

Nest sanitation in passerine birds: implications for egg rejection in hosts of brood parasites

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Abstract We reviewed information on nest sanitation (nest cleaning) by passerine birds because the act of cleaning nests is thought to be associated with egg rejection by hosts of brood parasites, and yet there has been no synthesis of the literature on nest sanitation. In the first part of the review, we summarized information on nest sanitation. We found that birds remove a variety of objects from nests such as egg shells, fecal sacs, pieces of vegetation, invertebrate parasites, dead chicks, uneaten food, and occasionally unhatched eggs. Fecal sac removal, the most commonly considered type of nest sanitation behavior, is not divided equally between the sexes across species; females remove more fecal sacs than males. In addition, larger species tend to carry fecal sacs farther than smaller species. In the second part of the review, we discuss the importance of nest sanitation in the evolution of egg rejection behavior of brood parasite hosts. Recent studies involving the experimental addition of non-egg-shaped objects to nests or to the vicinity of nests suggest that nest sanitation plays a role in host rejection of avian brood

parasitism. Most objects added to nests prior to hatching (usually hard) and after hatching (usually soft) were rejected. In a logistic regression model, shape and size were the significant factors in eliciting rejection for all hosts that received experimental non-egg objects added to their nests prior to hatching. Nest sanitation may be an exaptation for antiparasite defences and thus plays an important role in the host-parasite arms race.

Keywords Brood parasitism · Egg shell · Fecal sac · Nest cleaning · Object rejection · Passeriformes

Zusammenfassung Wir überprüften Daten zur Nesthygiene (Nestsäuberung) bei Singvögeln. Es wird angenommen, dass Nestsäuberung assoziiert ist mit der Zurückweisung von Eiern durch Wirte von Brutparasiten. Bislang gibt es jedoch keine Synthese der Literatur zur Nesthygiene. Daher fassen wir im ersten Teil der Arbeit die vorhandenen Informationen zur Nesthygiene zusammen. Wir fanden heraus, dass Vögel eine Vielzahl von Objekten aus ihren Nestern entfernen, beispielsweise Eierschalen, Kotpakete, Vegetationsteile, wirbellose Parasiten, tote Küken, Futterreste und gelegentlich nicht geschlüpfte Eier. Die Beseitigung von Kotpaketen, das am meisten beobachtete Nesthygieneverhalten, wird von den Geschlechtern nicht gleichverteilt durchgeführt. Weibchen entfernen mehr Kot aus den Nestern als Männchen. Darüber hinaus tendieren größere Arten dazu, Kotreste weiter weg zu bringen als kleinere Arten. Im zweiten Teil der Studie diskutieren wir die Bedeutung von Nesthygiene in der Evolution des Verhaltens der Gelegeablehnung durch Wirtsarten für Brutparasiten. Aktuelle Studien, bei denen experimentell nicht eierschalenförmige Objekte in die Nester oder in deren Nähe gelegt worden sind, deuten an, dass für die Wirtsarten Nesthygiene eine Rolle spielt bei

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der Vermeidung von Brutparasitismus durch andere Vogelarten. Die meisten Objekte, die vor (normalerweise harte) und nach dem Schlupf (normalerweise weiche) den Nestern hinzugefügt wurden, werden entfernt. In einem logistischen Regressionsmodell sind Form und Größe die entscheidenden Faktoren für die Zurückweisung der Eier durch die Wirtsvögel, deren Nestern vor dem Schlupf nicht-eierförmige Objekte hinzugefügt worden sind. Nesthygiene könnte eine besondere Anpassung (Exaptation) für Parasitenabwehr darstellen und spielt daher eine bedeutende Rolle in der Beziehung zwischen Wirt und Parasit.

Introduction

The earliest naturalists, such as Plutarch, noted that some birds remove and hide excrement, whereas others “teach” their young to defecate over the rim of the nest (Skutch 1976, p. 282). Similarly, most passerines do not tolerate objects other than eggs and nestlings in their nests (Welty 1982). Removal of fecal sacs and egg shells minimizes contamination of the nest’s contents and the conspicuousness of the nest to predators (Blair and Tucker 1941; Tinbergen et al. 1962; Petit et al. 1989). Not only are fecal sacs and egg shells removed from nests, however, but most birds immediately remove any object that does not resemble or look like an egg (i.e., non-egg object), which keeps the nest dry, warm, and free of parasites and pathogens (Thomson 1934; Welty 1982).

Nest sanitation was poorly understood until Thomson (1934) and Blair and Tucker (1941) reviewed the subject, and Weatherhead (1988) and Petit et al. (1989) studied the behavior in the field. These reviews and results of recent studies have increased our understanding of different components of nest sanitation, such as ingestion and dispersal of fecal sacs. However, Blair and Tucker (1941) only considered sanitation as the removal of fecal sacs, and the rudiments of nest sanitation are still not fully appreciated. Therefore, in the first part of our review, we summarize information available on all types of nest sanitation behavior and identify energetic and evolutionary implications.

The removal of non-egg-shaped objects has been considered a type of nest-sanitation behavior (Alvarez et al. 1976; Bártol et al. 2003; Moskát et al. 2003; Underwood and Sealy 2006a; Guigueno and Sealy 2009). Studies involving experimental addition of objects have given insight into the genetic basis of nest sanitation and its relationship with the rejection responses of some hosts of brood parasites (Smith 1943; Bártol et al. 2003; Moskát et al. 2003; Underwood and Sealy 2006a). The subject has not been reviewed, despite that the study of nest sanitation

has drawn increased interest (Ortega and Cruz 1988; Ortega et al. 1993; Bártol et al. 2003; Moskát et al. 2003; Underwood and Sealy 2006a; Guigueno and Sealy 2009). Results of studies on hosts of both Common Cuckoo and Brown-headed Cowbird (scientific names in Supplementary Material 1; classification follows Gill and Wright 2006) suggest a relationship between nest sanitation and rejection by hosts of avian brood parasites (Rothstein 1975; Moskát et al. 2003; Guigueno and Sealy 2009). Could egg rejection have been derived from nest sanitation behavior? Abundant evidence suggests that hosts respond to parasitic eggs under the pressure of brood parasitism (Sealy and Bazin 1995; Rothstein and Robinson 1998; Peer et al. 2007; Stoddard and Stevens 2010). Cuckoos have interacted with their hosts over greater evolutionary time than cowbirds and thus co-evolutionary adaptations are present in the hosts (better recognition of own eggs) and cuckoos (more perfect mimicry of host eggs) (Davies 2000; Stoddard and Stevens 2010). Regardless, nest sanitation behavior may be an important stage for the evolution of egg rejection in hosts. In the second part of our review, we examine the implications of nest sanitation for anti-parasite responses, which include implications of studies that tested responses to non-egg-shaped objects, and we identify gaps in our knowledge and additional research that will improve our understanding of the behavior involved in nest sanitation.

Methods

We defined nest sanitation (nest cleaning) as the removal of any object that is not an intact and viable egg or young from the nest cup or nest cavity, whether the adult birds ingest the object, carry it away, or bury it under new nest material. We compiled information on nest sanitation from papers published worldwide, whether sanitation was the main focus, or merely a section of the paper, and observed in species of the order Passeriformes. Most papers included in this review described different aspects of nest sanitation in detail, but we also included studies in which anecdotal observations were presented. We searched for the following key words: nest sanitation, nest cleaning, fe(a)cal sac, eggshell, and egg shell. Other studies referenced in papers were also included; however, we cannot guarantee all studies that mentioned fecal sac, egg shell, or removal of any other debris were included, as this was beyond the scope of this review. We also searched for information on nest sanitation in all *Birds of North America* species accounts for Passeriformes, as there was a section on nest sanitation in nearly all the accounts. We gathered information on 274 species of passerine birds from 40 families. We compiled information on the different types of nest

sanitation and examined the hypotheses posited to explain various components of this behavior.

In the first part of this review, we describe accounts of nest sanitation in which naturally occurring objects were removed from nests. The second part summarizes experiments involving addition of non-egg-shaped objects to nests of passerine birds. We searched for studies that reported the responses of passerines to hard or soft non-egg-shaped objects experimentally added to the nests or to the vicinity of the nests during the pre-nestling and nestling stages. We did not consider spheres as non-egg-shaped objects because brood parasites lay eggs that are generally more spherical than host eggs (Hoy and Ottow 1964; Picman 1989; Brooker and Brooker 1991; Underwood and Sealy 2006a).

We conducted several statistical analyses based on the data that emerged from our review. First, we conducted binomial tests to determine whether (1) fecal sacs were more likely to be eaten during the early part of the nestling stage and carried away later, (2) nest sanitation was reported in most species accounts for Passeriformes, and (3) one sex was more likely to carry out nest sanitation across multiple species. We also used linear regression to determine whether the distances that species of birds carried fecal sacs were correlated with body mass, and then, using the FLIGHT program (Kaiser 2007), we calculated the increased chemical energy expenditure by a small host of a brood parasite carrying a parasite's fecal sacs as opposed to the sacs produced by their own young. Finally, we used a general linear model (GLM) to determine which factors were more likely to elicit rejection of objects experimentally added to nests of multiple passerines. We controlled for phylogeny using PHYLIP (Felsenstein 1989). Further details of the statistical analyses are provided in the text.

Part I. The genetic bases of nest sanitation

Herrick (1900, p. 102) referred to nest sanitation as having a genetic basis, stating that cleanliness should be considered an “imperative instinct.” In some cases, this behavior may be influenced by hormones, as male Blue-headed Vireos with experimentally elevated levels of testosterone provided less parental care and nest sanitation (Van Roo 2004). Nest sanitation may have initially evolved with the swallowing of feces as a “gustatory act” (Selous 1933, p. 222) and with the swallowing of feces established, other actions, such as carrying them and other extraneous objects or debris away from the nest, also “evolved.” For example, fecal sac disposal occurs in distinct stages (Blair and Tucker 1941). In some cases, adult birds appear to wait for defecation (Herrick 1900; Gabrielson 1912; Selous 1933;

Smith 1950; Glück 1988; Ley and Williams 1998), whereas adults of other species stimulate defecation by prodding the cloacal region (Selous 1933; Erickson 1938; Smith 1942, 1947, 1950; Gill 1983; Conder 1948; Nice 1964; Nolan 1978; Islam 1994), tugging at the nestling's back (Smith 1942, 1950), or shaking the nestling's head vigorously (Smith 1942, 1950). Efforts to stimulate defecation vary during the nestling period, but seem greater earlier than later in this stage (Blair and Tucker 1941) when violent stimulation no longer seems necessary (Smith 1942).

The importance of releasers (extrinsic stimuli) in birds has been emphasized and described by Lorenz (1937) and Tinbergen (1939). However, the original definition of the cirlet of feathers surrounding the cloaca as a releaser for the removal of feces by adults was incorrect as fecal sac removal occurred before the feathers appeared (Rand 1942). Rather, the releaser may be the nestling's behavior, as many nestlings only attempt to defecate when the adult is present and often elevate the cloaca or tail so the parent can stimulate defecation (i.e., Brown Thrasher, Gabrielson 1912; Melodious Warbler, Selous 1933; Brown Creeper, Davis 1978). Willow Warbler chicks placed a dropping in a specific latrine, where feces accumulated, and were later removed by the parents (Blair and Tucker 1941). Nest sanitation may be stimulated by the presence of young birds such that carrying away fecal sacs continues until the young birds have left the nest (Spotted Flycatchers and Willow Warblers, Blair and Tucker 1941). Alternatively, the stimulus may be the nest itself such that regions occupied by post-fledging young are highly soiled (Meadow Pipits and Corn Buntings, Blair and Tucker 1941; Melodious Warblers, Selous 1933) and nests were cleaned even after young departed and when no re-nesting occurred (Woodlark: Smith 1950). In some cases, different sections of the nest were cleaned at different rates (Conder 1948).

Complete nest sanitation may be a derived behavior in certain species. The Poo-uli (family Drepanididae), which feeds principally invertebrates to its young instead of plants, keeps its nest clean, but other related species are not as fastidious (Kepler et al. 1996).

Types of nest sanitation behavior

Some birds do not clean their nests (Australian finches, Thomson 1934; weavers, Hindwood 1951; House Finch, Van Tyne and Berger 1971; Gill 1994), but the task of cleaning them may be carried out by other animals (Thomson 1934; Hindwood 1951; Chisholm 1952). No difference in cleanliness was observed in nests with cleaning beetles (*Platydema pascoei*), however, because nests harbored too few beetles to keep them clean (Hindwood 1951). Detritus-eating beetles may assist in cleaning the nest of soil cavity-nesting species, such as bee-eaters,

which frequently do not clean their own nest (Casas-Crivillé and Valera 2005). In addition, fringillids usually keep their nest clean only early in the nestling stage (Supplementary Material 2; references for supplementary material in Supplementary Material 5). In the rest of this section, we describe different types of nest sanitation for species that clean their nests.

Removal of egg shells and unhatched eggs

Soon after hatching, egg shells are commonly removed from the nest, carried away, and dropped (Smith 1950; Wallace and Mahan 1975; Welty 1982; Winkler 2004; Supplementary Material 2). Small passerines may carry egg shells some distance before dropping them, but other species break and eat the shells piecemeal and may use them as grit (Nethersole-Thompson and Nethersole-Thompson 1942; Supplementary Material 2). Whether shells are removed from the nest by ingestion or are carried away varies between individuals of the same species (Haldeman 1931; Nethersole-Thompson and Nethersole-Thompson 1942; Nice 1964) or between species (Supplementary Material 2).

Although many species eat hatched egg shells, they are probably of limited nutritional value to adults because embryos extract about 80% of their skeletal calcium from eggshell calcium (Simkiss 1961; Wallace and Mahan 1975; Jones 1976). Supplemental calcium has only a slight effect on the adults' reproductive output (Johnson and Barclay 1996), although the effect may be greater for species such as cowbirds that lay many eggs. At Delta Marsh, Manitoba, Canada, Brown-headed Cowbirds and other passerines that were collected for diet studies had pieces of egg shells and snail shells in their stomachs, and some adult female cowbirds were observed eating tiny pieces of egg shell removed from the bottom of old nests (S.G. Sealy, personal observation). Ankney and Scott (1980) recorded the presence of snail shells in the gizzards of nearly all laying female Brown-headed Cowbirds, in addition to a pronounced shift from a seed to an insect diet (more so in females than in males), therefore, nutrients for egg production were likely extracted directly from their diet (Ankney and Scott 1980).

Intact eggs may be removed by some species (Supplementary Material 2); however, they were frequently left in the nest (Eastern Bluebird, Hartshorne 1962, attempts at rejections recorded; Western Meadowlark, Shaver 1918; Wallace and Mahan 1975; Dunnock, Tomek 1988; Red-whiskered Bulbul, Islam 1994; Brown-capped Rosy Finch, Johnson et al. 2000; Great-tailed Grackle, Johnson and Peer 2001; Boat-tailed Grackle, Post et al. 1996; Dickcissel, Long et al. 1965; Lincoln's Sparrow, Ammon 1995; Prairie Warbler, Nolan et al. 1999). Broken eggs were usually

removed from the nest (Supplementary Material 2); if not, the bird may desert the clutch (Smith 1950). Broken eggs may leak their contents into the cup and "glue" eggs to the lining or to each other (Kemal and Rothstein 1988). Rejection of broken eggs declined abruptly at hatch, likely because it was not adaptive for birds to reject their own pipped eggs (Kemal and Rothstein 1988; McMaster and Sealy 1998). For this reason, Kemal and Rothstein (1988) did not support the idea that rejection of egg shells is generalized nest sanitation behavior. Nethersole-Thompson and Nethersole-Thompson (1942) also considered nest sanitation and shell disposal as separate, but possibly related, behaviors because nest sanitation is "practically confined" to passerines and their allies, whereas eggshell removal was also observed in other groups. However, the origins of these two behaviors may proceed along "parallel lines" and both behaviors may have uses in common (Nethersole-Thompson and Nethersole-Thompson 1942, p. 165). Indeed, birds that usually accepted parasitic eggs (Rothstein 1975) rejected broken egg shells during Kemal and Rothstein's (1988) study. This led them to suggest that egg rejection occurred in response to a more universal selection pressure than parasitism alone.

Egg-capping, the enclosing of an intact egg by a hatched egg shell, sometimes occurred if egg shells were not removed from the nest soon after hatching (Derrickson and Warkentin 1991; McMaster and Sealy 1998; Hauber 2003). Instances of egg capping varied from 0.2% ($n = 501$ nests) in Glaucous-winged Gulls (Verbeek 1996) to 2.6% ($n = 234$ nests) in American Coots (Arnold 1992). In nests parasitized by obligate brood parasites, however, the often-larger parasitic eggs that hatch earlier than host eggs may increase the frequency of egg-capping (Hauber 2003). Thirty-three percent of Eastern Phoebe nests parasitized by the Brown-headed Cowbird had hosts' eggs capped by the parasite's larger egg shell, and hosts removed fragments that capped eggs more quickly than fragments that did not (Hauber 2003).

Removal of other materials

Birds remove materials such as leaves and sticks, feathers and uneaten food (all infrequently reported; Supplementary Material 2), and dead chicks (frequently reported; Supplementary Material 2). A Striated Thornbill brooding eggs placed a feather back into position after it was deliberately misplaced, or it removed the feather altogether (Thomson 1934). Grinnell and Storer (1924) described an adult American Robin feeding a piece of liver to a nestling, but the nestling could not swallow it because it was too big. Part of the liver protruded from the nestling's mouth after it had swallowed as much as it could. The adult picked up the protruding part and carried both the food and the nestling

Table 1 Binomial tests summarizing differences in nest sanitation behaviors in passerine birds worldwide

Difference analyzed	Number of species in question	Total number of species	<i>P</i> value
Fecal sacs removed	227	229	<0.0001
Fecal sac ingestion occurring only in first half of nestling period	87	144	0.0035
Fecal sac removal only or mostly by females	33	39	<0.0001
Invertebrate removal only or mostly by females	11	11	0.0005

The first and second analyses test the frequency of specific types of behavior, regardless of sex, whereas the third and last analyses test whether there is a sex difference for two types of behavior

out of the nest. Brewer's Blackbirds disposed of dead chicks in areas regularly used for fecal sac disposal (Welty 1982). Similarly, some cavity nesters removed old nest material before building their own nest (Gowaty and Plissner 1997; Mazgajski et al. 2004). Eastern Bluebirds removed some old nesting material before the females started to build over the remains (Gowaty and Plissner 1997). European Starlings usually only removed the top layer of material in old nests, which increased interior space in the nest-box and decreased the number of parasites that may have overwintered in the old nests (Mazgajski et al. 2004).

Management of invertebrate parasites

At least 15 species of passerines from nine families are known to minimize the costs of invertebrate parasites by removing them from their nests (Supplementary Material 2). Objects removed from the nest, such as parasites, may be eaten (Tomek 1988). Probing the nest may have many roles: changing egg position, removing objects in the nest, repairing the nest, and clearing parasites from the nest; probing may decline as chicks get older (Tomek 1988; Deeming 2002). Results of experiments on tits have revealed a role of nest sanitation in parasite removal as female Blue Tits spent more time performing nest sanitation activities in nests parasitized by blowflies (*Protophthora* spp.) than in nests experimentally deparasitized (Hurtrez-Boussès 2000). Tits also buried and fluffed the nest structure to sift food remains and shed skin to the bottom of the nest cavity (Hurtrez-Boussès 2000) or searched actively for and killed hen fleas (*Ceratophyllus gallinae*) with their head dug into the nest material (Christie et al. 1996). Adult tits and their chicks may share the costs of blowfly parasitism because these parasites only attack the chicks; high parasitic loads forced tits to increase time devoted to sanitation activity, to decrease foraging time and to sleep less, which may reduce adult survival after the breeding period (Christie et al. 1996; Triplet et al. 2002). Searching for invertebrates has also been recorded in Florida Scrub-Jay (Woolfenden and Fitzpatrick 1996), Hawaiian Crow (Banko et al. 2002), Grey Catbird

(Gabrielson 1913), Eastern Bluebird (Gowaty and Plissner 1997), Yellow-headed Blackbird (Fautin 1941), Northern Cardinal (Halkin and Linville 1999), and Lazuli Bunting (Greene et al. 1996).

Fecal sac removal

Fecal sac removal is nearly universal among Passeriformes. Of the 229 *Birds of North America* species accounts that presented information on nest sanitation, only two species were not reported regularly to rid their nests of fecal sacs (Table 1). Passerines void their excrement in sacs that consist of dark intestinal excreta and white semisolid urine (uric acid) enclosed in a thick mucous membrane (Blair and Tucker 1941; Skutch 1976; Pettingill 1985; Winkler 2004). The sacs facilitate removal of excrement from the nest because the wastes are securely held together by the mucous membrane (Welty 1982; Gill 1994).

Blair and Tucker (1941) only considered fecal sac removal as nest sanitation and identified three stages. First, parents swallowed the feces voided by nestlings up to 3 days of age (Blair and Tucker 1941). During the second or intermediate stage, parents frequently prodded the nestlings to stimulate defecation and feces were carried away or swallowed (Blair and Tucker 1941). Active co-operation ensued between nestling and parent during the third stage; nestlings may adopt more than one of these options: (1) project feces away from the nest, (2) deposit feces in a selected area, to be swallowed or carried away by the parent, and (3) deliver feces directly to the parent, who again swallows or carries them away (Blair and Tucker 1941). Nonetheless, in some species, feces accumulated in the nest or on the rim later in the nestling period, and nest sanitation in these situations was not performed throughout the nestling period (Red-billed Quelea, Morel et al. 1957; Grey Warbler, Gill 1983; Barn Swallow, Spencer 2005; most species of the family Fringillidae; Supplementary Material 2). In other species, fecal sacs were either only swallowed or carried away [firecrest (Kirkpatrick 1984), laughingthrushes: Islam (1995); Supplementary Material 2].

After each feeding, parents usually waited for defecation and some even stimulated it (see "The genetic bases of nest

sanitation”). Therefore, parents usually removed sacs immediately after feeding young (93% of removals by Brown Thrashers, Gabrielson 1912; 98% by Common Yellowthroats, Shaver 1918). Feeding stimulated defecation, but defecation did not occur every time (defecation and removal at 50% of feeds for Nilgiri Laughingthrush, Islam 1994; 40% Grey-breasted Laughingthrushes, Islam 1995; 23% White Wagtails and 26% Japanese Wagtails, Nakamura et al. 1984; 33% Northern Parula, Moldenhauer and Regelski 1996; 79% Yellow-breasted Chat, Eckerle and Thompson 2001). The rate of fecal sac removal may depend on the rate at which feeding visits occurred and on the percentage of feeding trips where defecation occurred (Nice 1964; Morton 1979; Spencer 2005). The rate of fecal sac removal was greater in larger broods (Lombardo 1991).

Distance carried and energetic analyses Fecal sacs are ingested and/or carried varying distances from the nest (Supplementary Material 2). Distance carried by each species was proportional to the logarithm of body mass (Fig. 1). Larger species produced larger fecal sacs, therefore, we expected larger fecal sacs to be carried farther from the nest to minimize attraction to the nest by predators. Birds carrying fecal sacs probably incurred some energetic cost, especially those that removed sacs larger than those voided by their own young, as in the case of a small host removing fecal sacs voided by a larger brood-parasitic nestling. Based on the above relationship, a typical 11-g, frequently parasitized host species, the Yellow Warbler (Sealy 1995), would be expected to carry a fecal sac about 20 m. Using the above information, and assuming fecal sacs near fledging are 2.4% of nestling body mass (Morton 1979), a Yellow Warbler traveling its maximum speed would increase its chemical energy cost per fecal sac removal by 5.6% by carrying parasite (cowbird) fecal sacs

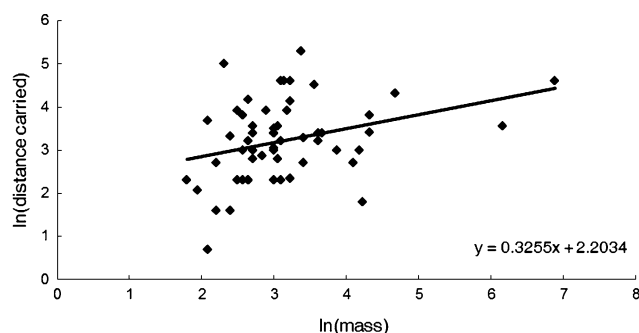


Fig. 1 Distance fecal sacs carried from the nest by different species of bird in the order Passeriformes. The logarithm of distance carried was proportional to the logarithm of body mass ($t_{55} = 2.53$, $P = 0.01$, $r^2 = 0.11$). Distance increased with increasing size of the species, possibly because fecal sacs are larger and must be transported farther to minimize attracting predators to the nest

compared to warbler fecal sacs (FLIGHT program with inputs from Kaiser 2007: weight 11 g, aspect ratio 4.91, wingspan 0.21 m; Pennycuick 2008).

Ingesting or carrying feces away cleans the nest (Blair and Tucker 1941; Skutch 1976; O’Connor 1984), but in the case of transported feces, how far should they be carried? Petit et al. (1989) reported that the closer feces were dropped, the higher was the incidence of predation at those nests. Ingesting or carrying feces a minimal distance (Supplementary Material 2), therefore, kept the nest cleaner and may reduce predation (Blair and Tucker 1941; Petit et al. 1989). Most passerines produce fecal sacs (Van Tyne and Berger 1971; Pettingill 1985; Winkler 2004) and this provides the parents the option of easily carrying the feces away rather than eating them (McGowan 1995). There may be other reasons, however, why fecal sacs are ingested rather than carried away.

Three hypotheses, which are not mutually exclusive, have been posited to explain why adults eat their nestlings’ feces. Feces may be nutritious (Herrick 1900; Kluijver 1950; Morton 1979; Kozłowski 1981; Glück 1988; McGowan 1995; Stake and Cavanagh 2001), they may provide water (Morton 1979; Glück 1988), or ingestion of them may be an economic alternative to the cost incurred when feces are carried away from the nest (Khacher 1978; Hurd et al. 1991; McGowan 1995).

Economic disposal hypothesis (McGowan 1995) Ingestion of fecal sacs may be an economical alternative to carrying them away from the nest when the adult birds are brooding or removing parasites (Hurd et al. 1991). Tree Swallows carried sacs in directions different from those traveled when foraging, which possibly cost parents time and energy (Weatherhead 1984, 1988; Quinney 1986; Hurd et al. 1991). Ingesting fecal sacs eliminates transportation costs and maximizes time at the nest, but this may be costly in itself because the sacs contain waste products, which when ingested may “tax” the adults’ digestive tract (Khacher 1978; Hurd et al. 1991, p. 70). According to the economic disposal hypothesis, this may be why adults stop ingesting sacs when the nestlings are older, because the sacs are possibly too large and, hence, possibly more costly for the adults to handle and ingest (Hurd et al. 1991). Adult Tree Swallows, American Robins and Red-winged Blackbirds ingested sacs regardless of variation in their nutritional content, because it was more costly to carry them away, stopping only when they became too large and too much of a burden on their digestive systems (Hurd et al. 1991). Furthermore, female robins ingested more fecal sacs when it was cooler, presumably when they had to brood more (Hurd et al. 1991). Nonetheless, results of other studies have not supported economic disposal (McGowan 1995; McKay et al. 2009).

Parental nutrition hypothesis (McGowan 1995) This hypothesis posits that adults ingest fecal sacs for nutritional benefit (Herrick 1900; Blair and Tucker 1941; McGowan 1995). When two parents are present when a fecal sac emerges, the female, who is likely the more nutritionally stressed, was more likely to eat it (McGowan 1995). In Spotted Towhees, fecal sac ingestion increased (1) during years of food shortage, (2) when food declined late in the breeding season, (3) when parents were in poor body condition, and (4) when their young were underweight (McKay et al. 2009). Calculations suggested that fecal sacs make up to 10% of energy intake of adult birds (Morton 1979). Parents usually consumed their offsprings' feces early in the nestling period when fecal energy content was high and offspring did not efficiently digest food, and feces were small (Kluijver 1950; Newton 1967; Glück 1988); once nestling digestive efficiency matched adult digestive efficiency, adults stopped consuming feces (Glück 1988). For example, albumen-rich fecal sacs (especially those voided by younger nestlings) could significantly contribute to the regeneration of albumen that was lost during egg production (Kozłowski 1981). In the present review, we found that, among all species in which fecal sac ingestion was reported, ingestion occurred significantly more frequently in the first half of the nestling period (Table 1).

Gain of water hypothesis (Morton 1979) Fecal sacs may enhance the adults' daily water balance (Morton 1979). Adult birds have greater reno-cloacal abilities than their young, therefore, young birds usually discharge a waste product with a lower concentration of solutes than their parents (Calder 1968; Skadhauge 1981). In nesting White-crowned Sparrows, water from fecal sacs may contribute half or more of the adults' daily water needs, which may be especially important for sparrows inhabiting xeric areas (Morton 1979). However, there has been no direct test of or support for this hypothesis.

In conclusion, fecal sacs may be ingested to enhance nutrition, as a hedge against hydration, or as an economic alternative to reduce transportation costs. Feces are usually consumed when they are smaller and contain less digested material, and carried away when they become larger and a greater burden on the adults' digestive tract. However, studies addressing these three hypotheses simultaneously are lacking.

Use of disposal sites At least 15 species of passerines have been reported to dispose of feces on various objects, including tree branches, cables, and poles (Supplementary Material 2). The record is 84 fecal sacs attached to a wooden pole by a Brown Creeper, with the sacs' density increasing with height and with the sacs distributed evenly around the pole, except for a bare strip, one-third of the

pole's width, running up one side (Washington 1986). Other species dropped their feces in water (Supplementary Material 2). Cliburn (1978) reported that Common Grackles made special trips to a lake to drop fecal sacs in the water, because the birds flew back to the woods after disposing of the fecal sacs; disposing feces in water could be a way to conceal the location of the nest (Cliburn 1978). As avian fecal matter may increase nutrient input and vegetation growth, it is also possible that, by depositing fecal sacs in appropriate microenvironments, birds alter local food webs to their own benefit (e.g., Maron et al. 2006).

Carrying fecal sacs away probably serves two major functions: nest sanitation and predator avoidance, although these functions likely are not mutually exclusive and ingestion also keeps the nest clean (Hendricks 1987; Petit and Petit 1987; Weitzel 2003). Petit et al. (1989) found a significant inverse relationship between predation frequency and distance between the feces and the quail (*Coturnix* spp.) eggs that they had positioned in woodlots. Carrying fecal sacs more than 5 m from the nest reduced the incidence of predation even more (Petit et al. 1989). These results supported the hypothesis that one function of fecal sac removal was to decrease nest predation, although the patterns of sac dispersion around the nest did not affect the likelihood of predation (Petit et al. 1989). Similarly, Water Pipits (Hendricks 1987) and Northern Wheatears (Brooke 1981) flew significantly farther when leaving the nest carrying fecal sacs compared to leaving without them. This suggests the point where the sac was dropped resulted in part from the requirement to reduce the visibility of the nest (Brooke 1981). Overall, a compromise likely exists between not attracting predators (by flying farther from the nest) and minimizing energy expenditure (Brooke 1981).

Weatherhead (1984) tested two hypotheses: (1) whether Tree Swallows nesting over land carried fecal sacs farther from their nests, and (2) whether these swallows dispersed them more widely than swallows nesting over water, because the sacs do not disperse as well on land as in water. His results supported the first hypothesis. Swallows that nested in terrestrial and aqueous habitats varied the direction of departure from the nest more when they carried fecal sacs (Weatherhead 1984). However, a re-analysis of the data, prompted by questions raised by Petit and Petit (1988), suggested a better interpretation: "... swallows nesting over water change the direction of their departures when carrying fecal sacs" (Weatherhead 1988, p. 519). Weatherhead (1988) suggested that these results, along with Petit and Petit's (1987) results, would not be expected if the only reason for fecal sac disposal was to sanitize the nest, thus suggesting these results support the idea that extra effort was made to minimize predation. This was also supported by the idea that fewer young were reared if the

costs of fecal sac dispersion were high (Weatherhead 1984). For example, Weatherhead (1984) reported that the female Superb Lyrebird only lays one egg, but must fly up to 100 m to deposit fecal sacs in streams and, where no streams were available, the female buried them (Skutch 1976).

Petit and Petit (1987) reported that when Prothonotary Warblers dropped fecal sacs over land, the distance they were carried from the nest was not significantly greater than the distance when sacs were dropped over water. However, the distribution of trips when the birds flew from the nest without a sac actually varied more than the distribution of trips with sacs (Petit and Petit 1987). This was similar to the behavior of Common Grackles reported by Weatherhead (1988). Every time a grackle flew away with a fecal sac, it flew straight to and dropped it into the same swimming pool (Weatherhead 1988). The direction of foraging trips, therefore, varied more when the birds left the nest without a fecal sac than when they left with one (Weatherhead 1988). According to Weatherhead (1988), the behavior and ecological situation of the Prothonotary Warblers studied by Petit and Petit (1987) resembled more closely those of Common Grackles than of Tree Swallows (Weatherhead 1984), as warblers and grackles consistently used the same disposal sites. Birds with available disposal sites (e.g., water) may behave differently from those that do not have a site available. Taken collectively, results from several studies suggest that fecal sac disposal is not merely a manifestation of nest sanitation, because birds exert extra effort attempting to reduce the risk of predation (Weatherhead 1988).

Western Bluebirds dropped fecal sacs 9.5–43 m from nest-boxes and 56% of sacs were dropped within 13–20 m (Weitzel 2003). Also, 69% of fecal sacs were disposed of in the one quadrant in which foraging occurred (Weitzel 2003). Thus, fecal sacs were not scattered randomly. As the young became older, parents carried the sacs progressively farther from the nest (Weitzel 2003). White-breasted Nuthatches dispersed fecal sacs 6–60 m from the nest; 56% were dropped 48–60 m and the greater dispersal distance in White-breasted Nuthatch, relative to Western Bluebird, may be attributed to the presence of predators, which were absent in Weitzel's (2003, 2005) study. Approximately 95% of fecal sac flights and 75% of flights without fecal sacs were to the foraging area; therefore, nuthatches did not randomly disperse fecal sacs 360° around the nest (Weitzel 2005). These results suggest the pattern of dispersal depended on ecological factors, such as the presence (White-breasted Nuthatch: greater dispersal distance) or absence (Western Bluebird: smaller dispersal distance) of predators and a dependable food source (Western Bluebirds and White-breasted Nuthatches: most fecal sacs were dropped in foraging area). The parents increased the

distance fecal sacs were dropped (Weitzel 2003, 2005) as the young developed. By contrast, Willie Wagtails dropped fecal sacs 1–1.5 m closer to the nest when the nestlings were older (Goodey and Lill 1993). Lang et al. (2002) reported Eastern Bluebirds leaving the nest-box with fecal sacs flew 21–52 m farther than the average distance recorded during a 30-min focal period, and concluded that fecal sac dispersal to these greater distances reduced cues used by predators to locate nests.

In conclusion, the farther feces were carried by various passerines, the lower the risk of predation. By carrying away fecal sacs, birds undoubtedly also cleaned their nests. The dispersal of fecal sacs around the nest depends on the ecology of the species. Birds that used a disposal site, such as water, or that had a dependable food source, were less likely to disperse fecal sacs randomly around the nest. Birds frequently exerted extra effort to reduce predation risk, and their method to reduce this risk was context-dependent.

Sex differences in nature

The task of nest sanitation is sometimes equally divided between females and males (Gabrielson 1912; Esten 1925; Goodey and Lill 1993; Bignal 1998; Lessells et al. 1998; Lang et al. 2002; Stevens 2005). For species in which the task was not equally divided between both members of a pair, females removed more fecal sacs and invertebrate parasites than males (Table 1); however, the sample size varied greatly from study to study (Supplementary Material 3). Other important sexual differences exist.

Parasite management was performed only by females in Blue Tits, possibly because these nest sanitation techniques evolved in tandem with nest construction behavior, which only females performed (Bañbura et al. 2001). Female tits may also have bills more suitably shaped for searching and killing fleas (Christie et al. 1996). The only aspect of nest sanitation performed by both males and females was removal of fecal sacs (Bañbura et al. 2001). Christie et al. (1996) reported that male Great Tits tending nests experimentally parasitized with hen fleas did not show typical sanitation behavior, but increased their rate of food provisioning by nearly 50%. More fecal sacs were removed by males, which may have been because they fed larger caterpillars to nestlings, which better stimulated defecation (Royama 1966).

In other species, one member of the pair cleaned the nest, whereas the other fed the nestlings (Herrick 1900; Selous 1933). Herrick (1900) observed a female Cedar Waxwing spreading her wings to shield the brood from the sun, whereas the male repeatedly fed the nestlings cherries. The female remained straddled over the nest, devouring excrement (Herrick 1900). Selous (1933) observed a male

Blackcap arrive at the nest without feeding the nestlings, but it had come to the nest for another purpose—to clean it. The male stimulated defecation in one nestling, retrieved the feces as they emerged and flew away with them (Selous 1933). During subsequent visits, the male stimulated defecation while the female fed the nestlings (Selous 1933).

In conclusion, nest sanitation is generally not equally divided between females and males. Males may perform different aspects of nest sanitation, may clean nests less often than females, or may not clean them at all, depending on the species and on the type of nest sanitation (Table 1; Supplementary Material 3). Males may be more preoccupied with defending their territory and thus feed the young less than females. Some types of nest sanitation behavior, such as searching for invertebrate parasites, resemble other female-only types of behavior, which may explain why females performed more nest sanitation than males in those situations.

Nest sanitation performed by individuals other than the parents

Intraspecific helping behavior

Especially in social groups, nest sanitation is not only carried out by the parents but also by helpers (Supplementary Material 2). This type of helping behavior was more frequently observed in social species, such as Green Jays, which travelled in flocks of 3–9 individuals (Alvarez 1975). Parents and helpers removed fecal sacs and debris, such as dry leaves and twigs (Alvarez 1975). Azure-winged Magpies breed in a highly flexible cooperative system, which includes helpers that remove fecal sacs from nests (Valencia et al. 2003). Other species in the family Corvidae whose helpers performed nest sanitation were Florida Scrub-Jay and American Crow (Supplementary Material 2). Within each group of Arabian Babblers, one breeding pair plus helpers fed nestlings and removed fecal sacs (Wright 1998). Noske (1980) observed the nest of a Varied Sittella, which was attended by a group of six individuals. Five members, including two juveniles from a brood fledged earlier in the season, fed the nestlings and removed fecal sacs, but most fecal sacs were removed by the primary pair, the putative parents (Noske 1980).

Although helping behavior was observed more in social groups, it has also been noted in territorial species, such as the House Wren (Timson and Farley 2003). House Wrens were territorial during the breeding season and helping behavior was rarely observed. However, Timson and Farley (2003) observed an unbanded juvenile House Wren carrying a spider to a nest-box and later removing a fecal sac, which suggested a second feeding. It was unknown

whether the helper was genetically related to wrens occupying an adjacent nest-box (Timson and Farley 2003).

Nest sanitation performed by other species

Individuals occasionally cleaned other species' nests (Ouellet 1991; Stake and Cavanagh 2001). Ouellet (1991) observed a Savannah Sparrow feeding Lapland Longspur nestlings and picking up fecal sacs. Once the male longspur started feeding the nestlings, however, the sparrow stopped feeding them and removing fecal sacs. Because of the small number of similar cases reported, this behavior may have been accidental or misdirected (Ouellet 1991). There are numerous records of misdirected parental care that include feeding young (Shy 1982; Sealy and Lorenzana 1997; Schaeffer et al. 2009).

Stake and Cavanagh (2001) published the first observations of adult cowbirds ingesting or transporting host fecal sacs from unparasitized nests (Supplementary Material 2). Brown-headed Cowbirds removed fecal sacs at three nests and ingested those removed from two nests (Stake and Cavanagh 2001). The cowbirds were also observed removing host nestlings at these nests, which may function to increase the likelihood of nest failure and to force the host to reneest, thus increasing future opportunities for parasitism (Arcese et al. 1996). Interestingly, a cowbird interrupted the handling of a nestling to remove a fecal sac (Stake and Cavanagh 2001). Possibly, the stimulus to remove fecal sacs was stronger than the need to remove host nestlings. There is no adaptive reason for cowbirds to ingest feces from nestlings other than for purposes of nutrition or water conservation, because cowbirds do not tend their own nestlings (Stake and Cavanagh 2001).

In conclusion, nest sanitation was usually performed by the parents; however, conspecific helpers from social and also territorial species may assist occasionally. Nest sanitation may also be performed by other species, including brood parasites, suggesting that this behavior is non-adaptive and is a relic from the time cowbirds built their own nests (Stake and Cavanagh 2001).

Part II. Experimental objects added to nests

Objects added to nests prior to hatching

Summarizing and analyzing results of multiple experiments allowed us to determine which properties of an object in a nest elicits nest sanitation behavior, i.e., removal of the object, and whether this behavior changes through the nesting period. We also applied the results of our analyses to investigate the importance of nest sanitation

behavior in the evolution of egg rejection by hosts of avian brood parasites.

Responses to object types

Several species rejected objects experimentally added to nests before hatching (Table 2). Differences in responses between the sexes have not been reported; however, female Great Reed Warblers and Yellow Warblers likely were responsible for burying objects because they exclusively build the nests. Some objects were standardized for weight and volume to simulate the characteristics of the host's or brood parasite's eggs (Moskát et al. 2003; Underwood and Sealy 2006a). The cubes used by Alvarez et al. (1976) were similar in weight and volume to Eurasian Magpie eggs. However, the non-egg-shaped objects used by Ortega and Cruz (1988), Ortega et al. (1993), and Bártol et al. (2003) were not standardized for weight or volume to match the characteristics of host or parasite eggs. Hoover (2003) placed dice in Prothonotary Warbler nests that were not standardized for weight, volume, or color. Guigueno and Sealy (2009) used objects of the same weight, volume, and color of cowbird eggs for one experiment, and half the weight and volume of cowbird eggs, but the same mass and volume of host eggs, for a second experiment. Larger objects were mostly buried only in pre-incubation, whereas smaller objects were mostly ejected during pre-incubation and incubation (Guigueno and Sealy 2009). In a related study, Honza and Moskát (2008) found that the type of material (plastic or painted host eggs) influenced whether hosts punctured the object (painted host egg) or pecked the object over and over to create a hole in the hard material (plastic egg); however, both object types were rejected at similar frequencies.

Cubical objects placed in nests of Eurasian Magpies were rejected more quickly than oval objects (Alvarez et al. 1976). Dice placed in Prothonotary Warbler nests during early egg laying were rejected 10% of the time, and warbler and cowbird eggs were not rejected at all (Hoover 2003). Great Reed Warblers rejected non-egg-shaped objects significantly more frequently than dummy cuckoo eggs, and large coins were buried significantly less frequently than small coins (Moskát et al. 2003). Bártol et al. (2003) found that Great Reed Warblers ejected reed stems and buried coins more frequently than cuckoo eggs under natural conditions. American Robins and Grey Catbirds rejected non-egg-shaped objects significantly more often and sooner than egg-shaped objects (Underwood and Sealy 2006a). Yellow Warblers rejected large stars more frequently than cowbird eggs only in pre-incubation, and rejected small stars more frequently than small dumbbells and foreign Yellow Warbler eggs during pre-incubation (nest complete) and incubation (Guigueno and Sealy 2009). The two pairs

of American Robins studied by Höhn (1993) did not remove the layer of leaves and settled onto their covered clutch, which suggests the urge to incubate was stimulated from the top half of the nest cup and from the nest rim (Höhn 1993). However, it was unknown for how long the robins continued to incubate and birds may sit on empty nests for some time (Owen 1940; Dhondt and Eyckerman 1978); therefore, the above conclusion must be interpreted cautiously. Large beads (holes filled-in, with or without visible holes, which consisted of a black dot painted over the filled-in hole) and dowels were almost always accepted by Red-winged Blackbirds, but stars and large beads with holes were generally ejected (Ortega et al. 1993). No clear pattern of response was recorded for small beads, but for all non-egg-shaped objects added to nests, there was no significant difference in the frequency of acceptance or rejection of colors (Ortega et al. 1993). Birds, however, see in the range of UV wavelengths, 300–400 nm, which are invisible to humans, and therefore birds may not perceive differences in color the same way humans do (Wright 1972). Indeed, differences in the UV spectrum between host and parasite eggs may influence the decision to reject (Honza and Polaciková 2008; Underwood and Sealy 2008). However, artificial colors usually do not reflect the UV spectrum, therefore, the non-egg-shaped objects used in studies summarized in this section likely did not simulate the natural colors of real eggs (Antonov et al. 2010).

We used PROC GLM in SAS (SAS Institute 1990) to determine the importance of three categorical factors (shape, size, and color) on the frequency of rejection in hosts listed in Table 2. Shape was considered more egg-like if the experimental object did not have any edges or flat surfaces, whereas it was less egg-like if there were edges and/or flat surfaces. Color was considered similar only if the color of the background and maculation were the same as host eggs. Size was considered similar if the dimensions or volume were the same as host eggs, whereas size was considered dissimilar if the experimental object was smaller or larger than the host egg. We controlled for phylogeny with independent contrasts using the contrast.exe subroutine of PHYLIP (Felsenstein 1989) and the phylogenetic hypothesis presented by Barker et al. (2002). The phylogenetically corrected independent variables were then analyzed using a GLM ($n = 29$). Shape ($F_{1,25} = 43.33$, $P < 0.0001$) and size ($F_{1,25} = 8.30$, $P = 0.0080$) affected rejection in seven hosts, but not color ($F_{1,25} = 0.26$, $P = 0.6113$; Fig. 2). Therefore, experimental objects differing from the host's own eggs in shape and size increased the probability of rejection across species. The least important factor in our model was color; however, this factor should not be ignored because it could have made a difference in American Robins and Grey Catbirds if color had varied (Underwood and Sealy 2006a; T.J. Underwood, personal communication).

Table 2 Responses of passerine birds to non-egg-shaped objects of different color and pattern experimentally added to their nests during different times within the pre-nestling stage

Species	Object type	Rejection % (n)	Type of rejection	Time model added	Source	
Eurasian Magpie	Magpie-egg colored wooden cubes	100 (16)	Ejection	Laying and incubation	Alvarez et al. (1976)	
Great Reed Warbler	Pieces of brown reed stems	88 (16)	Ejection	Pre-egg-laying	Bártol et al. (2003)	
	Big copper-colored coins	88 (16)	Ejection	Pre-egg-laying		
	Small copper-colored coins	94 (17)	Burial	Pre-egg-laying		
			Desertion			
	Polyester-covered sticks (beige background, sepia ^a and brown blotches)	93.5 (31)	Ejection	Pre-incubation		Moskát et al. (2003)
			Burial			
	Polyester-covered discs (beige background, sepia and brown blotches)	93.1 (29)	Ejection	Pre-incubation		
Burial						
American Robin	Deep layer (2 cm) of dead leaves, covering the eggs being incubated	0 (2)	NA	Incubation	Höhn (1993)	
Grey Catbird	White wooden or plaster cylinders, rectangles, and cubes	59.5 (42)	Ejection	Laying and incubation	Underwood and Sealy (2006a)	
Yellow Warbler	Dark green wooden or plaster cylinders, rectangles, and cubes	58.1 (43)	Ejection	Laying and incubation		
	Large stars (off-white with brown spots)	43.8 (32)	Burial	Pre-incubation	Guigueno and Sealy (2009)	
			Desertion			
	Large dumbbells (off-white with brown spots)	23.5 (34)	Burial	Incubation		
			Ejection			
	Small stars (off-white with brown spots)	28.8 (73)	NA	Pre-incubation and incubation		
Burial						
Small dumbbells (off-white with brown spots)	1.3 (80)	Ejection	Pre-incubation and incubation			
Prothonotary Warbler	Dice (white with black dots)	80 (10)	Deserted/ pushed to side	Pre-egg-laying	Hoover (2003)	
Red-winged Blackbird	White and sky blue pom-poms, large and small smooth beads, bumpy beads, oblong models, and stars	10 (80)	Deserted	Early egg-laying	Ortega and Cruz (1988)	
			Ejection	Egg laying and early incubation		
	Wooden dowels (off-white with brown maculation or white ^b)	8.7 (23)	Ejection	Egg laying and early incubation	Ortega et al. (1993)	
	Large wooden beads (filled in); off-white with brown maculation or white	0 (23)	NA	Egg laying and early incubation		
	Large wooden beads (with hole); off-white with brown maculation	83.3 (12)	Ejection	Egg laying and early incubation		
	Large wooden beads (with hole, white)	71.4 (14)	Ejection	Egg laying and early incubation		
Large wooden beads (with a painted black “hole”) (off-white with brown maculation or white)	0 (29)	NA	Egg laying and early incubation			
Wooden small beads (filled in) (off-white with brown maculation or white)	54.1 (37)	Ejection	Egg laying and early incubation			
Plastic stars (off-white with brown maculation or white)	95.5 (22)	Ejection	Egg laying and early incubation			

Table 2 continued

Species	Object type	Rejection % (n)	Type of rejection	Time model added	Source
Yellow-headed Blackbird	White and sky blue pom-poms, large and small smooth beads, bumpy beads, oblong models, and stars	100 (6)	Ejection	Egg laying and early incubation	Ortega and Cruz (1988)

Rejection may be by ejection (grasping the object between the mandibles), burial (superimposed nest built on the previous nest and eggs), or desertion (abandonment of the nest and nest site)

NA Not available

^a Color mimics Common Cuckoo egg background and maculation

^b Color mimics Brown-headed Cowbird egg background and maculation

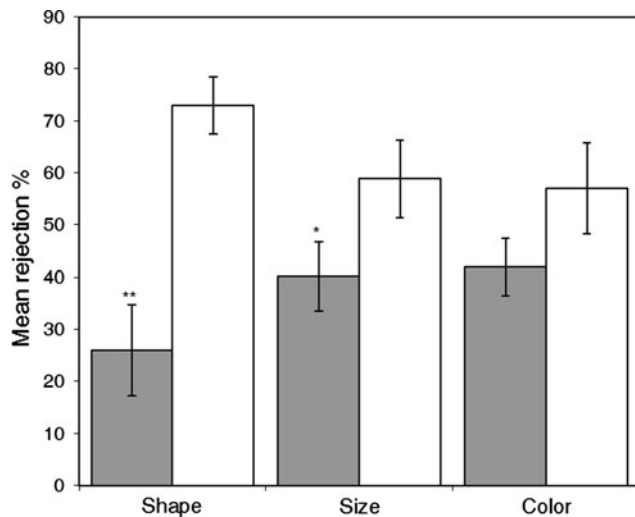


Fig. 2 Importance of shape, size, and color on mean frequency (\pm SE) of rejection of experimental objects similar to host eggs (*shaded*) compared to dissimilar (*unshaded*) experimental objects added to host nests before hatching. For *Shape*, “similar” represents non-egg-shaped objects without edges or flat surfaces, whereas “dissimilar” represents objects with edges and/or flat surfaces. *Color* was considered similar only if the colors of the background and maculation were the same as host eggs. *Size* was considered similar if the dimensions or volume were the same as host eggs, whereas size was considered dissimilar if the experimental object was smaller or larger than the host egg. We controlled for phylogeny using independent contrasts. Significance: $**P < 0.0001$, $*P < 0.01$; $n = 29$

These results are consistent with the hypothesis that nest sanitation may be a pre-adaptation for egg rejection in hosts of avian brood parasites (Moskát et al. 2003; Guigueno and Sealy 2009), because debris falling into the nest is more likely to differ in shape and size from host eggs than eggs of brood parasites. Hosts must frequently rely on differences in color and size to visually discriminate between a parasite’s egg and their own eggs (Rothstein 1975, 1982; Sealy and Bazin 1995; Underwood and Sealy 2006a, b), but only about 10% of cowbird hosts regularly eject non-mimetic cowbird eggs (Rothstein 1982; Peer and Sealy 2004a) because these hosts apparently have not had

long co-evolutionary histories with their parasites, as in cuckoo hosts (Davies and Brooke 1998). Although cowbird hosts reject non-egg-shaped objects resembling debris that could potentially fall into their nests, egg discrimination must be well developed before ejection could evolve from nest sanitation. We examine this hypothesis in greater detail below.

Nest stage effects

Moskát et al. (2003) reported that rejection frequencies did not differ significantly between pre-incubation [before egg laying (nest complete) plus egg laying] when there was a greater risk of natural parasitism and incubation (low risk), but the method of rejection changed. During incubation, ejection became more frequent, replacing nest desertion because it has been suggested that abandonment of a full clutch is too costly to sustain at this stage (Moskát et al. 2003). Prothonotary Warblers rejected any object (warbler egg, cowbird egg, or cubes) at frequencies up to 80% before egg laying, but once eggs were laid, they accepted all foreign eggs and rejected only a few cubes (Hoover 2003). This low response to foreign objects in nests with eggs may be an example of evolutionary lag, as Prothonotary Warblers have only recently been exposed to widespread parasitism by cowbirds (Hoover 2003). No significant difference in rejection frequencies between nesting stages was observed in Eurasian Magpies (Alvarez et al. 1976), and American Robins and Grey Catbirds (Underwood and Sealy 2006a). Yellow Warblers buried large objects in the pre-incubation stage, but not during incubation (Guigueno and Sealy 2009). Small objects were rejected at similar frequencies in pre-incubation and incubation, most by ejection and burial in which no host eggs were buried with the objects (“selective burial”; Guigueno and Sealy 2009, p. 253). Therefore, different forms of “nest sanitation” behavior may be expressed at different nesting stages and this behavior may be absent if it is more costly at a specific nesting stage, such as incubation. Responses to non-egg-shaped objects mirrored the responses to parasitic eggs. For example, Yellow Warblers

buried cowbird eggs early during laying but accepted them during incubation (Sealy 1995). Great Reed Warblers rejected cuckoo eggs at similar frequencies between pre-incubation and incubation, as was recorded for non-egg-shaped objects; however, rejection increased from pre-egg laying to the first egg-laying day when they observed the appearance of their own egg (Moskát et al. 2003; Moskát and Hauber 2007).

Experimental objects added to nests after hatching

Responses to object types

Supplementary Material 4 summarizes results from experiments that involved addition of objects to nests or the vicinity of the nest after hatching. Sample sizes were never more than a single nest and studies were conducted primarily in the first half of the twentieth century (Supplementary Material 4).

Sexual differences in rejection behavior of these objects have been described for Yellow Wagtail, White-throated Dipper, and Common Yellowthroat (Shaver 1918; Chislett 1933; Smith 1942, 1943). Female Yellow Wagtails rarely removed plasticene models and never removed lime or paper balls (Smith 1942, 1943), and usually only females removed real feces (Smith 1943). As for the dipper, males regularly fed the young and only they removed feces, as well as balls of tissue paper (Chislett 1933). However, usually the female Common Yellowthroat removed real feces and bits of paper added to the nest (Shaver 1918). As for the Dunnock, Song Sparrow, and Grey Catbird, it is not clear whether the objects added to nests were removed by the male or the female (Rand 1942; Tomek 1988).

Shaver (1918) reported that all bits of paper added to a Common Yellowthroat nest were carried away by the adult after its next visit. However, a dipper did not remove every ball of tissue paper placed under its nest (Chislett 1933). The smaller balls were disposed of in the stream where the male rinsed his bill. The same behavior was observed when real feces were removed. Chislett (1933, p. 9) increased the size of the tissue-paper balls to “the point of absurdity” and noted that the dipper no longer removed them from beneath the nest. As in the dipper, a male Yellow Wagtail did not remove all lime balls from near the nest (Smith 1942), except when they and wads of paper were revealed after the surrounding vegetation was parted around the nest site, but they ignored them when the vegetation was restored (Smith 1942). In another study, Smith (1943) added white plasticene models, resembling fecal sacs, to the latrine of the nests of Meadow Pipits and Yellow Wagtails (Smith 1943). Adult Meadow Pipits and one male Yellow Wagtail removed the “sacs” except when a nestling made pre-defecation movements, at which time the

adults froze and waited for the fecal sac to emerge. When the young were removed from the nest, the artificial sacs were ignored (Smith 1943). Wire added to a Dunnock’s nest was placed around a chick’s neck as part of another study. It was unexpectedly removed and dropped below the nest along with the chick (Tomek 1988). Rand (1942) did not identify any special stimulus that elicits nest sanitation in Grey Catbirds and Song Sparrows; however, young had to be present before nest cleaning occurred (Rand 1942). Nest sanitation and bringing food to the nest were complementary, but sanitation was the more generalized behavior because food was always brought to the nest, whereas a variety of items were carried away (Rand 1942).

These experiments demonstrated that all foreign materials near or at the nest were removed during the nestling stage. A more general urge to remove not only fecal sacs was advantageous, because a strict lock-and-key relationship, where a specific stimulus elicited a specific response, such as fecal sac removal, may result in removing only feces from the nest, whereas other materials would be left behind (Rand 1942).

Implications of nest sanitation on responses to avian brood parasitism

Because avian brood parasitism frequently impacts negatively on the reproductive effort of hosts (Lorenzana and Sealy 1999), selection has favored the development of defences to reduce the costs of parasitism (Rothstein and Robinson 1998; Davies 2000). Host species exhibit various rejection responses such as ejection of the parasitic egg or burial or desertion of a clutch that contains a parasitic egg (Rothstein 1990). Acceptor cowbird hosts usually accept nonmimetic eggs, as cowbird eggs usually do not mimic host eggs, whereas rejecters reject nonmimetic eggs (Rothstein 1975). However, acceptor species likely can perform the critical behaviors that are essential for the rejection of a parasitic egg (Rothstein 1982; Rasmussen et al. 2010).

The importance of nest sanitation behavior in the evolution of parasitic egg rejection has been described or mentioned in many studies in which non-egg-shaped objects were added to nests (Ortega and Cruz 1988; Moskát et al. 2003; Underwood and Sealy 2006a; Guigueno and Sealy 2009). The similarity between egg ejection and nest sanitation was noted long ago by Swynnerton (1918). Ejection and burial, antiparasite behaviors, seem more like general behaviors and not solely adaptations to brood parasitism (Rothstein 1975; Ortega and Cruz 1988; Bártol et al. 2003; Moskát et al. 2003; Guigueno and Sealy 2010). A general behavior would be used in many contexts (i.e., rejecting a foreign object), whereas specific behaviors are those used only in specific contexts (i.e., ejecting eggs).

Antiparasite responses, rather than adaptations per se, may have evolved under particular selective forces (i.e., benefits accrued by keeping the nest clean), but now are adaptive in another context (i.e., benefits accrued by removing parasite eggs; Mumme and Koenig 1991). Nest sanitation behavior may be an exaptation for egg rejection (Guigueno and Sealy 2009). However, egg rejection likely did not evolve solely from nest sanitation because hosts are subjected to selection from brood parasitism, which underlies the evolution of this behavior (Rothstein and Robinson 1998).

Under certain circumstances, ejection may be a more general behavior rather than only a specific antiparasite defense (Rothstein 1975; Moskát et al. 2003; Underwood and Sealy 2006a). Birds performing nest sanitation grasp egg shells, fecal sacs or other objects and remove them from the nest between their mandibles, swallow them or carry them from the nest and drop them at some distance (Peer and Sealy 2004a). This is similar to egg ejection except that parasitic eggs are usually carried away from the nest by rejecters, not swallowed (except in the case of puncture-ejecters, which may ingest them piecemeal; Sealy 1996), and they are occasionally gently placed on a substrate (Peer and Sealy 2004b). To become a rejecter, nest sanitation motor patterns must be released early in incubation and in response to alien eggs instead of refuse (Rothstein 1975; Ortega and Cruz 1988).

Underwood and Sealy (2006a) found the proportion of odd-shaped objects that are rejected was higher in American Robins and Grey Catbirds, two rejecter species, than in acceptor species. This suggests the tendency to discriminate foreign objects is refined in these two species, although the rejecter and acceptor that were compared were not closely related (Underwood and Sealy 2006a). Refinement of foreign object discrimination may also be the result of a similar parasitism pressure and not just a trait shared by related species.

Nest sanitation may be important in the burial of non-egg-shaped objects, behavior that may be a pre-adaptation to rejection of parasitic eggs (Bártol et al. 2003; Moskát et al. 2003; Guigueno and Sealy 2009). In their study of Great Reed Warblers, Bártol et al. (2003) concluded that egg burial was not a specific response to parasitic eggs but burial resembled nest sanitation behavior because warblers also buried coins placed into their nests. Thus, egg burial was not solely an adaptation against brood parasitism, and only round and flat objects (coins) were buried (Bártol et al. 2003). The Yellow Warbler, the only host of the Brown-headed Cowbird known to consistently bury cowbird eggs (Sealy 1995), buried non-egg-shaped objects, along with its own eggs, more frequently than egg-shaped objects, but ejected smaller objects of the same shape (Guigueno and Sealy 2009). The “nest sanitation” hypothesis, which posits that nest sanitation is a pre-adaptation for egg rejection,

predicts that (1) objects least similar to eggs are rejected more frequently than egg-shaped objects, (2) objects are removed from nests by ejection as this is the least costly rejection method, and (3) objects are removed from nests at similar rates throughout the pre-nestling stages, as nests should be kept clean throughout (Moskát et al. 2003; Guigueno and Sealy 2009, p. 248). In Guigueno and Sealy’s (2009) experiment with large objects, rejection (mostly by burial) was recorded only in pre-incubation, as warblers probably could not eject these objects. However, when small objects were added to nests, ejection was the most common type of rejection; debris-like objects were rejected more frequently than egg-like objects, and objects were removed at similar frequencies between pre-incubation and incubation. These results, therefore, supported the nest sanitation hypothesis (Guigueno and Sealy 2009). Moskát et al. (2003, p. 18) concluded nest sanitation behavior could be “an important evolutionary stage” leading to the rejection of parasitic eggs.

Moskát et al. (2003) added stick-shaped, disk-shaped, and cuckoo egg-shaped objects to nests during the stages of pre-incubation (high parasitism risk) and incubation (low parasitism risk). Cuckoo egg-shaped-objects were rejected (by burial, desertion, and ejection) less often than the non-egg-shaped objects in the pre-egg-laying and incubation stages, which supported the idea that hosts rejected objects dissimilar to their own eggs, but accepted similar objects (Moskát et al. 2003). Yellow-headed Blackbirds and Red-winged Blackbirds, acceptor species, ejected all non-egg-shaped objects (Ortega and Cruz 1988). Results of these studies confirm the importance of shape in the discrimination between foreign objects that are rejected, probably as a form of nest sanitation, and objects that are accepted.

Hosts of brood parasites are subjected to increased pressure that favors better egg recognition, which probably enhances detection of any foreign object (Moskát et al. 2003). Thus, it is important to compare the responses of hosts to non-egg-shaped objects in parasitized and unparasitized populations or to compare responses of closely related species-pairs (Moskát et al. 2003; Guigueno and Sealy 2009). More satisfactory conclusions regarding the evolution of antiparasite strategies in the context of nest sanitation would be achieved by comparing the responses of closely related rejecter and acceptor species of similar size to non-egg-shaped objects (Underwood and Sealy 2006a).

Future research

Nest sanitation merits further study. Although researchers have been interested in nest sanitation for many years, only

recently have certain components of nest sanitation, such as ingestion and dispersal of fecal sacs, been examined quantitatively. Researchers should investigate the types of nest sanitation behavior other than eggshell removal, fecal sac removal, and the management of invertebrate parasites, as most of the other types have been investigated only qualitatively and have generally appeared as anecdotal observations in papers that dealt with broader aspects of breeding biology. Studies involving experimental addition of natural objects in the nests of birds should be conducted, as Rothstein (1975) suggested. Also, the ingestion and transport of fecal sacs of brood parasites by smaller hosts should be analyzed to determine the effects on adult survival and body condition. Researchers should also continue to explore the relationship between nest sanitation and rejection behavior of hosts of brood parasites.

A striking difference between studies conducted prior to and after hatching is that most objects added in the early nesting stages were hard, whereas those added later were soft. This may be because researchers intended to add objects that differed slightly from eggs in the pre-nestling stage, when hosts of brood parasites reject eggs, and objects that differed slightly from fecal sacs during the nestling stage. This has made it impossible to test differences in rejection frequencies between the pre-nestling and nestling stages. It is important in future studies to test responses to the same object types, both hard and soft with shape and size constant, throughout all stages to identify any significant differences.

Studies in which objects were added to nests during the nestling stage generally have been based on only one or two breeding pairs (Shaver 1918; Smith 1942, 1943; Tomek 1988; Supplementary Table 3). Conversely, studies in which experiments were carried out prior to hatching involved larger numbers of nests tested once. Studies of nestlings sometimes involved many experiments on the same nest, resulting in pseudoreplication (Shaver 1918; Smith 1942, 1943); however, the number of replications was not specified. Future studies, therefore, should test responses of a statistically adequate number of breeding pairs during the nestling period to verify the trends in behavior reported by previous studies. Also, more species should be tested before and after hatching.

Studies like those suggested by Moskát et al. (2003), Underwood and Sealy (2006a), and Guigueno and Sealy (2009) may promote better understanding of the role of nest sanitation behavior in rejection of parasitic eggs and the origin of rejection behavior. This is because the suggestion that egg rejection is a type of nest sanitation is somewhat speculative at this point, as other motor patterns, not just egg rejection, resemble those involved in nest sanitation, such as foraging. However, the resemblance is greater for nest sanitation, as foraging birds do not pick up

an object with their bills, carry it some distance, and then drop it outside of their nest. Finally, greater rejection frequency of non-egg-shaped objects may be a side effect of selection due to brood parasitism (Moskát et al. 2003; Guigueno and Sealy 2009). If differences in rejection frequencies of non-egg-shaped (debris-like) objects between parasitized versus unparasitized populations are reported, this would more likely be due to differences in exposure to parasitism.

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