequence to establish the position of parasitic eggs in the laying sequence. There is a consistent pattern of intraclutch egg-size variation over the laying sequence in eiders (Robertson 1995a; Robertson and Cooke 1993). The amount of oviducal residue present on eggs also varied with laying sequence; first-laid eggs were usually covered with a thick layer, while third and fourth eggs had little residue. Length, breadth and the oviducal residue score were used to establish a discriminant function with known-sequence eggs from clutches laid by a single female. All eggs laid beyond the third position were pooled into a 'last' category. There were 254 first-sequence eggs, 219 second-laid eggs and 437 'last'-laid eggs available for analysis. The a priori probability of an egg being assigned to a particular laying position was set to be proportional to the occurrence in the data set (27% for first-laid eggs, 24% for second-laid eggs and 49% for last-laid eggs). Eggs identified as being laid parasitically ($n = 64$) were then entered into the discriminant function to determine from which laying sequence they were most likely to come. Since the discriminant function did not assign all known-sequence eggs to their correct laying sequence, some error is also expected in the assignment of parasitic eggs to a laying sequence. This error was calculated by examining the posterior error rate for each laying position. For example, if 66.6% of true first-laid eggs were assigned into the first-laid egg category, then the assignment of parasitic eggs to the first-laid egg category was assumed to have an error rate of 33.3%. Using these error rates, a minimum and maximum value was calculated for the number of parasitic eggs assigned to each category. These errors were not symmetrical, because some errors were biased towards a specific laying sequence (e.g. second-laid eggs may be misclassified as last-laid eggs more often than as first-laid eggs).

Results

Annual variation in parasitism rates, nest density and environmental conditions

Over 40% of nests were parasitized in 1991, while only 20–24% of nests were parasitized in 1992 and 1993 (Table 1). The reduced parasitism rate in 1992 and 1993 coincided with a reduction in nesting density in the colony, which was roughly half that in 1991. The reduced nest density in 1992 was a result of very poor environmental conditions (low temperatures during the egg-laying period and deep snow cover). In 1993, temperatures during the egg-laying period were low but very little snow cover was present and the birds nested over a wide area. The pattern of snow cover during nest initiation in 1991 probably concentrated the nesting of eiders into the study area.

Table 1 Annual variation in the parasitism rate (as a percentage of the total number of completed clutches), nest density of breeding female common eiders, and maximum temperature (Robertson 1995a) and snow cover at the time of nest initiation (see Fig. 1) (1991 data from Robertson et al. 1992)

Year	Percentage of parasitized nests (complete clutches)	Nest density (nests/ha)	Mean maximum daily temperature ±1 SD	Snow cover
1991	42.4 (153)	61.9	12.0 ± 9.3	Moderate
1992	20.2 (99)	30.8	5.4 ± 5.5	Deep
1993	23.4 (186)	34.4	5.8 ± 4.8	None

Timing of laying

The mean egg-laying date was not significantly different between parasitically and normally laid eggs ($F = 1.93$, $P = 0.165$, $df = 1{,}2110$) but did vary between years ($F = 444.7$, $P = 0.0001$, $df = 2{,}2110$) (Fig. 1). A marginally significant interaction ($F = 2.88$, $P = 0.053$, $df = 2{,}2110$) between egg type (parasitic or normal) and year was due to parasitically laid eggs being laid about 3 days later in 1992 than normally laid eggs (Fig. 1).

Timing of laying parasitical eggs with respect to the host's clutch

Over 75% of parasitic eggs were laid before the host laid her third egg (Fig. 2). Twenty eggs were laid before the host began her clutch (Fig. 2). Additionally, in some of the clutches where the parasitic egg was laid on the same day the host intiated, the parasitic egg could have been laid first. In 1991, that proportion could be calculated because we visited nests three times daily. In 8 of 13 (61%) nests, the parasitic egg was laid before the host egg (Robertson et al. 1992); this proportion is not different from the expected proportion of 0.5 ($G = 0.692$, $P = 0.405$, $df = 1$). Therefore, for all 3 years combined, it was assumed that half of the 75 parasitic eggs laid on the same day the host intiated were laid before the host egg. Including the 20 cases where the parasitic egg was present in the nest the day before the host initiated her clutch, 31% (57.5/188) of all parasitic eggs were laid before the host initiated her clutch.

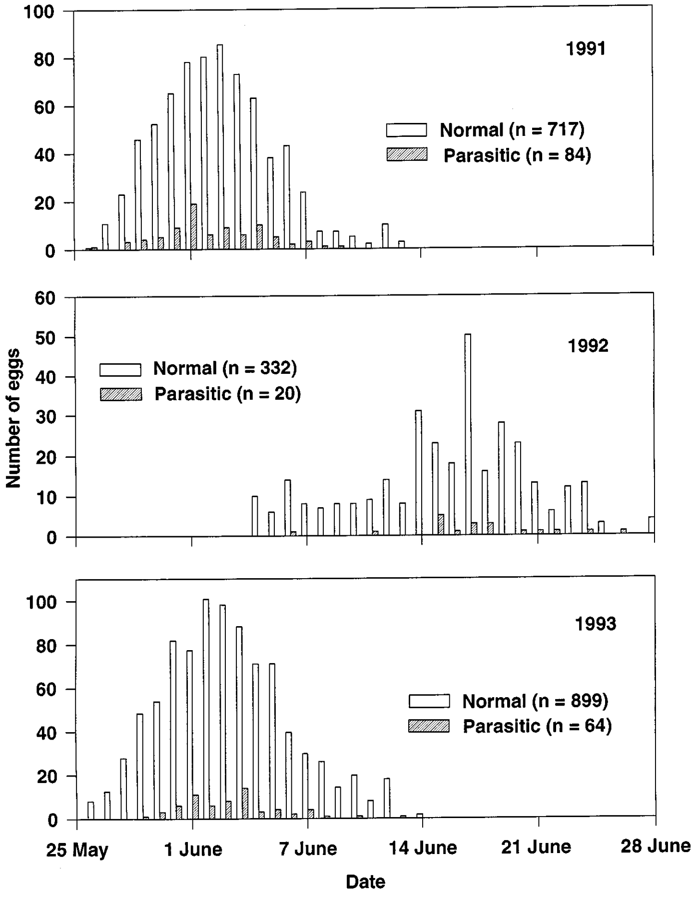

Fig. 1 Relative distribution of the number of normal and parasitically laid eggs over the nesting season in three years

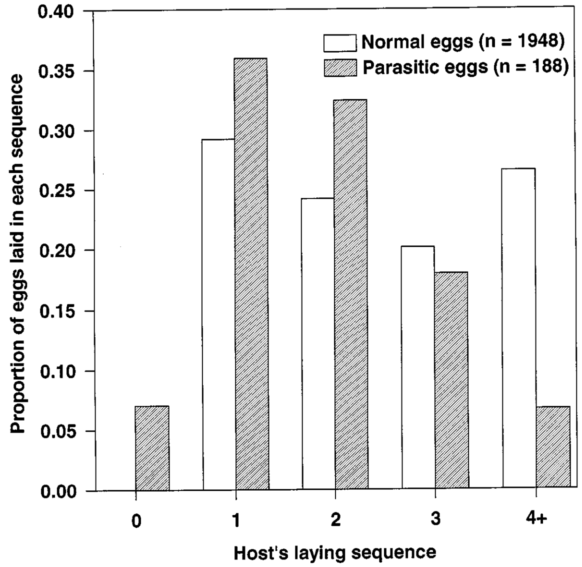

Fig. 2 Distribution of host eggs and parasitically laid eggs as a function of the host's laying sequence (*0* is the day before the host begins her clutch)

Laying sequence of parasitic eggs

The discriminant function created to establish which laying sequence parasitic eggs came from had a success rate of 69.4% in classifying known-sequence eggs into first-, second- or later-laid eggs. Of the sample of 64 parasitic eggs laid in 1993, 39 (61%) (min.–max. 26–44, 41–69%) were classified as first-laid eggs, 14 (22%) (6–25, 9–39%) were classified as second-laid eggs and only 11 (17%) (8–16, 13–25%) were classified as third- or later-laid eggs.

Early partial clutch depredation and parasitized nests

Nests in which one or more parasitic eggs were laid on the same or previous day as the host intiated had a 77.4% ($n = 93$) chance of avoiding predation before incubation began. In nests where no parasitic eggs were laid on the day the host initiated her clutch; the host egg had 53.5% ($n = 585$) chance of avoiding predation until incubation began. These proportions are significantly different ($G = 19.4$, $P = 0.001$, $df = 1$). Similar comparisons using parasitic eggs that were laid as the second, third or fourth host egg was laid showed no difference between the two groups ($P > 0.48$ in all cases).

Discussion

A number of hypotheses have been presented to explain the evolution and maintenance of nest parasitism in birds. Reviews by Yom-Tov (1980), Andersson (1984), Eadie et al. (1988) and Rohwer and Freeman (1989) provide good summaries of the hypotheses present in the literature. Predictions from the four most popular hypotheses are tested with the data collected on common eiders nesting at La Pérouse Bay.

Salvage strategy

For eiders nesting at La Pérouse Bay, the parasitism rate was highest in a year when nesting densities were high and environmental conditions were favourable. Parasitism and nesting density decreased in years with poor environmental conditions. In contrast, more geese lay parasitically in years with adverse environmental conditions because more individuals are in poor condition (Lank et al. 1989). Nesting density also decreases, due to the reduced number of normal breeders (Lank et al. 1989, 1990).

Coulson (1984) found evidence of extensive nonbreeding by adult eiders at a colony in Scotland. Eiders, like other sea ducks (Tribe: Mergini) exhibit a high-survival and low-fecundity life history (Goudie et al. 1994) and may defer breeding instead of resorting to parasitism in years with bad environmental conditions. Young eiders and eiders in poor body condition are known to lay later in the breeding season than good-quality birds (Baillie and Milne 1982; Laurila and Hario 1988). At La Pérouse Bay, parasitically laid eggs were laid at the same time of year as normally laid eggs in 2 of 3 years. Therefore, a salvage strategy is probably not the mechanism that accounts for the occurrence of most nest parasitism in eiders. In 1992, however, parasitic eggs were laid later in the season, so in extremely bad years a few females may resort to parasitism as a salvage strategy. Additionally, in all years, some parasitic eggs were laid at later stages in the host's laying sequence, also suggesting that a few parasitic eggs may be laid as a salvage strategy (Bjørn and Erikstad 1994). It is possible that females that lay parasitically only lay one or two eggs, because most parasitic eggs are the first- or second-laid eggs.

Enhancement strategy

When an enhancment strategy is employed, parasitic individuals obtain the highest reproductive output, as they are able to pursue two methods of reproduction (Kendra et al. 1988). Generally, but not necessarily, parasitic eggs are laid earlier in the season, relative to the population of nesting birds, because there is a general decline in nesting success as the season progresses (Sorenson 1991). However, the timing of parasitic egg-laying coincides with the time that normally nesting eiders lay. Furthermore, enhancement strategies are only used by birds that are in good body condition and can lay extra eggs. As eiders are determinate egg-layers (Erikstad and Bustnes 1994; Swennen et al. 1993) and rely exclusively on accumulated reserves for egg-laying and incubation (Korschgen 1977; Parker and Holm 1990), they may be unable to increase the number of eggs they lay beyond what they can carry as reserves (no more than six eggs). Erikstad et al. (1993) showed that female eiders in the best body condition lay large clutches, incubate quickly and do not abandon their young into crèches. The best option for eiders in top body condition is to lay a large clutch early and raise the young herself rather than resorting to nest parasitism.

Mixed ESS

A pure intraspecific parasitic strategy (an individual only parasitizes throughout her life) has never been documented in birds, and it is highly unlikely that such a strategy exists (Eadie 1989, Lank et al. 1990). A strategy where individuals switch between two strategies in successive years is more likely and has been proposed for Barrow's (*Bucephela islandica*) and common goldeneye (*Bucephela clangula*) (Eadie 1989). Mixed ESSs do not make any predictions about the mechanism by which the alternative behaviour is manifested, a problem with testing ESS models (Austad 1984). It is thus difficult to prove alternative behaviours have evolved as an ESS, and stating a behavioural set has evolved to an ESS provides no insights into the mechanism of how the alternative behaviour is achieved.

Nevertheless, certain data suggest that parasitism in eiders may not be the result of a mixed ESS. Clutches (31%) exist where the very first egg in the nest is the 'parasitic' egg. If parasitism is an ESS, it would seem to be risky to lay a parasitic egg in a nest site that is not currently being used by any other female. In the case of cavity nesters, one may expect that a suitable cavity would be eventually used by a nesting female, and that parasitizing a cavity may be a viable option. Eiders, however, nest on the ground on any suitable terrain (personal observation). Laying an egg in a possible nest site would not be a successful strategy if only a small percentage of these nest sites were subsequently used by host females. Unfortunately, data for the lifetime reproductive success of parasitic and normally nesting eiders are not available; therefore the possibility that intraspecific nest parasitism has evolved to an ESS cannot be dismissed.

Nest site competition and takeover

In eiders, parasitically laid eggs are laid early in the laying sequence of the host's clutch. This observation is consistent with two or more females competing for the same nest site early in their laying cycles. Parasitic eider eggs also tended to be the first- or second-laid eggs of the 'parasitic' females, implying that only a proportion of some eider clutches are laid parasitically, which is also consistent with the nest site competition and takeover hypothesis. Furthermore, nest parasitism rates increase in years with higher nest densities. Wood ducks (*Aix sponsa*) show higher levels of parasitism with increasing nest density, which may be the result of joint egg-laying as females compete for the limited number of available nest sites (Semel et al. 1988). However, there are a variety of reasons why aggressive nest site competition and takeovers are probably not occurring in eiders. First, nest sites are probably not limiting in this species, because eiders nest on the ground, on any dry habitat, which is widely available. Second, in the first year of this study, there was no observed reduction in the hatching success of eggs laid in parasitized nests (Robertson et al. 1992) contrary to what is usually seen when females are competing for limited nest sites [in the other 2-years only very few (< 5%) nests hatched successfully (Robertson 1995b)]. If nest sites are limited in number and/or quality, then it is expected that females will actively compete for these nest sites. In these interactions, eggs may be damaged and large clutches can be laid in these nests with a reduction in the hatching success (Eriksson and Andersson 1982; Hines and Mitchell 1984; Semel et al. 1988).

Egg adoption

The most common explanations of nest parasitism in the literature do not satisfactorily explain the occurrence of most of the 'parasitic' eggs laid by common eiders. It appears that two or more females initiate egg-laying in the same nest cup. A likely scenario is that two females begin to lay in the same nest cup with at least one female beginning to lay in a nest site which already contains another female's egg(s). Eiders begin to incubate their clutch after they lay their second or third egg (Swennen et al. 1993). Apparently, one female incubates the clutch and the other female lays the remainder of her clutch elsewhere. Although these observations are consistent with a nest site competition and takeover hypothesis, in approximately 160 h observing nesting common eiders, no aggressive interactions were seen between nesting females, and at least two parasitized nests were included in this sample (L. Yoshida, unpublished data). In eiders, none of the typical negative consequences of nest site takeovers, such as extremely large clutch sizes, nest abandonment, egg breakage or egg loss occur (Semel et al. 1988). Females incubating foreign eggs may not suffer any costs and joint egg-laying may be an inadvertent selection of the same nest site by two females. However, nest sites that contain parasitic eggs have lower probabilities of having their first eggs removed by predators. An inadvertent joint egg-laying hypothesis cannot explain this result.

Active egg adoption could be advantageous because first-laid eggs are vulnerable to avian predators. First- and, to a lesser degree, second-laid eider eggs are highly susceptible to avian predation (Bjørn and Erikstad 1994; Robertson and Cooke 1993). Eiders lay their first egg in a nest bowl and cover it with twigs and leaves in an attempt to hide the egg. The next day she returns and begins to attend her clutch (Swennen et al. 1993; L. Yoshida, unpublished data). It is only the first or second egg that are vulnerable because female eiders at their nest can defend their clutch from aerial predators such as gulls and jaegers (Schamel 1977). Female eiders prospecting for a nest site may preferentially choose a site that already contains an egg. If a female eider chooses a site that contains another concealed eider egg, then she has some assurance that the nest site is offering protection to eggs. Nest sites with more cover have reduced chances of being depredated (Choate 1967; Gorman 1974). Alternatively, the visits by two females to the same nest site while they lay their first eggs may increase the amount of time the eggs in the nest are protected. Therefore, it may be advantageous for a female to choose a safe nest site at the expense of having to incubate one, or rarely two, extra eggs. The female that has her egg(s) adopted is not disadvantaged as the host female will protect her eggs from aerial predators as she begins to attend her own clutch. Eiders tend to be philopatric to a general nesting region, yet not to specific nest sites (Bustnes and Erikstad 1993; Milne 1974). They can nest at very high densities, with nearest-neighbor distances of less than 2 m. The female which does not incubate the clutch may only have to move a very short distance to lay the rest of her clutch. Eiders also prospect for nest sites before laying, so females will already be familiar with alternative nest sites (Schamel 1977). Egg attendance in eiders is based on the number of eggs a female has laid and not on the number of eggs in the female's nest (Swennen et al. 1993). Therefore, the female that does not incubate the joint clutch can begin to attend the remainder of her clutch immediately at a new nest site because she has already laid one or two eggs.

If females could simply protect their first-laid eggs themselves then they would not need to actively adopt eggs to find a good nest site. Physiological constraints such as hormonal balances (i.e. prolactin) needed for egg-laying and incubation may preclude females from starting nest attendance at the first egg (Haywood 1993). Additionally, nest attendance at the first egg may cause the nest to hatch asynchronously and increase the chances that last-laid eggs are abandoned (Flint et al. 1994). Finally, a foraging bout on the day the first egg is laid may be important in topping up nutrient reserves that must last for approximately 28 days.

Egg adoption occurs in other birds. Female geese will roll eggs that are outside of their nest back in to retrieve eggs that have accidentally rolled out of the nest bowl. Parasitic geese have taken advantage of this behaviour by laying their eggs outside the actual nest bowl, if they cannot displace the host from her nest. In snow geese (*Chen caerulescens*), Lank et al. (1991) showed that females will roll a parasitic egg into the nest that has been laid outside their nest bowl. Given the choice of incubating a foreign egg or having a glaring white egg outside the nest which will attract predators, the best option is to accept the parasitic egg into the nest. Eiders may actually use foreign eggs as assessments of nest site quality and adopt foreign eggs in a good nest site at no apparent cost to themselves or the parasite. Incubation ability (Erikstad et al. 1993; Robertson et al. 1995; Rohwer 1992; but see Erikstad and Tveraa 1995) and brood rearing (Bustnes and Erikstad 1991; Lazarus and Inglis 1986; Munro and Bédard 1977; Williams et al. 1994) do not constrain annual reproductive success of Arctic breeding geese and eiders. It is the amount of nutrient reserves that can be carried to the nesting grounds and consequent clutch size which largely determines the reproductive output of these birds (Alisauskas and Ankney 1992). Incubating and rearing foreign eggs and young are probably not constraining the reproductive output of the host female.

Lyon (1993) found that American coots (*Fulica americana*) laid parasitically in three different contexts: non-territorial floater females, birds which had lost their nests, and normal nesters laying parasitically. In all three cases, the coots were truly parasitizing their hosts because the presence of parasitic eggs and young in the nest negatively influenced the reproductive output of the host. In eiders, I believe that there are two fundamentally different behavioural mechanisms occurring, both of which lead to what is described as 'nest parasitism' in the literature and neither of which is likely to be detrimental to the host. One is a stable strategy used by nesting females to ascertain the quality of a chosen nest site, where both the host and the parasite achieve equal or slightly elevated fitness gains. This egg adoption is a behavioural tactic exhibited by the putative 'host' female rather than the putative 'parasite'. This strategy is used extensively in good environmental conditions when high nesting densities occur and there are many available eggs to adopt. The other mechanism is a classic salvage strategy used by females who are not in sufficient condition to nest normally. This strategy is used less frequently, although it may be more prevalent in populations nesting in more northerly (and presumably harsher) locations (Bjørn and Erikstad 1994).

Further investigations of taxa where brood care does not involve high costs and there are nest site quality differences may reveal more instances of egg adoption as a method of gaining a high-quality nest site with no fitness loss to the individual who loses her eggs.

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