Journal of Ethology (2018) 36:251–258
https://doi.org/10.1007/s10164-018-0555-y

ARTICLE

Costs and response to conspecific brood parasitism by colonial red-breasted mergansers

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Received: 24 April 2018 / Accepted: 22 July 2018 / Published online: 31 July 2018

Abstract

Costs of conspecific brood parasitism (CBP) are expected to be influenced by a species' life history traits. Precocial birds lay large clutches, and clutches that have been enlarged by CBP can affect host fitness through a longer incubation period, displaced eggs, and lower hatching success. We examined costs and response to CBP by hosts in a population of colonial red-breasted mergansers (*Mergus serrator*; $n = 400$ nests over 8 years) within which 29% of parasitized clutches were enlarged considerably (≥ 15 eggs). Length of the incubation period did not increase with clutch size. The mean number of eggs displaced from a parasitized nest during incubation (2.8) was 2× greater than at an unparasitized nest (1.4). Hatching success declined by 2% for each additional egg in the nest. Thus, for a nest with ≥ 15 eggs, one or more fewer host eggs hatch relative to an unparasitized nest with the same number of host eggs, assuming equal probability of success for all eggs. Hosts were 40% more likely to desert nests receiving 2 or 6 experimental eggs relative to unparasitized control nests, although it is unknown whether hens deserting a nest renested elsewhere. Our study indicates that costs of CBP to hosts during nesting may be limited to those red-breasted mergansers incubating the largest clutches (≥ 15 eggs), and it raises questions about the adaptive significance of deserting a parasitized clutch.

Keywords Breeding behavior · Colonial nesting · Conspecific brood parasitism · Fitness costs · *Mergus serrator* · Red-breasted merganser

Introduction

The laying of eggs in the nest of another individual of the same species, known as conspecific brood parasitism (CBP), can succeed as a reproductive tactic if it leads to fitness advantages for the parasite (Lack 1968; Eadie et al. 1988; Pöysä et al. 2014). CBP, however, may depress the fitness of the host, who must care for its offspring and those of the parasite (Payne 1977). The type of costs of CBP to hosts is expected to vary with different patterns of parental care (Rohwer and Freeman 1989). Altricial birds lay small clutches and invest much energy into caring for their young (Jetz et al. 2008). Enlarged broods thus increase demand for parental care and can reduce host fledgling success (Tucker et al. 2017). To counter these negative effects, altricial birds have evolved defense against nest parasitism, using tactics such as ejection of foreign eggs (Lombardo et al. 1989).

In contrast to altricial birds, the costs of caring for additional newly hatched young are small for species with self-feeding young (Sayler 1992), which may help to explain the common occurrence of CBP among precocial birds and notably waterfowl (Anseriformes; Rohwer and Freeman 1989; Eadie and Savard 2015; Lyon and Eadie 2017). CBP has been documented in ~ 50% of Anseriformes (Yom-Tov 2001). Waterfowl can tend large broods without compromising fledging success (Eadie 1989; Briggs 1991) or recruitment (Dugger and Blums 2001). CBP may even benefit some hosts. For example, parasite-derived hatchlings can dilute the risk of predation to the host's young (Munro and Bédard 1977).

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Contrary to the brood-rearing period, CBP is potentially costly to precocial birds during nesting. Waterfowl lay large clutches (Jetz et al. 2008), and clutches that have been considerably enlarged by nest parasitism can take longer to incubate, forcing females to expend more energy in incubation (Hepp et al. 1990; Roy Nielsen et al. 2006). Hatching success can be reduced when incubation of large clutches is incomplete or if eggs are broken or displaced from the nest (Eadie 1989; Waltho and Coulson 2015). Hosts can avoid prospects of poor reproductive success in large clutches by abandoning a nest (Weller 1959; Jaatinen et al. 2009), and nest desertion can be adaptive if a host abandons her clutch early on and lays her remaining eggs in a new nest (McRae 1995).

A number of studies have addressed costs and responses to CBP in waterfowl using observational data (reviewed in Sayler 1992). Observations at unmanipulated nests can reveal interesting correlations between CBP and host behavior, but they do not provide direct evidence that a particular behavior is caused by the addition of foreign eggs, as it may be related to factors other than nest parasitism such as timing of breeding or female quality (Dugger and Blums 2001). In contrast, the experimental addition of eggs to a nest can reveal a cause-and-effect relationship between CBP and host behavior. Few studies have incorporated both experimental and observational data in their assessment of costs and response to nest parasitism (but see Eadie 1989; Briggs 1991; Dugger and Blums 2001). Accordingly, the net effect of enlarged clutches on precocial hosts remains poorly understood (Lyon and Eadie 2008).

The frequency of CBP can be particularly high for waterfowl that breed colonially, and this is likely reflected in the ease by which parasitic females encounter nests and potential hosts. Coloniality thus provides an interesting ecological context for the study of costs of CBP. We examined nest parasitism among colonial red-breasted mergansers (*Mergus serrator*) at Kouchibouguac National Park in eastern Canada. Here, birds breed at high density (up to 30 nests ha^{-1}) and CBP is frequent. Young and Titman (1988) estimated that 64% of nests at the site were parasitized, and that 40% of all nests exceeded mean host clutch size (9 eggs) by ≥ 3 eggs. We used experimental nest parasitism and observations at unmanipulated nests to: (1) determine whether CBP is costly to host red-breasted mergansers (e.g., longer incubation period, eggs displaced from the nest, lower hatching success); and (2) to determine whether nest abandonment during the egg-laying cycle represents a potential behavioral response to nest parasitism.

Materials and methods

Study area

We studied red-breasted mergansers nesting on the Tern Islands at Kouchibouguac National Park, New Brunswick (46.7769°N, 64.8752°W). The Tern Islands consist of 3 small, neighboring islands (total 3 ha) composed of sand. Red-breasted mergansers nest on the ground in dense stands of marram grass (*Ammophila breviligulata*; Craik and Titman 2009). During our study, an average of 50 nests (range 32–83) were monitored annually at the site (Table 1).

Field procedures

Observations at unmanipulated nests

During 2003–2006 and 2013–2016, red-breasted merganser nests were found by searching on foot, beginning in May with initiation of the first nests (Fishman et al. 2011). Each nest was revisited every 6–7 days during 2003-2006 and every 3–4 days during 2013-2016. Dates of nest initiation were estimated by backdating using a laying rate of 1 egg 1.5 $days^{-1}$ (Craik et al. 2015). At each visit, we recorded clutch size and noted any eggs outside the nest. Predicted hatching dates were estimated by floatation of incubated eggs (Westerskov 1950).

Table 1 Number of nests observed, nest densities, rates of conspecific brood parasitism (CBP), and proportion of nests abandoned during egg laying for red-breasted mergansers (*Mergus serrator*) on the Tern Islands, New Brunswick, Canada, 2003–2006 and 2013–2016

Year	Number of nests observed	Nest density (nests ha^{-1})	Proportion of nests parasitized[a]	Proportion of nests abandoned during egg laying
2003	48	17.2	0.83 (10/12)	0.38
2004	43	15.4	0.23 (3/13)	0.33
2005	73	26.2	0.38 (6/16)	0.40
2006	83	29.8	0.51 (20/39)	0.40
2013	41	14.7	0.42 (8/19)	0.19
2014	43	15.4	0.46 (11/24)	0.44
2015	32	11.5	0.45 (9/20)	0.29
2016	37	13.3	0.53 (8/15)	0.43

[a]From those nests at which parasitism status (parasitized or unparasitized) was determined. See "Materials and methods" for how nest parasitism was assessed in the field

We estimated the length of the incubation period by comparing hatching date to date of incubation initiation. For most nests during 2014–2016, we numbered each egg following its addition to the nest. The fate of a nest was categorized as: successful if at least one egg hatched; abandoned; or depredated, if all eggs were removed. Nest visits during egg laying occurred after 1000 hours ADT because nest video data indicated that egg-laying red-breasted mergansers are typically at the nest between 0500 and 0900 hours ADT (S. R. Craik unpublished data).

A nest was classified as parasitized if eggs were added at a rate exceeding 1 egg 1.5 days^{-1} (Craik et al. 2015). We typically noted intra-clutch variation in egg color, size, and shape for nests classified as parasitized (Sorenson 1993). In contrast, egg morphology was relatively uniform in unparasitized nests. We only considered active nests discovered during the earliest stages of egg laying (≤4 eggs; median 2 eggs). We may have missed some nest parasitism at the beginning of the host laying cycle prior to nest discovery. DNA microsatellite analyses from a sample of 10 nests indicated that our field method for detecting nest parasitism was accurate; 9 of 10 nests were classified similarly by field and genetic data (S. R. Craik unpublished data).

Experimental nest parasitism

We simulated CBP by adding painted chicken eggs to 10 active nests in 2016. Chicken eggs were generally similar in color, size, and shape to those of red-breasted mergansers. We added eggs during the earliest stages of nesting ($\bar{x}=3$ host eggs nest^{-1}) to assure that hosts had time to respond to the manipulation (Andersson and Eriksson 1982). Two treatment groups were used: (1) moderate parasitism ($n=5$ nests), in which one experimental egg was added to a nest on each of 2 days over a 3-day period (total of 2 eggs added); and (2) heavy parasitism ($n=5$ nests), in which 3 eggs were added on each of 2 days over a 3-day period (total of 6 eggs added). The magnitude of experimental nest parasitism reflected natural rates of egg additions at parasitized red-breasted merganser nests on the Tern Islands (up to 6 eggs added over 3 days). Control nests ($n=8$) received no new eggs, although they were visited at the same frequency as treatment nests to control for disturbance effect. Both treatment and control nests were selected randomly throughout the entire nest-initiation period to control for effect of timing of breeding on nest abandonment.

Data analyses

Costs of CBP

We examined whether CBP was associated with each of the following 3 potential costs to hosts: (1) greater length of incubation period; (2) greater number of eggs lost from the nest during incubation; and (3) lower hatching success for successful nests. We used linear models to determine whether each of the three cost types varied between parasitized and unparasitized nests. Year was included as a fixed effect for analyses of incubation length and hatching success. All data for the number of eggs lost at a nest were combined because of small sample sizes in some years. We also explored the relationship between clutch size (i.e., a measure of magnitude of CBP) and each of the 3 cost types using polynomial regressions (linear and quadratic). Analyses for each of the three potential costs were performed individually because different combinations of nests provided data for each cost type.

Host response to CBP

We examined the level of association between abandonment of unmanipulated nests during egg laying and: (1) the occurrence of CBP at a nest; and (2) the magnitude of CBP, measured by egg-laying rate and clutch size. Specifically, we compared the frequency of nest parasitism (% of nests parasitized) between abandoned and incubated nests with a test of equality of proportions with continuity correction. Potential differences in the magnitude of CBP between abandoned and incubated nests were examined with linear models for which egg-laying rate and clutch size were response variables, nest type (abandoned or incubated nest) was an explanatory variable, and year was a fixed effect. An analysis of covariance (ANCOVA) was used to control for covariation between clutch size and date of nest initiation because red-breasted merganser clutch size on the Tern Islands declines throughout the season (Craik and Titman 2009), and abandoned nests are initiated an average of 6 days earlier than nests reaching incubation ($t_{68}=-3.4$, $P<0.001$; 2-sample t-test). Dates of nest initiation were standardized within each year by assigning ‘Day 1’ to the day the earliest nest was initiated. We focused on host response during egg laying because nest desertion during incubation was relatively uncommon (~20% of deserted nests).

Data for the moderate and heavy nest parasitism experiments were combined because rates of nest abandonment were similar between the egg-addition treatments.

The hypothesis that raw data and regression residuals are normally distributed was evaluated with Shapiro–Wilk tests and by inspection of quantile–quantile probability plots. Variables were log transformed if normality needed to be improved. Homogeneity of variances were verified with Bartlett’s tests. We set significance levels at $P<0.05$. Analyses were performed in R 3.3.1 (R Development Core Team 2015). Values reported in the Results are mean ± SD.

Results

Rates of CBP

We confirmed nest parasitism status (parasitized or unparasitized) at 158 nests over the 8-year study. Mean annual proportion of nests that were parasitized by conspecifics was 48 ± 17% (Table 1). Most parasitic eggs were added during the egg-laying period; of 50 successful nests with marked eggs, only 5 (10%) nests received eggs after the first few days of incubation (range 1-3 foreign eggs nest^{-1}). Annual nest density varied considerably, but it did not affect the frequency of nest parasitism ($r^2 = 0.01$, $F_{1,6} = 0.01$, $P = 0.97$) or mean clutch size at incubated nests ($r^2 = 0.07$, $F_{1,6} = 1.2$, $P = 0.31$; Table 1).

Costs of CBP

Both parasitized ($n = 13$) and unparasitized nests ($n = 9$) had a mean incubation period of 31 days ($F_{3,18} = 10.1$, $P = 0.39$; ANOVA; Table 2), and incubation period was unaffected by clutch size ($r^2 = 0.01$, $F_{1,30} = 0.1$, $P = 0.72$). At the extremes, 2 females incubated successful clutches of 16 eggs for 31 and 32 days, respectively, and 2 females incubated clutches of 9 eggs for 32 days. Sixty percent of 54 parasitized nests lost ≥ 1 egg during incubation, whereas only 22% of 63 unparasitized nests lost eggs. Of nests losing ≥ 1 egg, the number of egg losses at parasitized nests was twice that of unparasitized clutches ($F_{2,42} = 4.8$, $P = 0.01$; Table 2; ANOVA), and the number of eggs lost increased with clutch size ($r^2 = 0.11$, $F_{1,44} = 6.4$, $P = 0.01$).

Considering host and parasite eggs together, hatching success at parasitized nests was similar to that at unparasitized nests ($F_{3,102} = 0.7$, $P = 0.57$; ANOVA; Table 2). Parasitized nests generally produced more ducklings than unparasitized nests, at least partially because clutch size at parasitized nests was ~ 50% larger than for the latter (mean difference of 4.4 eggs; Fig. 1). The proportion of all eggs that hatched in a clutch decreased by 2% for each additional egg ($Y = 0.83 - 0.02X$; $r^2 = 0.04$; $F_{1,105} = 5.6$, $P = 0.02$; Fig. 2). Based on this finding, hosts would hatch one or more fewer of their own eggs when total clutch size was ≥ 15, relative to an unparasitized nest with the same number of host eggs (assuming equal hatching success for host and parasite eggs; see "Discussion").

Host response

Unmanipulated nests

We determined the fate of 400 nests (Table 1). All nest losses during egg laying were attributed to abandonment, except for 4 nests that were depredated. On average, 36 ± 8% of nests were abandoned during the egg-laying period annually (Table 1). An abandoned nest was not more likely to be parasitized than a nest reaching incubation ($\chi^2_1 = 0.9$, $P = 0.33$, $n = 158$; test of equality of proportions). Magnitude of CBP, measured by egg-laying rate, varied between the two nest types; the egg-laying rate at parasitized nests that were eventually abandoned was 20% greater than at parasitized nests reaching incubation ($F_{1,68} = 4.8$, $P = 0.03$; ANOVA; Table 3). Clutch size at abandoned and incubated nests was similar, even after controlling for effect of date of nest initiation on clutch size ($F_{1,66} = 0.1$, $P = 0.75$; ANCOVA). Egg-laying rates and clutch sizes did not vary among years.

Experimental nest parasitism

All eight unparasitized control nests were incubated. In contrast, 4 of the 10 (40%) nests receiving 2 or 6 experimental eggs during early egg laying ($\bar{x} = 3$ host eggs nest^{-1}) were either abandoned immediately following experimental additions or they received 1-3 eggs irregularly following experimental egg additions. The irregular

Table 2 Mean (± SD) incubation period (days), number of eggs lost from the nest during incubation, and egg hatching success of successful nests between parasitized and unparasitized red-breasted merganser (*Mergus serrator*) nests on the Tern Islands, New Brunswick, Canada, 2003–2006 and 2013–2016

	Parasitized nests	Unparasitized nests	All nests
Mean incubation period (days)	30.5 ± 2.8 (13) Range 26–35	31.7 ± 1.7 (9) Range 29–34	31.0 ± 2.4 (22) Range 26–35
Mean number of eggs lost during incubation[a]	2.8 ± 2.5 (32) Range 1–11	1.4 ± 0.6 (14) Range 1–3	2.4 ± 2.2 (46) Range 1–11
Mean clutch size	13.3 ± 2.3 (49) Range 8–19	8.9 ± 1.9 (58) Range 3–12	10.9 ± 3.0 (107) Range 3–19
Mean hatching success	0.62 ± 0.25 (49) Range 0.07–1.00	0.67 ± 0.19 (58) Range 0.13–1.00	0.65 ± 0.22 (107) Range 0.07–1.00
Mean number of ducklings leaving nest	8.1 ± 3.1 (49) Range 1–13	6.0 ± 2.1 (58) Range 1–10	7.0 ± 2.80 (107) Range 1–13

Number of nests used to calculate descriptive statistics are indicated in parentheses

[a]For nests that lost ≥ 1 egg

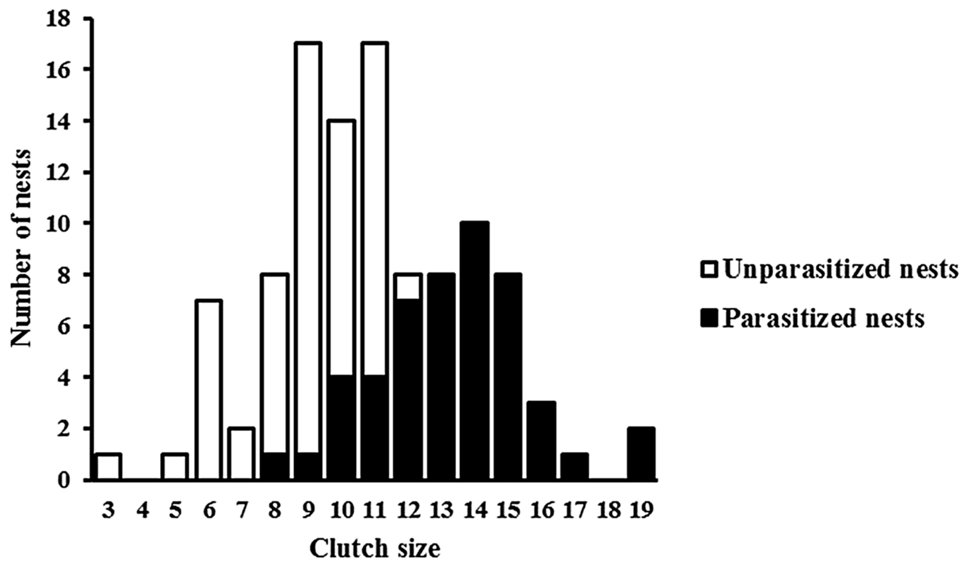

Fig. 1 Frequency distribution of clutch sizes at 58 unparasitized and 49 parasitized red-breasted merganser (*Mergus serrator*) nests on the Tern Islands, New Brunswick, Canada, 2003–2006 and 2013–2016

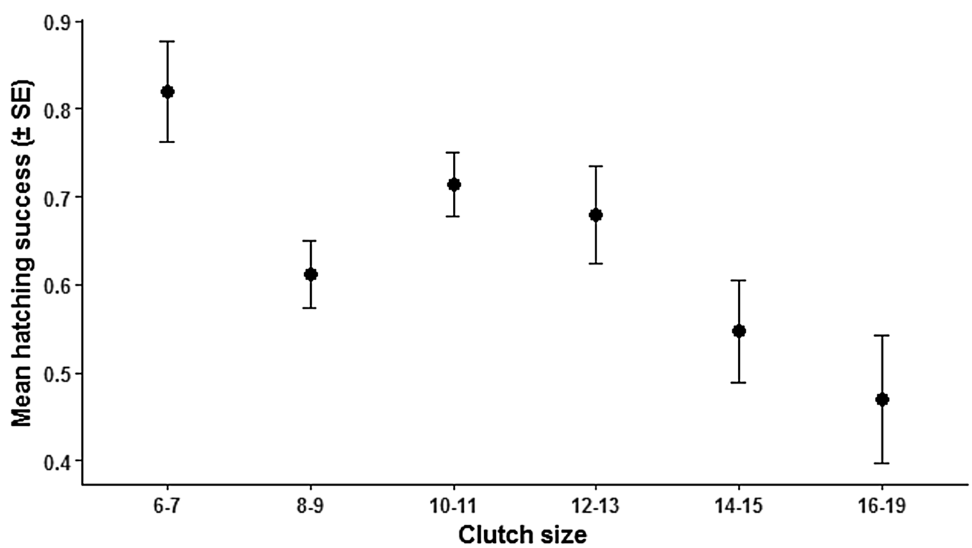

Fig. 2 Mean hatching success (± SE) declined linearly with clutch size at 105 incubated red-breasted merganser (*Mergus serrator*) nests on the Tern Islands, New Brunswick, Canada, 2003–2006 and 2013–2016

Table 3 Rates of conspecific brood parasitism (CBP) and mean (± SD) egg-laying rates and clutch sizes at abandoned and incubated red-breasted merganser (*Mergus serrator*) nests on the Tern Islands, New Brunswick, Canada, 2003–2006 and 2013–2016

	Nests abandoned during egg laying ($n = 18$)	Incubated nests ($n = 140$)
Proportion of all nests parasitized	0.61	0.46
Mean egg-laying rate (eggs laid day^{-1}) for parasitized nests	1.20 ± 0.49 Range 0.75–2.50	0.97 ± 0.25 Range 0.56–1.81
Mean clutch size for parasitized nests	12.6 ± 4.4 Range 9–25	12.4 ± 3.2 Range 6–24

additions were possibly the result of parasitic hens ‘dumping’ eggs in abandoned nests. We did not detect natural nest parasitism during the egg-laying cycle (i.e., > 1 red-breasted merganser egg added over a 1.5-day period) for each of the 4 abandoned nests and for 5 of 6 experimental nests reaching incubation.

Discussion

Costs of CBP to hosts

Determining the costs of caring for foreign eggs and young is critical for understanding the overall effect of CBP on host fitness (i.e., is CBP a truly parasitic behavior?), and the level of costs influences predictions about the evolution of nest parasitism behavior (e.g., role of kin selection; Andersson 2001; Lopez-Sepulcre and Kokko 2002). Despite this, there has been little effort to address costs of CBP in colonial waterfowl (but see Waltho and Coulson 2015). Using data from an 8-year field study and an egg addition experiment, we examined costs and response of CBP in a colonial population of red-breasted mergansers.

Egg hatching success for red-breasted mergansers on the Tern Islands declined with clutch size; egg hatchability in the largest clutches (19 eggs) was nearly 40% lower than for the smallest clutches. Reduced egg success at enlarged clutches often results from poor survival of parasite eggs added after the onset of incubation (Eadie 1989; Roy Nielsen et al. 2006), or for some species by the purposeful rejection of parasite eggs (Lyon 2003; McRae 2011). Laying by parasitic red-breasted mergansers was generally well timed with the host laying cycle as parasite eggs were rarely added after the first few days of incubation (10% of nests), and of those incubated nests receiving new eggs, all but one received ≤ 2 eggs. If a parasite egg is costly to host fitness, selection should favor its rejection shortly after being added (McRae 1995). We found little evidence that hosts rejected foreign eggs during egg laying; a total of one egg from 46 nests with marked eggs was displaced during laying, and only one experimental nest lost a chicken egg prior to incubation (S. R. Craik personal observation). Together, these observations suggest that parasitic red-breasted merganser eggs do not suffer disproportionate mortality relative to host eggs.

There were potentially important fitness costs to host red-breasted mergansers incubating heavily parasitized nests. The following example, derived from our estimates of clutch-size specific hatching success and based on equal hatchability of host and parasite eggs, illustrates these potential costs. From an unparasitized clutch of 9 eggs, 6–7 eggs may hatch. In contrast, a nest with 9 host eggs and 9 parasitic eggs should hatch 9–10 young of which only 4–5 will be those of the host. Thus, the addition of 9 parasitic eggs reduces host fitness by up to 40%. For a nest with ≥ 15 eggs, one or more fewer host eggs hatch relative to an unparasitized nest with the same number of host eggs. There may thus be a limit to the number of foreign eggs that can be added without affecting host (and parasite) hatching success. This suggestion is supported by the observation that 6 of 9 (67%) nests abandoned during incubation had ≥ 17 eggs (S. R. Craik personal observation). Nevertheless, clutches of ≥ 15 eggs represent only 29% of incubated nests that were parasitized during our study (and 13% of all incubated clutches), so host hatching success may not be affected at the majority of parasitized nests.

Deleterious effects of CBP on hatching success have been observed in other waterfowl for which nest parasitism can be frequent, notably colonial common eiders (*Somateria mollissima*; Robertson et al. 1992; Waltho and Coulson 2015) and cavity-nesting goldeneye (*Bucephala* spp.; Eadie et al. 1998) and wood ducks (*Aix sponsa;* Haramis and Thompson 1985; Semel et al. 1988). Among cavity nesters, population increases can raise the frequency of CBP and clutch sizes, which results in a decline in egg hatching success (Semel et al. 1988; Eadie 1989). In contrast, frequency and magnitude of CBP by red-breasted mergansers were unaffected by nest density, despite considerable annual variation in nest numbers on the Tern Islands. The social and/or demographic factors influencing CBP locally for red-breasted mergansers and other colonial waterfowl remain largely unexplored; their identification will contribute to our understanding of how nest parasitism behavior ultimately affects host fitness under different ecological settings (e.g., cavity nesting, ground nesting, coloniality).

What factors were responsible for greater hatching failure at enlarged red-breasted merganser clutches? More eggs can die in large clutches because of inefficient incubation (Weller 1959). Parasitized red-breasted merganser clutches with ≥ 11 eggs always have unhatched eggs, and some of these eggs fail to hatch because of embryo mortality during incubation (Young and Titman 1988). Egg losses during incubation were particularly common at parasitized nests; an average of 2.8 eggs was displaced from a parasitized nest and the rate of egg loss increased with clutch size. Predation by corvids (*Corvus* spp.) is a source of egg loss on the Tern Islands (Craik and Titman 2009), but it likely represents a small amount of total loss given that nest depredation is rare (4 of 400 nests). Eggs can be broken during incubation activities, and especially in large clutches (Weller 1959). Although we rarely witnessed broken or leaking eggs in a nest, damaged eggs can go undetected because hosts quickly remove them from the nest (Semel and Sherman 1986). Regardless of their source, displaced eggs contribute considerably to lower hatching success at enlarged red-breasted merganser clutches.

Host response to CBP

Nest abandonment was associated with magnitude of CBP but not with the occurrence of nest parasitism. We found that egg-laying rates (i.e., a measure of magnitude of CBP) at unmanipulated parasitized nests that were eventually abandoned were 20% greater than at parasitized nests reaching incubation. However, interpreting an association between CBP and nest abandonment is not straightforward because desertion of an unmanipulated nest may not necessarily be related to the addition of foreign eggs (Dugger and Blums 2001). Our nest parasitism experiment controlled for factors other than CBP that can affect a female's decision to abandon a nest (e.g., timing of breeding), allowing for the potential establishment of a cause-and-effect relationship between host behavior and nest parasitism. Indeed, red-breasted merganser nests receiving 2 or 6 experimental eggs early during the host laying cycle were 40% more likely to be abandoned than unparasitized control nests. Although our nest parasitism experiment was based on a small sample of nests ($n = 18$), it provides the first evidence that nest desertion by red-breasted mergansers can potentially reflect a host response to moderate-to-heavy CBP early during the laying cycle.

Nest abandonment can be an adaptive response to CBP if a host renests (Sorenson 1997). In her study of moorhens (*Gallinula chloropus*), McRae (1995) found support for a model predicting that when hosts are parasitized early during laying, they produce a greater number of their own offspring by abandoning the nest and completing their clutch in a new nest, relative to remaining at a parasitized nest. The renesting potential of red-breasted mergansers on the Tern Islands is unknown. However, if deserting hosts do not lay the remainder of their clutch elsewhere (i.e., in a new nest or parasitically), then egg failure in the deserted nest would constitute a cost of nest parasitism to the host.

Our assessment of costs of CBP to host red-breasted mergansers is consistent with expectations based on life history traits of waterfowl. Red-breasted mergansers lay large clutches and hatching success can be affected when clutches are parasitized. Despite this, measurable costs of CBP to host hatching success were only predicted for the ~ 30% of hens incubating the largest parasitized clutches (≥ 15 eggs). Accordingly, negative impacts of nest parasitism to fitness of the majority of hosts during nesting are likely negligible, assuming females that respond to CBP by abandoning their nest lay the remainder of their eggs elsewhere. The study provides insight into how frequent CBP can be maintained in colonial waterfowl, and it raises questions about the adaptive significance of deserting a parasitized clutch.

Acknowledgements The authors are grateful for field assistance provided by A. Beaudet, D. Bilodeau, A. Comeau, A. Constantineau, M. Deveau, K. Francis, J. Haché, A. Hanks, P-É Hébert, N. Laplante, F. LeBlanc, S. Lefrançois, B. Martin, A. Rousseau, S. Seaborn, B. Spinney, E. Titman, R. Titman, S. Titman, and A. Wood. The late O. Fraser provided sea kayaks. M. Guigueno, F. Leighton, J. Eadie, and an anonymous reviewer provided valuable comments on earlier versions of the manuscript. Funding was provided by Bird Protection Quebec, Bishop's University, Canadian Wildlife Federation, Delta Waterfowl Foundation, McGill University, Natural Sciences and Engineering Research Council of Canada (NSERC), New Brunswick Wildlife Trust Fund, North American Sea Duck Joint Venture, and Université Sainte-Anne. All grants were awarded to SRC and RDT except that from NSERC (awarded to NT). None of the funders had any influence on the content of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution at which the studies were conducted (permits # 1926 and #7329 at McGill University).

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