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CONSPECIFIC BROOD PARASITISM IN COMMON EIDERS (*SOMATERIA MOLLISSIMA*): DO BROOD PARASITES TARGET SAFE NEST SITES?

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Abstract.—Several hypotheses have been proposed to explain the evolution of conspecific brood parasitism (CBP), and recent studies suggest that nest predation may be an important factor in shaping this behavior. We assessed whether individuals that engage in parasitic laying preferentially deposit their eggs in safe nest sites (i.e., risk assessment hypothesis). We tested the predictions of this hypothesis using a population of Common Eiders (*Somateria mollissima dresseri*) nesting at Table Bay, Labrador, Canada, in 2007. Common Eiders at this location nest in three habitats (dense woody vegetation, open grassy vegetation, and nest shelters) that vary in their exposure to avian predators. We used isoelectric focusing electrophoresis of egg albumen to quantify the frequency and distribution of CBP among habitats. Nest-site safety did not explain patterns of CBP among habitats, given that nests in dense woody vegetation had the highest probability of survival (0.70; 95% confidence interval [CI]: 0.50–0.89) yet had the lowest frequency of CBP (33%). There was also no indication that parasitized and nonparasitized nests differed in their probability of nest survival (0.65 [95% CI: 0.41–0.83] vs. 0.58 [95% CI: 0.33–0.80]). We propose explanations for why our data did not support the risk assessment hypothesis. *Received 20 October 2009, accepted 8 April 2010.*

Key words: Common Eider, conspecific brood parasitism, habitat selection, nest predation, nest survival, protein fingerprinting, *Somateria mollissima*.

Le parasitisme conspécifique de nid chez *Somateria mollissima*: les parasites de nid ciblent-ils les sites de nidification sûrs?

Résumé.—Plusieurs hypothèses ont été proposées afin d'expliquer l'évolution du parasitisme conspécifique de nid (PCN). Des études récentes suggèrent que la prédation des nids puisse être un facteur important dans l'élaboration de ce comportement. Nous avons évalué si les individus qui se livrent à la ponte parasitaire déposaient préférentiellement leurs œufs dans des nids sûrs (hypothèse d'évaluation des risques). Nous avons testé les prédictions de cette hypothèse sur une population de *Somateria mollissima dresseri* nichant à Table Bay, au Labrador, Canada, en 2007. À cet endroit, *S. mollissima* niche dans trois habitats (végétation arborescente dense, végétation herbacée ouverte et abris pour les nids) qui diffèrent en termes d'exposition aux prédateurs aviens. Nous avons utilisé l'électrophorèse isoélectrique de l'albumen des œufs afin de quantifier la fréquence et la répartition du PCN entre les habitats. La sécurité des sites de nidification n'a pas expliqué les patrons de PCN entre les habitats, car les nids situés dans la végétation arborescente dense avaient la probabilité de survie la plus élevée (0,70; intervalle de confiance [IC] à 95%: 0,50–0,89) et la plus faible fréquence de PCN (33%). De plus, il n'y avait aucune indication que les nids parasités et non-parasités différaient dans leur probabilité de survie (0,65 [IC 95%: 0,41–0,83] vs 0,58 [95% IC: 0,33–0,80]). Nous proposons des explications sur le pourquoi nos données ne supportaient pas l'hypothèse d'évaluation des risques.

Parental investment is energetically costly (King 1974, Andersson 1984) and can expose adults to additional mortality risks during nest attendance (Sargeant and Raveling 1992). Brood-parasitic individuals avoid these costs. Female birds that lay their eggs in the nests of other females, such that the care of the eggs and offspring is provided by others, may live longer and produce more offspring over a lifetime (Andersson 1984, Åhlund and Andersson 2001). However, because brood parasites abandon the care of their offspring to others, the selection of suitable hosts to raise their young has direct fitness consequences. Determination of where females choose to lay their eggs and how their decisions are made is important in our understanding of brood-parasite behavior.

If brood parasitism is to be evolutionarily advantageous, the parasites should select host species and nest sites that maximize the probability of their offspring's survival (Hauber 2000). Some parasitic species are generalists that employ a "shotgun" strategy

to randomly distribute their eggs among host nests (e.g., *Molothrus* spp.; Rothstein 1976, Kattan 1997). However, this approach may be favored only when host defenses in the avian community are not highly developed and when brood parasites have especially high fecundity. When host defenses are present or when brood parasites have low fecundity, specialized strategies and nonrandom host selectivity should evolve over time (Rothstein 1990, Davies 2000, Krüger 2007).

Brood parasites must overcome several challenges to be successful. They should select host species that have an appropriate diet to feed their offspring and that have an incubation length greater than or equal to their own. Suitable hosts must be in sufficient abundance and density to make parasitic laying possible, and the breeding cycle of the brood parasite must be in synchrony with that of the host. Brood parasites must also avoid or overcome host defenses such as aggressive nest defense and egg rejection (Rothstein 1990, Sealy and Bazin 1995, Sorenson 1997). Brood parasites may increase their fitness further if they are able to make finer-scale laying decisions such that they parasitize higher-quality parents (Soler et al. 1995, Avilés 2008, Polačiková et al. 2009) or preferentially lay in safer nest sites (Hauber 2001, 2009; Pöysä 2006).

Many of the challenges of selecting suitable hosts are resolved when brood parasites lay their eggs in the nests of conspecifics. Conspecific brood parasitism (CBP) accounts for 70% of all known taxonomic diversity of brood parasitism (234 species CBP vs. 100 obligate interspecific brood parasites; Yom-Tov and Geffen 2006) because fewer adaptations are required to parasitize individuals of the same species. However, CBP still requires sufficient availability of host nests (Lyon 2003) and that hosts are capable of incubating and caring for additional young. This may explain why CBP is biased toward colonial species with precocial young (Rohwer and Freeman 1989, Yom-Tov 2001). However, even in CBP it may be evolutionarily advantageous for parasites to discriminate among potential hosts to find the optimal location to deposit their eggs.

Nest predation is a primary selective force in shaping avian nesting behavior (Ricklefs 1969; Martin 1988, 1993), and recent studies have examined how nest predation influences the frequency and distribution of parasitic eggs among nest sites (Pöysä 2003, 2006; Roy Nielsen et al. 2008). The "risk assessment hypothesis" posits that when nest predation differs among nest sites, individuals may be able to increase an egg's probability of survival by preferentially laying in safe nest sites (Pöysä 1999, Pöysä and Pesonen 2007). To date, empirical support for this hypothesis has been restricted to cavity-nesting birds, and it is unknown whether this concept can be generalized to other groups, such as ground-nesting species.

We attempted to assess whether or not Common Eiders (*Somateria mollissima dresseri*) that engage in parasitic laying preferentially deposited their eggs in safe nest sites (i.e., sites with low predation risk). Conspecific brood parasitism is frequent in Common Eiders (Robertson et al. 1992, Bjorn and Erikstad 1994, Waldeck et al. 2004), and birds at our study area nest in habitats that vary in their vulnerability to nest predation. Our objectives were to (1) compare rates of CBP among nesting habitats, (2) determine whether levels of CBP were correlated with differences in reproductive success among those habitats, and (3) determine whether parasitized and nonparasitized nests differed in their probability of nest survival. Assuming that nest parasites preferentially lay eggs in safe nest sites, we predicted higher rates of CBP at nest sites that offered the most protection from predators.

Methods

Study site.—Our study was conducted in Table Bay (53°40′N, 56°26′W; Fig. 1), Labrador, Canada, in 2007. This area supports the largest number of nesting Common Eiders of the *dresseri* subspecies on the Labrador coast (Lock 1986). Common Eiders nest on small (<12 ha) coastal islands in three main habitat types: (1) dense woody vegetation of dwarf spruce (*Picea* spp.) and Balsam Fir (*Abies balsamea*) that ranges from 1 to 3 m in height; (2) open habitats characterized by a mix of grassy, herbaceous, and heath vegetation (e.g., Common Cowparsnip [*Heracleum maximum*], Scottish Licorice-root [*Ligusticum scoticum*], and Black Crowberry [*Empetrum nigrum*]) that rarely exceeds 40 cm in height; and (3) artificial wooden nest shelters ($1.2 \times 0.9 \times 0.25$ m). Approximately 700 artificial nest shelters were located on study islands in the Table Bay area at the time of our study. Although the number and placement of shelters varied, our sampling regime (see below) enabled us to obtain a representative sample of nests across our study islands.

Nest searches.—Islands were searched systematically for nests during the early laying period. We limited the total number of marked nests to every other nest during each island visit in order to minimize disturbance of the population. For each marked nest, we recorded the number of eggs present and numbered the eggs with indelible ink according to the degree of egg staining (Cooper 1978). The darkest or dirtiest egg was assumed to have been laid first. Nest age was determined by candling eggs (Weller 1956). We marked nest bowls using a small wooden stake pushed
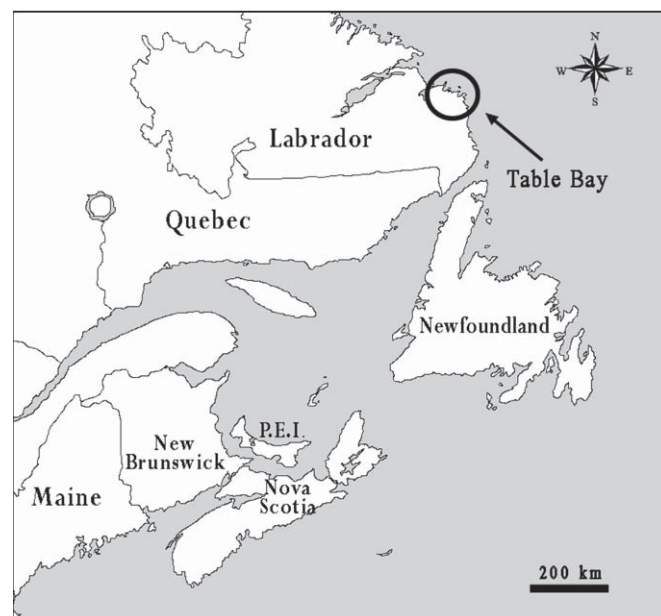

Fig. 1. Map showing the Table Bay study area (circled) in Labrador, Canada, where our study of Common Eider nest survival and conspecific nest parasitism was conducted in 2007.

into the ground under the nest bowl and recorded nest locations using a global positioning system to facilitate revisits. Nest initiation dates (NID) and predicted hatch dates were calculated by assuming an incubation length of 26 days (Guignion 1968) and a laying interval of one egg per day (Cooch 1965, Swennen et al. 1993). Before leaving the nest site, we covered the eggs with down and nest materials to insulate them and reduce their visibility to avian predators. We revisited nests periodically (every 3 or 4 days) during laying to determine nest status and to check for additional eggs. The revisitation rate was selected to limit observer effect on nest survival and CBP. Final clutch size (CS) was the number of eggs present when incubation began.

Nests were revisited after hatch to determine nest fates. Nests were considered successful if they contained eggshell fragments and egg membranes that separated easily from the shell (Klett et al. 1986, Mabee 1997). We assumed that nests had failed if they lacked signs of successful hatching or contained depredated eggs (broken eggshells with yolk or blood on them) or abandoned eggs. We excluded nests that could not be relocated ($n = 3$) and nests that we suspected were abandoned as a result of our research activities (specifically, when the female was flushed from the nest during egg laying and the nest was found abandoned on the subsequent visit; $n = 3$).

Albumen sampling and electrophoresis.—We used isoelectric focusing (IEF) electrophoresis of egg albumen to identify clutches that contained parasitic eggs. We obtained egg albumen samples from every nest we encountered that was <5 days into incubation, until we reached target sample sizes in each of the three main nesting habitats (~15 nests habitat^{-1}). Albumen samples were collected over 8 days (8–16 June). Previous work had shown that albumen sampling does not affect egg hatchability if it is done early in incubation (Andersson and Åhlund 2001, Waldeck et al. 2004), and therefore we limited sampling to nests that were <5 days into incubation. A small hole was made in the blunt end of the egg using a sterile pushpin, and ~0.3 mL of albumen was extracted using a syringe. The hole was sealed with cyanoacrylate glue (super glue) and was left to dry before the eggs were returned to the nest. We obtained albumen from all eggs within a clutch beginning at the date of nest discovery. We revisited nests 3 or 4 days after the initial visit to obtain albumen samples from any new eggs, and we continued nest visits until albumen had been obtained from the entire clutch. Albumen samples were stored frozen until electrophoresis. We did not analyze albumen from nests that failed before incubation had begun, because final CS could not be determined. However, these nests were included in the analysis of nest survival (see below).

Albumen samples were run on gels with a broad-range pH gradient (Ready-Gel pH 3–10; Bio-Rad, Hercules, California). The IEF methods were optimized for protein load and staining–destaining methods. Five microliters of each albumen sample was buffered with 10 µL of 50% v/v glycerol. Two Ready-Gels were loaded into a Bio-Rad Miniprotean apparatus. Cathode buffer (20 mM lysine [free acid, Sigma L5501] and 20 mM arginine [free acid, Fluka 11009]) was added to the upper chamber, and anode buffer (7 mM phosphoric acid) was added to the lower chamber. The wells of the precast gel were rinsed with buffer prior to loading the samples. All eggs from the same clutch were run side by side on the same gel. One well per gel was loaded with 5 µL of IEF

standard (BroadRange pI 4.45–9.96; Bio-Rad). Gels were run in a stepwise manner with voltages of 100 V for 60 min, 250 V for 60 min, and 500 V for 30 min, at a current of 5–25 mA. After electrophoresis, each gel was placed in 50 mL of IEF staining solution (Bio-Rad) and incubated for 45 min on a shaking platform. The stain was then removed and 50 mL of destaining solution (40% methanol, 10% acetic acid) was added to each gel. Gels continued to be incubated on the shaking platform and the destaining solution was changed every 2 to 3 hours until all background stain had been removed from the gel. Gels were placed in distilled water overnight before banding patterns were analyzed. The IEF trials were repeated twice to determine that the numbers of visible bands were consistent among gel runs.

Albumen proteins are exclusively of maternal origin (White 1991). All eggs from a single female have identical protein band patterns, and differences in albumen protein band patterns can be used to identify eggs laid by different females (Andersson and Åhlund 2001, Pilz et al. 2005, Waldeck and Andersson 2006). We scored a nest as being parasitized if it contained at least one egg of different maternal origin. The most common albumen banding pattern in a clutch was considered to have originated from the host (Andersson and Åhlund 2001, Waldeck et al. 2008). We did not explore relatedness between hosts and parasites.

Statistical analyses.—We tested for normality of CS and NID data using the Shapiro-Wilks statistic (PROC UNIVARIATE; SAS Institute 2001). The CS and NID data were not normally distributed, and transformations did not improve normality. Therefore, we used Kruskal-Wallis tests to check for differences in CS and NID among habitats (PROC NPAR1WAY; SAS Institute 2001) and used Bonferroni-adjusted Wilcoxon two-sample tests for post hoc comparisons.

We conducted two separate nest-survival analyses to estimate daily survival rates (DSR) for (1) all nests encountered and (2) the subsample of nests in which we determined egg maternity using IEF. We used the Nest Survival option in program MARK (White and Burnham 1999) to estimate DSR and used the logit-link function for all models. Model selection was based on quasi-likelihood Akaike's information criterion (AIC) adjusted for sample size and overdispersion (QAIC$_c$; Akaike 1973, Burnham and Anderson 2002). Models were adjusted for overdispersion using the variance inflation factor ($\hat{c}$) from our most parameterized model (Anderson et al. 1994, Burnham and Anderson 2002). There is currently no consensus on how to estimate extrabinomial variation in nest survival data (Dinsmore et al. 2002), but $\hat{c}$ can be used as a conservative method of estimating overdispersion (Schmidt et al. 2006) to avoid selecting a more parameterized model than is supported by the data (Anderson et al. 1994).

In the analysis of all nests encountered, we constructed a set of 18 candidate models in a three-step procedure. First, we examined the effects of nest habitat, island, and albumen sampling on nest survival. We compared the fit of models in which DSR was constant across all nests {S } or varied according to nest habitat {S$_{Hab}$} or island {S$_{Island}$}. We also examined models in which DSR varied according to whether the nests had been sampled for egg albumen {S$_{Alb}$}. We included additive and interactive models between both nest habitat and island with albumen sampling.

Second, for the most parsimonious model {S$_{Hab}$}, we tested for variation in DSR in relation to nest age. Because nesting was highly

synchronous (see below), the effects of nest age and calendar date on DSR could not be differentiated. We assumed that temporal trends reflected the effect of nest age on DSR. We used the following three forms of models to constrain DSR as a function of nest age: (1) linear, where nest survival changed in relation to nest age at a constant rate; (2) quadratic, where nest survival was highest during mid-incubation and lower toward the beginning and end of incubation; and (3) pseudothreshold, where nest survival increased at a constant rate to a point at which the effects of nest age neared, but did not reach, an asymptote. The pseudothreshold model allowed us to account for changes in DSR that were due to differences in female behavior between the laying and incubation periods.

Finally, we added CS and NID as covariates to the most parsimonious model {$S_{Hab+LnAge}$}. All covariates were standardized in MARK. We considered CS as both a linear and a quadratic covariate and assessed the interaction between linear and quadratic CS covariates and nest habitat. Quadratic covariates allowed us to test for the presence of an optimal CS (see Franklin et al. 2000). Because of nest failure during the initiation period, we were unable to obtain final CS values for some nests ($n = 17$; open habitats = 7, woody vegetation = 6, nest shelters = 4). For these nests, we replaced the missing CS values with the mean CS for the nests' habitat category. Doing so reduces the variance slightly but does not change the mean of the observed values (Little and Rubin 2003). We used model averaging to obtain estimates of DSR for nests (Burnham and Anderson 2002). We obtained overall nest survival probabilities for habitats and CS values using the product of model-averaged DSRs and derived confidence limits using the delta method (Seber 1982).

We used the chi-square test for goodness-of-fit to test whether nest parasitism was randomly distributed among habitats, and MARK to calculate overall nest survival probabilities for parasitized and nonparasitized clutches using the subsample of nests used in the IEF analysis ($n = 40$). Sample size limited the complexity of candidate models; therefore, we pooled nests from all habitats and estimated nest survival and compared 95% confidence intervals (CI) using a model with a single fitted parameter for parasitism.

Results

We monitored 239 Common Eider nests during the study (Table 1). Clutch size differed among habitats ($\chi^2 = 17.37$, df = 2, $P < 0.01$), with nests in shelters having larger clutches than nests in open habitats or woody vegetation (Table 1; nest shelters vs. open habitats: $Z = 3.92$, $P < 0.01$; nest shelters vs. woody vegetation: $Z = 2.70$, $P = 0.07$; open habitats vs. woody vegetation: $Z = -1.89$, $P = 0.06$). Nest initiation dates ranged from 31 May to 20 June 2007 and differed among habitats ($\chi^2 = 18.71$, df = 2, $P < 0.01$). Post hoc comparisons revealed that nests were initiated earlier in shelters than in the two other habitats (nest shelters vs. open habitats: $Z = -3.15$, $P < 0.01$; nest shelters vs. woody vegetation: $Z = -4.15$, $P < 0.01$; open habitats vs. woody vegetation: $Z = -0.68$, $P = 0.50$). The NIDs did not differ between albumen-sampled nests and non-albumen-sampled nests in nest shelters ($Z = 0.29$, df = 1, $P = 0.78$) or in open habitats ($Z = -0.64$, df = 1, $P = 0.53$), but they were earlier in albumen-sampled nests than in nonsampled nests in woody vegetation ($Z = -3.80$, df = 1, $P < 0.01$). Hence, our sampling was biased toward earlier nesters in the latter habitat. However, the overall timing of IEF sampling did not differ among habitats ($\chi^2 = 4.02$, df = 2, $P = 0.13$).

Overall apparent nest success for the laying and incubation period was 75% (180 of 239). Nest failure was caused by predation (69%; 41 of 59 marked nests) and nest abandonment (31%; 18 of 59 marked nests). Only avian predators were present at our study site—for example, Greater Black-backed Gulls (*Larus marinus*), Herring Gulls (*L. argentatus*), and Common Ravens (*Corvus corax*). The results of model selection suggest that nest survival varied among habitats, rather than among nesting islands (Table 2). Albumen sampling did not negatively affect nest survival. Top models (QAIC$_c$ weight ≈ 1.00) for nest survival included additive effects of habitat, clutch size, pseudothreshold age trend, and NID, as well as interactions between habitat and CS (Table 2). Daily nest survival was lowest during the egg-laying period and increased over the course of the nesting period (Fig. 2). Nests initiated earlier had higher survival than those initiated later ($\beta_{NID} = -0.09$; 95% CI: -0.18 to 0.002). Model-averaged nest survival estimates indicated that nest survival was highest in woody vegetation (0.70; 95% CI: 0.50–0.89), followed by nest shelters (0.51; 95% CI: 0.28–0.75) and nests in open habitats (0.34; 95% CI: 0.09–0.58). The results of model averaging suggest that nest survival was highest for clutches slightly below mean CS, with a general decline in nest survival as CS increased (Fig. 3). Nest survival for all clutch sizes was lower in open habitats than in nest shelters or dense woody vegetation (Fig. 3).

Nest parasitism.—In total, 55% of sampled nests (22 of 40) contained eggs from multiple females, and 18% of eggs (37 of 200)

TABLE 1. Number of nests, mean nest initiation dates, and mean final clutch sizes for Common Eiders nesting in three habitats (nest shelters, open grassy vegetation, and dense woody vegetation) at Table Bay, Labrador, Canada, in 2007.

Parameter	Overall[a]	All nests			Albumen-sampled nests[b]		
		Nest shelters	Open grassy vegetation	Dense woody vegetation	Nest shelters	Open grassy vegetation	Dense woody vegetation
Nests (*n*)	239	79	72	88	14	11	15
Nest initiation date (NID)	8 June	7 June	9 June	9 June	7 June	8 June	7 June
Julian date ± SD	159.2 ± 3.6	157.9 ± 4.0	159.7 ± 3.5	160.0 ± 3.0	157.8 ± 2.1	159.2 ± 1.9	157.6 ± 1.2
Clutch size (CS) ± SD	4.5 ± 1.4	4.9 ± 1.6	4.0 ± 1.3	4.4 ± 1.2	5.5 ± 1.1	4.4 ± 0.8	5.0 ± 2.1
Minimum CS	1	1	1	2	4	3	3
Maximum CS	10	10	8	10	7	6	10

[a] Includes nests from all habitats.
[b] Nests from which albumen samples were analyzed, a subset of the total 239 surveyed nests (see text).

TABLE 2. Candidate models of Common Eider nest survival for 239 sampled nests at Table Bay, Labrador, Canada, in 2007. Parameter estimates included nest habitat (Hab), nesting island (Island), the effect of albumen sampling (Alb), linear age trend (Age), quadratic age trend (Age^2), pseudothreshold age trend (LnAge), nest initiation date (NID), optimal nest initiation date (NID^2), clutch size (CS), optimal clutch size (CS^2), and constant daily survival. Models are ranked in accordance with QAIC$_c$ values ($ĉ$ adjusted to 1.22) and are denoted as additive models (+) or models with single and interactive effects (*). K = number of estimable parameters.

| Model	K	ΔQAIC$_c$[a]	QAIC$_c$ weights	QDeviance
$S_{(Hab+LnAge+NID+CS^2)}$	8	0.00	0.26	235.12
$S_{(Hab+LnAge+NID+CS)}$	7	0.10	0.25	237.23
$S_{(Hab+LnAge+NID+CS^2+Hab*CS^2)}$	12	0.93	0.17	228.00
$S_{(Hab+LnAge+CS^2)}$	7	1.30	0.14	238.42
$S_{(Hab+LnAge+CS)}$	6	1.90	0.10	241.03
$S_{(Hab+LnAge+NID+CS+Hab*CS)}$	9	3.93	0.04	237.04
$S_{(Hab+LnAge)}$	5	5.21	0.02	246.35
$S_{(Hab+LnAge+NID)}$	6	6.52	0.01	245.66
$S_{(Hab+Age)}$	5	7.00	0.01	248.14
$S_{(Hab+Age^2)}$	6	7.94	0.00	247.07
$S_{(Hab)}$	4	11.69	0.00	254.84
$S_{(Hab+Alb)}$	5	13.60	0.00	254.74
$S_{(.)}$	2	14.50	0.00	261.66
$S_{(Alb)}$	3	16.44	0.00	261.59
$S_{(Island)}$	8	16.63	0.00	290.61
$S_{(Hab*Alb)}$	7	17.18	0.00	254.30
$S_{(Island+Alb)}$	9	18.61	0.00	290.57
$S_{(Island*Alb)}$	12	23.94	0.00	289.77

[a] Lowest QAIC$_c$ value = 251.71.
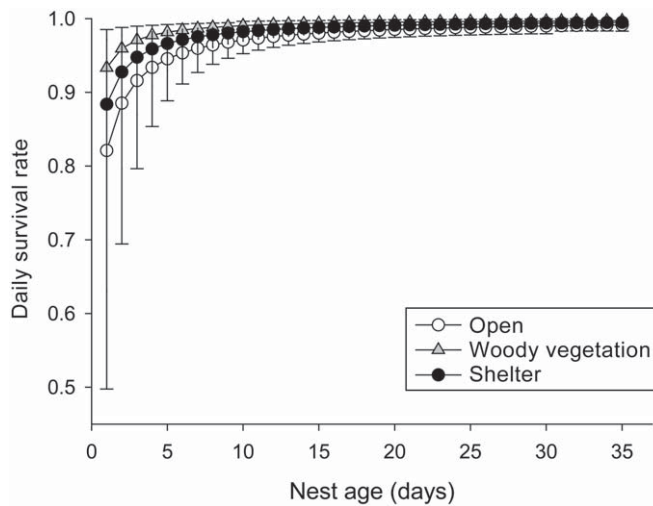
FIG. 2. Estimates of daily survival rates of Common Eider nests and 95% confidence intervals from three different nesting habitats at Table Bay, Labrador, Canada, in 2007. Values were calculated using the logit-link function and are the weighted averages based on 18 candidate models.
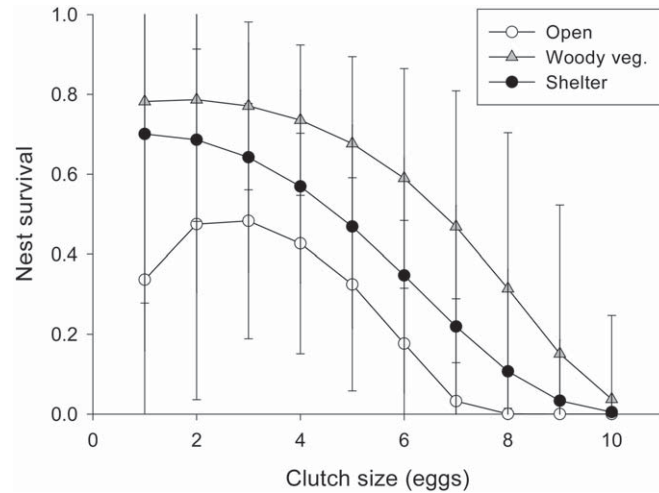

FIG. 3. Influence of clutch size on nest survival as predicted by models for Common Eider nests in three different habitats at Table Bay, Labrador, Canada, in 2007. The relationship is based on weighted model averages. Data were backtransformed from the logit scale, and confidence limits were derived using the delta method.

were laid parasitically. An average of 1.7 eggs nest^{-1} were added to parasitized nests. Most nests of mixed maternity contained a single foreign egg (55%; 12 of 22 nests). Five nests contained two parasitic eggs, and another five nests contained three parasitic eggs. Three nests contained eggs from three different females. Parasitic laying was not distributed evenly among habitats ($\chi^2 = 18.64$, df = 2, $P < 0.01$). Nests in shelters had the highest frequency of brood parasitism (78%; 11 of 14 nests), versus 54% of nests (6 of 11) in open habitats and 33% of nests (5 of 15) in woody vegetation. Overlapping 95% CIs suggest that nest survival of parasitized nests and nonparasitized nests did not differ (0.65 [95% CI: 0.41–0.83] and 0.58 [95% CI: 0.33–0.80], respectively). All parasitic eggs were deposited during the egg-laying period or during the first days of incubation, and most parasitic eggs (73%; 27 of 37) were laid before our initial nest visits. We were unable to determine the exact timing of brood parasitism during the egg-laying sequence because we found few nests at the one-egg stage, and our nest visits were limited to once every 3 to 4 days. However, because we conducted nest checks throughout incubation, we could confirm that no eggs were deposited in nests after the main egg-laying period.

DISCUSSION

Our estimated rate of CBP (55%) is among the highest reported for Common Eiders (cf. 42% and 31%, respectively, in Robertson et al. 1992, Waldeck and Andersson 2006). Nest parasitism at our study site was not evenly distributed among habitats and did not follow the pattern predicted by the risk assessment hypothesis (Pöysä 1999, 2006; Pöysä and Pesonen 2007). Nests in dense woody vegetation had the highest rates of nest survival but the lowest frequency of CBP—results that were inconsistent with our initial predictions. On the other hand, we observed higher-than-normal rates of CBP in nest shelters, compared with other habitats. Although nest shelters were a relatively safe nesting environment in

comparison to open habitats, we suggest that visibility and availability of suitable host nests (Semel et al. 1988, Lyon 2003, Roy Nielsen et al. 2006a) played more important roles than nest safety in influencing where nest parasites deposited their eggs.

Nest-site safety vs. visibility.—Nest safety is a primary selective force in shaping habitat selection (Ricklefs 1969; Martin 1988, 1993) and, thus, can influence CBP behavior (Pöysä and Pesonen 2007, Roy Nielsen et al. 2008). Recent studies suggest that brood parasites can increase the probability of their eggs' survival by preferentially depositing eggs in safe nest sites (risk assessment hypothesis; Pöysä 1999, 2006; Pöysä and Pesonen 2007). Central to this hypothesis is the premise that nest parasites gain information about nest-site safety through nest prospecting (Robertson 1998, Pöysä 2006, Roy et al. 2009). Information gathered during prospecting, such as the presence of a female at a site (Wilson 1993), the presence of eggs, or evidence of past success, may be useful cues when a safe nest site is selected. However, unlike cavity nesters that prospect for nest sites at the end of the season (Eadie and Gauthier 1985, Zicus and Hennes 1989, Pöysä 1999), Common Eiders prospect upon arrival at breeding areas (Robertson 1998). We suggest that shelters are used more by parasites because they (1) are highly visible and easily found and observed for host activity, (2) provide protection against avian nest predators and increase the probability that a parasite will find a host nest during laying, and (3) protect evidence of previous nesting attempts from being scattered by wind and precipitation, making shelters attractive to both normal nesters and parasites (see Roy et al. 2009, Fast et al. 2010). This supports the notion that nest visibility strongly influences CBP (Semel et al. 1988, Semel and Sherman 1995) and that nests in open areas are more likely to be parasitized than those in more concealed locations (Payne 1977). Although brood parasites could have potentially benefited from laying in the safest sites (i.e., nests in dense woody vegetation), the benefits may have been outweighed by the increased effort required to locate these nests (Rohwer and Freeman 1989).

In the absence of parasite strategies that target more concealed nests (e.g., Fiorini et al. 2009), nests in more exposed areas would, by chance alone, have been more likely to receive greater prospecting than more concealed nests. Recent evidence suggests that parasitic laying in combination with normal nesting (i.e., dual strategy; Sorenson 1991) may be a commonly used strategy (Reichart et al. 2010). Because normal nesting reduces the opportunity for individuals to parasitize the nests of others (Westneat and Sherman 1993), we suggest that individuals that engage in a dual strategy would benefit most if they used highly visible nest sites because this minimizes time spent searching for suitable host nests so that most of their time is spent attending to their own nests. This may be particularly important for colonial-nesting species that exhibit synchronous nest initiation.

Nest availability.—Successful parasitism requires temporal and spatial nest-site availability (Lyon 2003, Shaw and Hauber 2009). Because of the synchronous nature of nest initiation in Common Eiders (Cooch 1965, Swennen et al. 1993, present study), parasites have a relatively small window of opportunity to find suitable host nests. Common Eiders also exhibit a high degree of nest attendance before clutch completion and almost continuous attendance once incubation has begun (Swennen et al. 1993, Criscuolo et al. 2002, Bolduc and Guillemette 2003). Although

these behaviors are thought to have evolved to reduce the potential for egg predation (see Korschgen 1977, Andersson and Waldeck 2006), they likely limit exposure to brood parasites. Our results seem to support this idea, given that nest survival increased considerably at the onset of incubation and no eggs were laid parasitically after the main egg-laying period.

Behaviors that restrict opportunities for CBP and the small clutch size of Common Eiders ($\bar{x}$ = 4.5) likely contributed to the relatively low number of parasitic eggs per nest. We found no reductions in nest survival attributable to CBP, despite an overall high frequency of CBP (see also Robertson 1998, Roy Nielsen et al. 2006b). This may partially explain why aggressive interactions between female Common Eiders do not seem to occur (Robertson 1998), in contrast with other host–parasite systems (e.g., Sorenson 1997).

Conclusions and future studies.—Brood parasites appear to be selective in choosing where they lay their eggs. However, the choice of nest site seems to be based on overall nest visibility rather than nest-site safety. Although IEF helped to determine the frequency of nest parasitism, genetic data combined with molecular techniques will be necessary to understand whether Common Eiders employ dual nesting strategies (e.g., Reichart et al. 2010). Future studies that examine differences between hosts and brood parasites in terms of embryo quality and incubation effects (e.g., Pilz et al. 2005, DuRant et al. 2010) and recruitment of parasite and host young would be helpful in elucidating the ultimate benefits of CBP.

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