

## Article

# Nest sanitation behavior does not increase the likelihood of parasitic egg rejection in herring gulls

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## Abstract

Birds' behavioral response to brood parasitism can be influenced not only by evolution but also by context and individual experience. This could include nest sanitation, in which birds remove debris from their nests. Ultimately, nest sanitation behavior might be an evolutionary precursor to the rejection of parasitic eggs. Proximately, the context or experience of performing nest sanitation behavior might increase the detection or prime the removal of parasitic eggs, but evidence to date is limited. We tested incubation-stage nests of herring gulls *Larus argentatus* to ask whether nest sanitation increased parasitic egg rejection. In an initial set of 160 single-object experiments, small, red, blocky objects were usually rejected (18 of 20 nests), whereas life-sized, 3D-printed herring gull eggs were not rejected whether red (0 of 20) or the olive-tan base color of herring gull eggs (0 of 20). Next, we simultaneously presented a red, 3D-printed gull egg and a small, red block. These nests exhibited frequent nest sanitation (small, red block removed at 40 of 48 nests), but egg rejection remained uncommon (5 of those 40) and not significantly different from control nests (5 of 49) which received the parasitic egg but not the priming object. Thus, performance of nest sanitation did not shape individuals' responses to parasitism. Interestingly, parents were more likely to reject the parasitic egg when they were present as we approached the nest to add the experimental objects. Depending on the underlying mechanism, this could also be a case of experience creating variation in responses to parasitism.

**Key words:** brood parasitism, egg rejection, herring gull, nest sanitation behavior

Avian brood parasitism imposes costs on hosts, including reductions in nestling growth or survival and increases in parental workload (Dearborn 1999; Hoover and Reetz 2006; Kruger 2007; Lyu and Liang 2021). Consequently, hosts can experience strong selective pressure to reject parasitic eggs, and many host species are effective at doing so (Rothstein 1990; Yang et al. 2010; De Marsico et al. 2013). Nonetheless, host responses to parasitism vary, with rejection conspicuously absent in some species, populations, or individuals (Rothstein 1990; Medina and Langmore 2016). This variation in rejection is typically framed in the context of evolutionary lag, evolutionary equilibrium, or evolved tolerance (Peer and Sealy 2004;

Feeney et al. 2014; Medina and Langmore 2016; Stokke et al. 2016). However, rejection behavior could also be shaped by events within the lifetime of an individual host, such as learning (Soler et al. 1999; Hauber et al. 2006; Shizuka and Lyon 2010), hormone levels (Abolins-Abols and Hauber 2020a), attributes of the current clutch (Moskát et al. 2014; Yang et al. 2014; Abolins-Abols and Hauber 2020b), or interactions with the adult parasite (Strausberger and Burhans 2001). In this framework, nest sanitation behavior is a factor that could influence individuals' likelihood of rejecting parasitic eggs. Nest sanitation is the removal of debris such as fecal sacs, eggshells, plant matter, and other foreign objects that have potential

to damage eggs, facilitate microbial growth, or interfere with incubation effectiveness (Kemal and Rothstein 1988; Petit et al. 1989; Evans et al. 2016). Debris removal requires similar recognition ability and motor patterns as parasitic egg rejection (Rothstein 1975; Luro and Hauber 2017), which has 2 possible implications. First, in an ultimate sense the Nest Sanitation Hypothesis has proposed that nest sanitation behavior may be an evolutionary pre-adaptation for the recognition and removal of parasitic eggs (Rothstein 1975; Guigueno and Sealy 2012; Poláček et al. 2013; Yang et al. 2015b; Guigueno and Sealy 2017). Second, the Nest Sanitation Hypothesis also predicts a proximate, mechanistic link between the performance of nest sanitation behavior and the performance of egg rejection. This proximate link might arise in at least 2 ways. One possibility is rooted in recognition, such that nest sanitation could cause host individuals to pay more attention to nest contents and thereby become more likely to reject a parasitic egg (Yang et al. 2015a; Feng et al. 2019). Another possibility is a priming effect (Goto et al. 2014; Payne et al. 2016), in which the actual performance of nest sanitation behavior by an individual could increase the likelihood of that individual then rejecting a parasitic egg (Poláček et al. 2013).

Irrespective of mechanism, variation in nest sanitation behavior could underlie variation in rejection behavior, including how long it takes rejection behavior to evolve when a species is newly exposed to strong selective pressure from brood parasitism. This makes it valuable to study the connection between sanitation and rejection across a wide range of life histories, ecologies, and parasitism levels. To date, there have been only 4 direct tests of a proximate link between nest sanitation and egg rejection. In barn swallows *Hirundo rustica*, birds were more likely to reject an experimental parasitic egg if it was added to their clutch simultaneously with a sanitation object than if only the egg was added (Yang et al. 2015a). In contrast, the 3 other studies found no proximate effect of nest sanitation on egg rejection. In American robins *Turdus migratorius*, birds that were initially induced to remove a sanitation object from the nest did not subsequently reject a parasitic egg at higher rates than birds who were given the 2 objects in the reverse order (Luro and Hauber 2017). In brown-breasted bulbuls *Pycnonotus xanthorrhous*, rejection rate for a nonmimetic parasitic egg was not affected by the simultaneous addition of a sanitation object (Su et al. 2018). Lastly, in red-winged blackbirds *Aegialais phoenicius*, hosts never rejected an experimental egg of a brown-headed cowbird *Molothrus ater*, regardless of whether or not a sanitation object was simultaneously added (Peer 2017). An additional study falls into a more ambiguous category, in which common tailorbirds *Orthotomus sutorius* were more likely to reject a mimetic parasitic egg if a nonmimetic egg was simultaneously introduced (Feng et al. 2019); because the accompanying object in that study was an egg rather than a nonegg object, this is arguably not testing for an effect of nest sanitation. Regardless, it is clear that the hypothesized proximal effect of nest sanitation on egg rejection has been infrequently tested and with mixed results.

Here, we experimentally test for a proximate connection between nest sanitation and egg rejection in the herring gull (Charadriiformes: *Larus argentatus*), a colonially nesting species for which research on eggs and reproductive behavior dates back to Tinbergen (1953). Herring gulls likely experience minimal selective pressures from brood parasitism, which makes it interesting to assess the rejection rate of nonmimetic eggs and whether this rate can be increased by nest sanitation. Specifically, interspecific brood parasitism is extremely rare (Perry 1982; Weseloh et al. 2020), and conspecific brood parasitism (CBP) has not been documented as far as we

are aware—though a low level of CBP might be unsurprising given reports of it in several congeners (Conover et al. 1979; Yom-Tov 2001; Ležalová-Piálková and Honza 2008).

We used 2 types of experiments to explore nest sanitation behavior and its possible effect on egg rejection in herring gulls. First, we conducted a set of single-object experiments to identify object types that induce frequent or infrequent rejection. Based on these results, we designed a second experiment to test whether a conspicuous parasitic egg is more likely to be rejected when it is presented simultaneously with a frequently rejected piece of debris. Our experiment also provides a correlational test of 2 other contextual factors that might impact hosts' response to brood parasitism. The first is the possible contribution of host clutch size, for example, to a discordancy effect (Moskát et al. 2010; Yang et al. 2014). Under a discordancy mechanism, hosts reject eggs that are most dissimilar to other eggs in the nest, and this effect could potentially be influenced by the ratio of host eggs to parasitic eggs (Abolins-Abols and Hauber 2020b). The second possible contextual factor is whether the adult gull remains near the nest during the experimental placement of the parasitic object. For example, encountering researchers at the nest could prompt a change in parental behavior that impacts egg rejection (Hanley et al. 2015), or a physiological trait such as corticosterone dynamics could influence both risk-taking behaviors (Martins et al. 2007) and egg rejection (Abolins-Abols and Hauber 2020a).

## Materials and Methods

### Study site and species

This study was conducted at the Bowdoin Scientific Station on Kent Island, Canada, in the Bay of Fundy (44°34'55"N 66°45'22"). The island is 2.8 km long, with an area of roughly 100 ha, and is 7 km southwest of the inhabited island of Grand Manan. The most common waterbirds nesting on the island are herring gulls, Leach's storm-petrels *Oceanodroma leucorhoa*, and common eiders *Somateria mollissima* (a potential interspecific parasite of herring gulls; Perry 1982), with smaller numbers of great black-backed gulls *Larus marinus* and black guillemots *Cepphus grylle*. The herring gull population on Kent Island has been one of the largest in eastern Canada (Ronconi and Wong 2003); in 2015, there were approximately 3,000 breeding pairs nesting in ~47 ha of nonforest habitat, with most of those nests concentrated in 15 ha of shoreline areas (Bennett et al. 2017).

Herring gull eggs are incubated by both adults, though females typically spend more time on the nest than do males (Burger 1987; Morris 1987). Clutch size in our population is typically 2 or 3 eggs (mean 2.3–2.5; Bennett et al. 2017; Weseloh et al. 2020). Herring gulls regularly encounter a variety of anthropogenic debris, both during their intertidal foraging and during nesting. On Kent Island, gulls nest primarily on the perimeter of the island, either on the rocky shore or in the treeless vegetated areas. The 7-m tidal flux brings the usual array of garbage—lobster traps and crates, bait bags, floats, gloves, shoes, bottles, jugs, PVC pipe, rope, Styrofoam, and lumber. An annual beach cleanup of the roughly 8 km of shoreline typically yields circa 8 m<sup>3</sup> of garbage.

Experiments 1 and 2 took place in June 2016 and May 2019, respectively. Nests were included only if they contained 2 or 3 eggs that were being actively incubated. Within each experiment, nests were used only once to avoid pseudoreplication. Overlap in the use of individual birds between Experiment 1 (in 2016) and Experiment 2 (in 2019) are not known because birds were not individually

tagged, but the 2 experiments were conducted 3 years apart, were analyzed separately, and addressed different questions.

### Experiment 1: Factors affecting object removal

This first experiment was designed to assess what physical factors of an object elicit removal from the nest and to identify an object with high rejection rate in order to pair it with an egg in Experiment 2. We tested 4 classes of objects, each in 2 different colors: small piece of wood ( $9 \times 5.5 \times 0.4$  cm, 5.5 g), large block of wood ( $8 \times 8 \times 4$  cm, 54 g), small egg ( $3.3 \times 2.5$  cm, 15 g), and large egg ( $7 \times 5$  cm, 92 g). Eggs were made of plastic, and the dimensions and shape of the large eggs were modeled from herring gull eggs collected on Kent Island (University of California Museum of Vertebrate Zoology, accession # 4667) and created with a 3D printer. The mass of the large egg was matched to that of a real herring gull egg by adding weights to the 3D-printed model. Objects were either painted olive-tan, to be generally similar to the ground color of natural herring gull eggs, or painted red to have a markedly different reflectance spectrum as measured with an Ocean Optics Jaz reflectance spectrophotometer and pulsed xenon light source (Ocean Insight, Orlando, FL, USA).

We used at least 6 different exemplars of each object type. Each nest was tested only once in Experiment 1 and was randomly assigned to receive one of the 8 types of object. After noting the number of eggs and number of adults present at the nest, we placed the object into the nest without rearranging the existing nest contents. In pilot experiments (A. Blunt and D. Dearborn, unpublished data), 25% of birds removed nonegg objects within 15 min of returning to the nest. To keep close temporal proximity between object removal and potential egg removal, and to balance the tradeoff between experiment duration and sample size, we used a 1-day window to test for object rejection. Thus, nests were revisited 24 h later, at which point the object was classified as accepted or rejected (see below). Each object type was tested at 20 nests, for a total of 160 trials, all at unique nests.

### Experiment 2: Nest sanitation and egg rejection

This second experiment compared a control treatment and a sanitation treatment. In both treatments, we measured the rejection frequency of a 3D-printed herring gull egg of realistic size and shape but painted red for high contrast with natural eggs. In the control treatment, a red egg was simply added to an existing nest in which 2 or 3 real eggs were being incubated. In the sanitation treatment, a red egg was placed in the nest simultaneously with a nonegg object that gulls would remove via nest sanitation. Because the first experiment showed that small, red pieces of wood were removed with a very high frequency (see Results section), we used this as the sanitation object.

As in Experiment 1, we used gull eggs from this population to model our 3D printing, creating experimental eggs that were  $67.9 \pm SE \ 2.2$  mm  $\times$   $48.0 \pm 2.1$  mm ( $n = 50$ ). One change from Experiment 1 is that the eggs in Experiment 2 were lighter, weighing only  $26.8 \pm 1.8$  g in comparison to natural herring gull egg mass of circa 92 g. This was to ensure that any absence of egg removal was not due to host difficulty in lifting the 3D printed egg.

We used at least 24 different exemplars of each object type. Each nest was tested only once and was systematically assigned to receive either the control treatment ( $n = 49$  nests) or the sanitation treatment ( $n = 48$  nests). After noting the number of eggs and number of adults present at the nest, we placed the object(s) into the nest

without rearranging the existing nest contents. As in Experiment 1, nests were revisited 24 h later, at which point objects were classified as accepted or rejected.

In both Experiments 1 and 2, objects were classified as rejected if they were missing, located outside of the nest, located on the nest rim at least 10 cm from the incubated eggs (rare), or selectively buried in the nest (uncommon). Counts of rejected vs. accepted objects were compared across attributes or across treatments in  $2 \times 2$  contingency tables using Fisher's exact tests.

Research was conducted following the Ornithological Council's Guidelines for the Use of Wild Birds in Research (Fair et al. 2010) and under Institutional Animal Care and Use Committee permits from Bowdoin College.

### Data Availability Statement

Data are available at Harvard Dataverse <https://doi.org/10.7910/DVN/EHUODJ>.

## Results

### Experiment 1

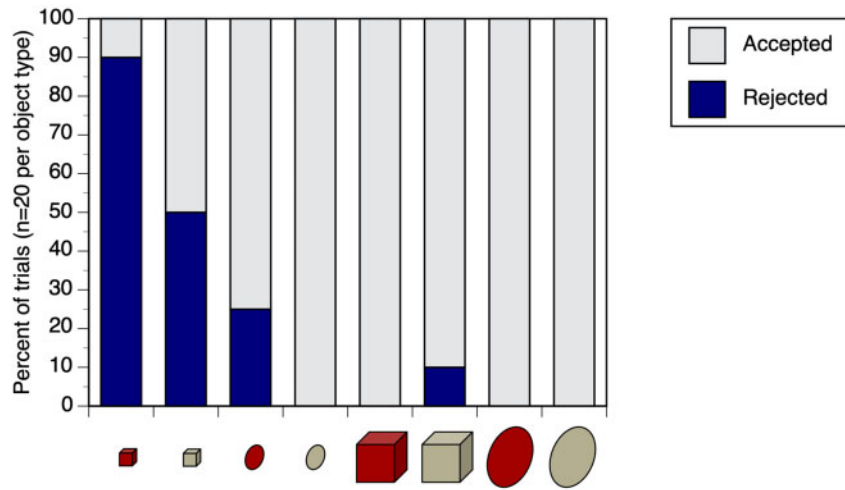
The 8 types of objects varied widely in their removal rates, ranging from 0% rejection for large eggs of either color to 90% rejection for small, red pieces of wood (Figure 1). Pooling across other attributes, rejection was more likely for small objects (47.5% for  $n = 80$  small objects, vs. 2.5% for  $n = 80$  large objects; Fisher's exact test,  $P < 0.0001$ ) and for blocky wooden objects (37.5% for  $n = 80$  pieces of wood, vs. 6.25% for  $n = 80$  artificial eggs; Fisher's exact test,  $P < 0.0001$ ). Color was not a significant overall predictor of rejection (27.5% for  $n = 80$  red objects, 15% for  $n = 80$  tan objects; Fisher's exact test,  $P = 0.081$ ), though the difference was significant when restricting the data to only the small objects (the first 4 columns of Figure 1: 57.5% for  $n = 40$  red objects, 25.0% for  $n = 40$  tan objects; Fisher's exact test,  $P = 0.006$ ).

To inform Experiment 2, the key results here are that the small, red piece of wood was almost always removed from the nest (18 of 20 trials), but the natural-shaped and visually conspicuous red egg was never rejected. Thus, Experiment 2 used a small, red piece of wood as a frequently rejected nonegg object, to ask whether egg rejection is more likely in the context of nest sanitation.

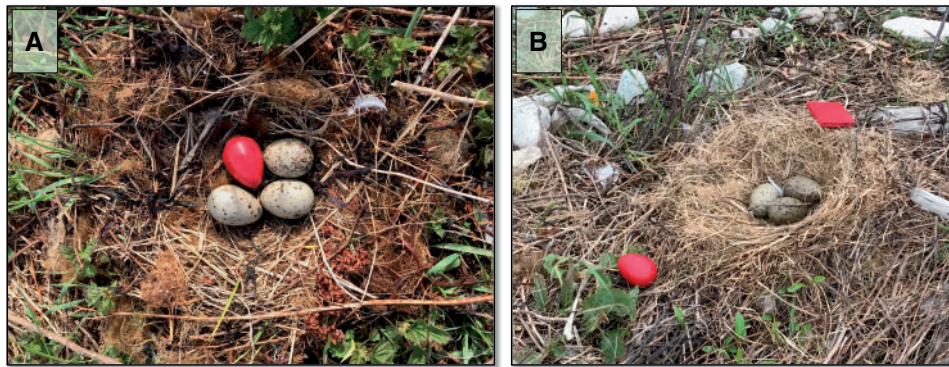
### Experiment 2

In this second experiment, gulls regularly performed nest sanitation (Figure 2) but this did not increase their likelihood of performing egg rejection. In the nests assigned to the sanitation treatment (i.e., egg + sanitation object), nest sanitation occurred at a high frequency: the small, red piece of wood was removed at 40 of 48 nests. However, parasitic egg rejection remained uncommon and did not differ between treatments: egg rejection occurred at 5 of those 40 successfully sanitized nests (12.5%) compared with 5 of 49 control nests (10.2%) which received the parasitic egg but not the sanitation object (Fisher's exact test,  $P = 0.749$ ; Figure 3). Thus, neither the observation of the sanitation object nor the performance of nest sanitation seemed to shape individuals' responses to parasitism.

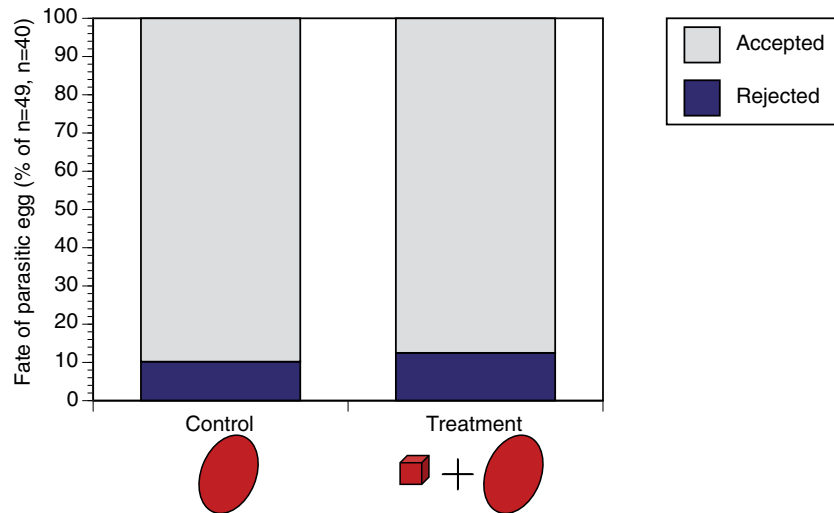
Across all treatment and control nests in Experiment 2, nests with 2 host eggs and nests with 3 host eggs did not differ significantly in the frequency with which the red parasitic egg was rejected (4.2% vs. 15.1%,  $n = 24$  and  $n = 73$ , respectively; Fisher's exact test,  $P = 0.283$ ). However, the continued presence of an adult during



**Figure 1.** Frequency of rejection of 8 types of objects in Experiment 1. Objects were placed individually in herring gull nests during incubation ( $n = 20$  nests tested per object type). Left to right: small red block, small tan block, small red egg, small tan egg, large red block, large tan block, large red egg, and large tan egg.



**Figure 2.** Nests from the sanitation treatment in Experiment 2. (A) The bird removed the sanitation object (not visible) but not the parasitic egg. (B) In contrast, this bird removed both the sanitation object and the parasitic egg.



**Figure 3.** Frequency of rejection of a red parasitic egg did not differ between control nests (parasitic egg added alone,  $n = 49$ ) and sanitized nests (bird successfully performed nest sanitation of nonegg object,  $n = 40$ ). At 8 additional nests, birds failed to remove the nonegg object; in two of those 8 cases, the experimental egg was rejected.

the experimental manipulation did affect the outcome. Specifically, if an adult remained near the nest during the brief disturbance caused by our approaching the nest and placing the object(s), subsequent egg rejection was more likely than if no adult remained at the nest (22.5% vs. 5.3%,  $n = 40$  and  $n = 57$ , respectively; Fisher's exact test,  $P = 0.025$ ).

## Discussion

Nest sanitation did not increase the likelihood of a bird rejecting a parasitic egg. In our first experiment, we used single-object trials with 8 different object types to explore the response to different object attributes. That experiment identified small, red pieces of wood as nonegg objects that were routinely removed. We also found that realistically sized and shaped 3D-printed gull eggs were infrequently rejected, whether painted an olive-tan to resemble the ground color of herring gull eggs or painted red for contrast. In our second experiment, we compared a nest sanitation treatment against a control, and found that the rejection rate of red 3D-printed gull eggs was not increased by simultaneous presentation with a frequently rejected nonegg object. Thus, egg rejection was not affected by either the visual stimulus of the nonegg object or by the actual performance of nest sanitation. Importantly, there was variation to examine: nest sanitation occurred at a high rate but was not ubiquitous, and egg rejection was uncommon but not absent. Nonetheless, there was no evidence of a proximate connection between nest sanitation and egg rejection.

The results of Experiment 1 are consistent with broad patterns in prior work on object removal from birds' nests (reviewed in [Guigueno and Sealy 2012, 2017](#); [Luro and Hauber 2017](#)). Specifically, we found higher rejection for blocky wooden objects than for egg-shaped objects, and higher rejection for smaller objects than for larger objects. Across a range of bird species, experiments have typically found greater rejection of objects that do not closely resemble eggs in shape or size ([Guigueno and Sealy 2012, 2017](#)). Color was a less strong predictor of object rejection in our experiment, consistent with the meta-analysis of [Guigueno and Sealy \(2012\)](#), though we did see greater rejection of red objects than tan when restricting the analysis to the set of small objects.

In Experiment 2, the simultaneous addition of a nonegg object—and its subsequent removal by the birds—did not increase the rejection rate for nonmimetic eggs. We used the small, red piece of wood as the sanitation object in Experiment 2 because it was by far the most frequently rejected object in Experiment 1. We paired this with the red version of the life-sized gull egg to simplify the interpretation if rejection was infrequent: failure to reject a red egg should not be attributable to perceptual difficulties in visually discriminating between the red egg and the herring gulls' own olive-tan eggs ([ten Cate et al. 2009](#); [Vidal et al. 2018](#)). Infrequent rejection of the red egg in Experiment 2 is also unlikely to be due to mechanical difficulties of manipulating the egg. One line of evidence against mechanical limitations is that 12% of those eggs were rejected. Another line of evidence comes from data on herring gulls' diet, which includes items as large as conspecific nestlings, duck nestlings, and adult storm-petrels ([Weseloh et al. 2020](#) and personal observations)—all more than twice the mass of the 3D-printed eggs in the second experiment. We have also observed herring gulls' dexterity as they open the backpacks of unwary beachgoers (D. Dearborn, personal observation). Thus, instead of being limited by visual acuity or the mechanics of moving an egg, it seems likely that failure to reject the red gull-shaped egg is the result of a decision rule to retain egg-like objects

that are approximately the correct size and shape, even if color differs markedly from their own eggs. The performance of nest sanitation behavior did not appear to soften that decision rule. Although it is possible that more egg rejection overall would be seen in a longer window of time (e.g., the 5-day period used in many egg rejection experiments), we think it unlikely that increased rejection would be disproportionately greater at treatment nests, because the egg rejection would be even more removed in time from the nest sanitation event.

At this stage, it is still difficult to generalize about a possible proximate connection between nest sanitation and egg rejection because the few existing studies differ in design, results, or both. For example, the barn swallow study and the brown-breasted bulbul study used similar methods but with contrasting results: in bulbuls, the simultaneous introduction of a peanut shell had no impact on the rejection rate of a nonmimetic egg ([Su et al. 2018](#)), but the same design in barn swallows ([Yang et al. 2015a](#)) resulted in nearly a doubling of the egg rejection rate compared with controls without the peanut shell (44% vs. 27%). The actual timing of the bird's sanitation behavior and the egg rejection is not known in those 2 studies, but the presentation of the 2 objects was simultaneous. Thus, the effect observed in barn swallows could be priming or could be the attention/recognition mechanism proposed by [Yang et al. \(2015a\)](#). In contrast, no effect of sanitation behavior was seen in American robins ([Luro and Hauber 2017](#)) in a comparison between birds that were sequentially tested either with plant debris then a nonmimetic egg or with a nonmimetic egg then plant debris—that is, researchers exposed birds to the second object only after the first object was found to have been accepted or rejected. Lastly, hosts in the blackbird study accepted 100% of experimentally placed cowbird eggs, regardless of nest sanitation treatment ([Peer 2017](#)). As with our study, nest sanitation by blackbirds did not detectably shift the decision rule about egg rejection. However, an important difference is that not a single bird rejected the parasitic egg in the blackbird study, which suggests that the decision rule is firmer or that the boundary around what constitutes your own egg is more encompassing in that species. At this point, then, 3 key questions remain open: the commonality of a connection between nest sanitation and parasitic egg rejection, the mechanism underlying such a connection (attention vs. priming), and the duration of any impact of performing nest sanitation behavior.

The selection pressure associated with parasitism is also interesting to consider. Although there are some cases of herring gulls being parasitized by common eiders ([Perry 1982](#)), in precocial species including gulls it is more common to see facultative CBP ([Yom-Tov 2001](#); [Lyon and Eadie 2008](#)). In contrast to parasitism by cowbirds or cuckoos, the cost of CBP is lower ([Dearborn et al. 2009](#)) and egg recognition is more difficult ([Rothstein and Robinson 1998](#)). Consequently, species that are not hosts to interspecific brood parasites might possess a stronger behavioral boundary between the responses to debris vs. a parasitic egg, such that nest sanitation is less likely to push a bird across that boundary. This idea has parallels to tests of the strength of nest sanitation in hosts of obligate interspecific brood parasites, where the expectation is that nest sanitation should be more pronounced in rejector species than in acceptor species ([Luro and Hauber 2017](#))—either because stronger sanitation tendencies made it easier to evolve rejection behavior, or because the evolution of rejection behavior had the side effect of exaggerating nest sanitation ([Guigueno and Sealy 2017](#)). Clearly, a robust comparative approach will require data from more species across a range of life history strategies and contexts.

In addition to considering the effect of nest sanitation, our study offers a correlational test of 2 other contextual factors that might impact birds' responses to parasitism. First, we found no difference in egg rejection at nests with 2 vs. 3 host eggs. A relationship between egg rejection and the ratio of host eggs to parasitic eggs could exist under either a discordancy mechanism or a template mechanism (Moskát et al. 2014). One possibility is higher rejection in 2-egg nests because the parasitic egg would make up a larger proportion of the eggs in the nest and thus be more recognizable (Akre and Johnsen 2014; Abolins-Abols and Hauber 2020b). An alternate possibility is lower rejection in 2-egg nests because these could be less experienced birds (Stokke et al. 2008) or because of recognition being impacted by the narrower host-egg majority—a phenomenon that has been extended to explain a lower rejection rate in multiply parasitized vs. singly parasitized nests (Stevens et al. 2013). Regardless of these predictions of opposing relationships, we did not find any connection between egg rejection and the ratio of host eggs to parasitic egg in our experiment.

The second contextual factor is the behavior of the adult at the start of the experiment. At 41% of nests, a bird remained close to the nest rather than flying away while we placed the experimental object(s), and those nests had a 4-fold higher egg rejection rate. Multiple mechanisms could be hypothesized to contribute to this difference: (1) males and females might differ in both nest defense (Weseloh et al. 2020) and egg rejection (Liang et al. 2012), and our experimental nests likely vary in whether the male or the female was incubating when we placed the experimental object(s); (2) local nest density varies widely across the island (unpublished data) and might influence both nest defense and the threshold for parasitic egg rejection; (3) birds on different parts of the island could be differentially habituated to humans because of proximity to walking paths, buildings, and research sites, causing habituated birds to encounter us at the nest during experimental placement, thereby cueing egg rejection (Hanley et al. 2015); and (4) a personality syndrome with physiological underpinnings such as corticosterone dynamics (Cockrem 2007) could influence both risk-taking behaviors (Martins et al. 2007) and egg rejection (Abolins-Abols and Hauber 2020a). With additional data and new experiments, these mechanisms are all testable and could shed more light on the contextual basis for responses to brood parasitism.

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## References

Abolins-Abols M, Hauber ME, 2020a. Endocrine regulation of egg rejection in an avian brood parasite host: endocrine regulation of host behaviour. *Biol Lett* 16:20200225.

- Abolins-Abols M, Hauber ME, 2020b. Proximate predictors of variation in egg rejection behavior by hosts of avian brood parasites. *J Comp Psychol* 134:412–422.
- Akre KL, Johnsen S, 2014. Psychophysics and the evolution of behavior. *Trends Ecol Evol* 29:291–300.
- Bennett JL, Jamieson EG, Ronconi RA, Wong SNP, 2017. Variability in egg size and population declines of herring gulls in relation to fisheries and climate conditions. *Avian Conserv Ecol* 12:16.
- Burger J, 1987. Selection for equitability in some aspects of reproductive investment in herring gulls *Larus argentatus*. *Ornis Scand* 18:17–23.
- Cockrem JF, 2007. Stress, corticosterone responses and avian personalities. *J Ornithol* 148:S169–S178.
- Conover MR, Miller DE, Hunt GL, 1979. Female-female pairs and other unusual reproductive associations in ring-billed and California gulls. *Auk* 96:6–9.
- De Marsico MC, Gloag R, Ursino CA, Reboreda JC, 2013. A novel method of rejection of brood parasitic eggs reduces parasitism intensity in a cowbird host. *Biol Lett* 9:20130076.
- Dearborn DC, 1999. Brown-headed cowbird nestling vocalizations and the risk of nest predation. *Auk* 116:448–457.
- Dearborn DC, MacDade LS, Robinson S, Dowling Fink AD, Fink ML, 2009. Offspring development mode and the evolution of brood parasitism. *Behav Ecol* 20:517–524.
- Evans JK, Griffith SC, Klasing KC, Buchanan KL, 2016. Impact of nest sanitation on the immune system of parents and nestlings in a passerine bird. *J Exp Biol* 219:1985–1993.
- Fair J, Paul E, Jones J, 2010. *Guidelines to the Use of Wild Birds in Research*. Washington (DC): Ornithological Council.
- Feeney WE, Welbergen JA, Langmore NE, 2014. Advances in the study of coevolution between avian brood parasites and their hosts. *Annu Rev Ecol Syst* 45:227–246.
- Feng CZ, Yang CC, Liang W, 2019. Nest sanitation facilitates egg recognition in the common tailorbird, a plaintive cuckoo host. *Zool Res* 40:466–470.
- Goto K, Bond AB, Burks M, Kamil AC, 2014. Visual search and attention in blue jays *Cyanocitta cristata*: associative cuing and sequential priming. *J Exp Psych Anim Behav* 40:185–194.
- Guigueno MF, Sealy SG, 2012. Nest sanitation in passerine birds: implications for egg rejection in hosts of brood parasites. *J Ornithol* 153:35–52.
- Guigueno MF, Sealy SG, 2017. Implications of nest sanitation in the evolution of egg rejection. In: Soler M editor. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. Cham, Switzerland: Springer, 385–399.
- Hanley D, Samaš P, Heryán J, Hauber ME, Grim T, 2015. Now you see it, now you don't: flushing hosts prior to experimentation can predict their responses to brood parasitism. *Sci Rep* 5:9060.
- Hauber ME, Moskát C, Bán M, 2006. Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. *Biol Lett* 2:177–180.
- Hoover JP, Reetz MJ, 2006. Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. *Oecologia* 149:165–173.
- Kemal RE, Rothstein SI, 1988. Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. *Anim Behav* 36:175–183.
- Kruger O, 2007. Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. *Phil Trans R Soc Lond B Biol Sci* 362:1873–1886.
- Ležalová-Piálková R, Honza M, 2008. Responses of black-headed gulls *Larus ridibundus* to conspecific brood parasitism. *J Ornithol* 149:415–421.
- Liang W, Yang C, Antonov A, Fossey F, Stokke BG et al., 2012. Sex roles in egg recognition and egg polymorphism in avian brood parasitism. *Behav Ecol* 23:397–402.
- Luro AB, Hauber ME, 2017. A test of the nest sanitation hypothesis for the evolution of foreign egg rejection in an avian brood parasite rejecter host species. *Sci Nat* 104:14.
- Lyon BE, Eadie JM, 2008. Conspecific brood parasitism in birds: a life-history perspective. *Annu Rev Ecol Syst* 39:343–363.
- Lyu N, Liang W, 2021. Parasitism is always costly to the host. *Zool Res* 42:217–220.

- Martins TLF, Roberts ML, Giblin I, Huxham R, Evans MR, 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Horm Behav* 52:445–453.
- Medina I, Langmore NE, 2016. The evolution of acceptance and tolerance in hosts of avian brood parasites. *Biol Rev* 91:569–577.
- Morris RD, 1987. Time-partitioning of clutch and brood care activities in herring gulls: a measure of parental quality? *Stud Avian Biol* 10:68–74.
- Moskát C, Bán M, Székely T, Komdeur J, Lucassen RWG et al., 2010. Discordancy or template-based recognition? Dissecting the cognitive basis of the rejection of foreign eggs in hosts of avian brood parasites. *J Exp Biol* 213:1976–1983.
- Moskát C, Zólei A, Bán M, Elek Z, Tong L et al., 2014. How to spot a stranger's egg? A mimicry-specific discordancy effect in the recognition of parasitic eggs. *Ethology* 120:616–626.
- Payne BK, Brown-Iannuzzi JL, Loersch C, 2016. Replicable effects of primes on human behavior. *J Exp Psych General* 145:1269–1279.
- Peer BD, 2017. Nest sanitation does not elicit egg ejection in a brown-headed cowbird host. *Anim Cog* 20:371–374.
- Peer BD, Sealy SG, 2004. Correlates of egg rejection in hosts of the brown-headed cowbird. *Condor* 106:580–599.
- Perry P, 1982. The use of gull nests by eiders. *Br Birds* 75:360–365.
- Petit KE, Petit LJ, Petit DR, 1989. Fecal sac removal: do the pattern and distance of dispersal affect the chance of nest predation? *Condor* 91:479–482.
- Poláček M, Griggio M, Bartíková M, Hoi H, 2013. Nest sanitation as the evolutionary background for egg ejection behaviour and the role of motivation for object removal. *PLoS One* 8:e78771.
- Ronconi RA, Wong SNP, 2003. Estimates of changes in seabird numbers in the grand manan archipelago, new Brunswick, Canada. *Waterbirds* 26:462–472.
- Rothstein SI, 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250–271.
- Rothstein SI, 1990. A model system for coevolution: avian brood parasitism. *Annu Rev Ecol Syst* 21:481–508.
- Rothstein SI, Robinson SR, 1998. *Parasitic Birds and Their Hosts: Studies in Coevolution*. New York (NY): Oxford University Press.
- Shizuka D, Lyon BE, 2010. Coots use hatch order to learn to recognize and reject conspecific brood parasitic chicks. *Nature* 463:223–226.
- Soler JJ, Sorci G, Soler M, Møller AP, 1999. Change in host rejection behavior mediated by the predatory behavior of its brood parasite. *Behav Ecol* 10:275–280.
- Stevens M, Troscianko J, Spottiswoode CN, 2013. Repeated targeting of the same hosts by a brood parasite compromises host egg rejection. *Nat Commun* 4:e2475.
- Stokke BG, Hafstad I, Rudolfson G, Moksnes A, Møller AP et al., 2008. Predictors of resistance to brood parasitism within and among reed warbler populations. *Behav Ecol* 19:612–620.
- Stokke BG, Røskaft E, Moksnes A, Møller AP, Antonov A et al., 2016. Disappearance of eggs from nonparasitized nests of brood parasite hosts: the evolutionary equilibrium hypothesis revisited. *Biol J Linn Soc* 118:215–225.
- Strausberger BM, Burhans DE, 2001. Nest desertion by field sparrows and its possible influence on the evolution of cowbird behavior. *Auk* 118:770–776.
- Su T, Yang C, Chen S, Liang W, 2018. Does nest sanitation elicit egg rejection in an open-cup nesting cuckoo host rejecter? *Avian Res* 9:27.
- ten Cate C, Bruins WS, den Ouden J, Egberts T, Neevel H et al., 2009. Tinbergen revisited: a replication and extension of experiments on the beak colour preferences of herring gull chicks. *Anim Behav* 77:795–802.
- Tinbergen N, 1953. *The Herring Gull's World: A Study of the Social Behaviour of Birds*. London: Collins.
- Vidal MN, Segovia Y, Victory N, Navarro-Sempere A, García M, 2018. Light microscopy study of the retina of the yellow-legged gull, *Larus michahellis*, and the relationship between environment and behaviour. *Avian Biol Res* 11:231–237.
- Weseloh DV, Hebert CE, Mallory ML, Poole AF, Ellis JC, et al., 2020. Herring gull *Larus argentatus*, version 1.0. In: Billerman SM editor. *Birds of the World*. Ithaca (NY): Cornell Lab of Ornithology.
- Yang C, Chen M, Wang L, Liang W, Møller AP, 2015a. Nest sanitation elicits egg discrimination in cuckoo hosts. *Anim Cog* 18:1373–1377.
- Yang C, Liang W, Cai Y, Shi S, Takasu F et al., 2010. Coevolution in action: disruptive selection on egg colour in an avian brood parasite and its host. *PLoS One* 5:e10816.
- Yang C, Møller AP, Røskaft E, Moksnes A, Liang W et al., 2014. Reject the odd egg: egg recognition mechanisms in parrotbills. *Behav Ecol* 25:1320–1324.
- Yang C, Wang L, Liang W, Møller AP, 2015b. Nest sanitation behavior in hirundines as a pre-adaptation to egg rejection to counter brood parasitism. *Anim Cog* 18:355–360.
- Yom-Tov Y, 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. *Ibis* 143:133–143.

