



Implications of Nest Sanitation in the Evolution of Egg Rejection

21

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Abstract

Nest sanitation or nest cleaning behaviour in Passeriformes has been widely reported in the literature. It was proposed that this behaviour is a preadaptation for the evolution of egg rejection behaviour in hosts of avian brood parasites, which are primarily passerines. Indeed, the same motor skills underlie nest sanitation and egg rejection behaviours. This “nest sanitation hypothesis” predicts that non-egg-shaped objects (i.e. simulated debris) are rejected more frequently than egg-shaped objects (i.e. simulated parasitic eggs), and the frequency of rejection mirrors the expected frequency of debris falling into the nest, rather than the risk of parasitism. We update information on nest sanitation processes (e.g. timing of defecation relative to faecal sac removal) and synthesize lists of objects removed from nests by passerines in non-experimental and experimental contexts. In the former, passerines remove various objects from their nests, including faecal sacs, parasitic invertebrates, vegetation and dead nestlings. Results of experiments reveal that non-egg-shaped objects, especially those most resembling debris, were more frequently rejected from nests, and that rejection of non-egg-shaped objects was generally constant among nesting stages prior to hatching.

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21.1 Introduction

Passerine birds have long been reported to remove objects from their nests that are neither eggs nor live nestlings (hereafter “debris”), such as faecal sacs and eggshells (i.e. Plutarch *in* Skutch 1976). Nest sanitation behaviour, or nest cleaning behaviour, likely plays a crucial role in keeping nests dry and free of parasites, reduces attraction of predators and facilitates egg turning during incubation (Guigueno and Sealy 2012). Birds may ingest debris or grasp it between their mandibles and drop it at a distant disposal site. Birds may push debris aside (Hoover 2003), which provides eggs or nestlings access to the main part of the cavity, or they may desert their nest and nest site altogether. These responses resemble egg rejection, a behaviour that is reported in many hosts of brood parasites. Nest sanitation behaviour may be a preadaptation to egg rejection behaviour, as hypothesized by Guigueno and Sealy (2012). Here, we review new information on nest sanitation behaviour and extend implications for its importance in the evolution of egg rejection behaviour within the context of avian brood parasitism.

How nests are ridded of debris depends on the type to be removed. Faecal sacs produced by younger nestlings may be consumed at the nest by the parents, who gain water (Morton 1979) and enhanced nutrition (McGowan 1995), in addition to conserving energy that would be required to carry faecal sacs far enough away to avoid attracting predators (McGowan 1995; Guigueno and Sealy 2012). As chicks age and become larger, with more effective digestive tracts, parents may carry the sacs away (Guigueno and Sealy 2012). Not all debris can be grasped and carried away, however, especially when it is large relative to the size of the birds. For example, yellow warblers (*Setophaga petechia*) buried experimentally added, large non-egg-shaped objects, but ejected smaller objects of the same shape (Guigueno and Sealy 2009). Burial is a form of clutch abandonment in which the adult bird buries the foreign object (debris or egg) along with its own eggs and superimposes a new nest above the previous nest and eggs (Mico 1998; Guigueno and Sealy 2010). Thus, the bird abandons its nest but not the nest site. Nest desertion is another form of clutch abandonment in which the bird deserts its nest and nest site (Guigueno and Sealy 2010). When cleaning their nests, therefore, passerines may ingest debris, carry it away, bury it in their nest (hereafter burial) or desert their nest and nest site (nest desertion).

Anti-parasite defences resemble responses to debris. Yellow warblers, hosts of brown-headed cowbirds (*Molothrus ater*), and great reed warblers (*Acrocephalus arundinaceus*), hosts of common cuckoos (*Cuculus canorus*), have been reported to bury and desert parasitic eggs and experimentally added non-egg-shaped objects in the context of studies on nest sanitation (Bártol et al. 2003; Moskát et al. 2003; Guigueno and Sealy 2009). In both yellow warblers and great reed warblers, burial and desertion are also considered anti-parasite strategies (Sealy 1995; Lotem et al. 1995; Moskát and Honza 2002). In a study of 60 populations from 35 host species of brown-headed cowbirds, Hosoi and Rothstein (2000) concluded that desertion is an evolved response to brood parasitism—hosts that incur large costs when parasitized have higher desertion rates among non-forest species, which more frequently

encounter cowbirds, than among forest species. Few or no cowbird hosts desert solely in response to the cowbird egg (Sealy 1995; Hosoi and Rothstein 2000). Interaction with the parasite may be a necessary cue for nest desertion as has been reported in yellow warblers (Guigueno and Sealy 2011) and meadow pipits (*Anthus pratensis*), the latter, hosts of the common cuckoo (Moksnes and Røskoft 1989). Unlike hosts that eject parasitic eggs, visual egg discrimination is not necessary for hosts to bury or desert parasitized clutches. Recent research has demonstrated that these hosts rely more on tactile cues than ejectors to assess clutch volume before determining whether to bury or desert parasitized clutches (Guigueno and Sealy 2012; Guigueno et al. 2014). Tactile input from debris in the nest may also elicit nest sanitation, as yellow warblers that ejected star-shaped objects first settled on their clutch before removing them (Guigueno and Sealy 2009). As such, tactile input, that is, assessment of the volume and shape of debris or parasitic egg relative to the size of the nest cavity, may be implicated in determining whether debris or a parasitic egg is removed by ejection, burial or desertion, all methods used in the context of both nest sanitation and brood parasitism.

21.2 Non-experimental Objects Removed From the Nests

21.2.1 Faecal Sacs

Passerines constantly encounter debris in their nests that may or may not be removed. Faecal sacs are the most frequently reported debris removed from nests (Table 21.1). In fact, many researchers measure only faecal sac removal when quantifying nest sanitation behaviour. The removal of faecal sacs is widespread among passerines, with 227 *Birds of North America Online* species accounts out of 229 reporting faecal sac removal (Guigueno and Sealy 2012). In Table 21.1, we listed 37 passerine families in which faecal sac removal has been reported, more than any other type of non-experimental object removed from nests.

Parents remove faecal sacs by ingesting them or carrying them to a distant drop site. Faecal sacs of passerines are encapsulated in a mucous covering, which provides a physical barrier from the pathogenic enteric bacteria inside the sac (Ibáñez-Álamo et al. 2014a). Recently, Quan et al. (2015) demonstrated that nestling defecation is stimulated by feeding in red-whiskered bulbuls (*Pycnonotus jocosus*), rather than occurring at a set time after feeding. Such plasticity minimizes soiling of the nest and its contents and allows for cooperation between the adults and nestlings, described earlier by Blair and Tucker (1941). Nestlings wait for a feeding to defecate, at which time the parent is available to either ingest or carry away the faecal sac (Quan et al. 2015). Ingesting faecal sacs eliminates transportation and disposal costs, but because faecal sacs contain waste products, they may tax the adults' digestive tract (Hurd et al. 1991), even though the mucous covering of faecal sacs has been shown to have an antimicrobial function (Ibáñez-Álamo et al. 2014a). As such, adults normally shift from ingesting smaller faecal sacs early in the nestling period to carrying larger faecal sacs away when nestlings are older (Guigueno and Sealy 2012). Adults must carry

Table 21.1 Objects removed by passerines in a non-experimental context

Object	Passerine families		References
Faecal sacs	Tyrannidae	Sittidae	Guigueno and Sealy (2012)
	Furnariidae	Certhiidae	
	Menuridae	Nectariniidae	
	Acanthizidae	Mimidae	
	Neosittidae	Sturnidae	
	Laniidae	Muscicapidae	
	Vireonidae	Turdidae	
	Rhipiduridae	Muscicapidae	
	Corvidae	Cinclidae	
	Paridae	Passeridae	
	Remizidae	Ploceidae	
	Hirundinidae	Motacillidae	
	Alaudidae	Fringillidae	
	Pycnonotidae	Parulidae	
	Phylloscopidae	Icteridae	
	Leiothrichidae	Calcariidae	
	Regulidae	Emberizidae	
	Troglodytidae	Cardinalidae	
Polioptilidae			
Invertebrates	Tyrannidae	Turdidae	Guigueno and Sealy (2012)
	Vireonidae	Prunellidae	Bolopo et al. (2015)
	Corvidae	Parulidae	Cantarero et al. (2013)
	Paridae	Icteridae	
	Sittidae	Cardinalidae	
	Mimidae		
Eggshells	Tyrannidae	Sturnidae	Guigueno and Sealy (2012)
	Corvidae	Prunellidae	
	Picathartidae	Fringillidae	
	Phylloscopidae	Parulidae	
	Leiothrichidae	Icteridae	
	Mimidae	Emberizidae	
	Turdidae		
Feathers	Acanthizidae		Guigueno and Sealy (2012)
Leaves, twigs and other vegetation	Corvidae		Guigueno and Sealy (2012)
	Acrocephalidae		Bolopo et al. (2015)
	Emberizidae		
Uneaten food	Tyrannidae	Turdidae	Guigueno and Sealy (2012)
	Corvidae		Bolopo et al. (2015)

(continued)

Table 21.1 (continued)

Object	Passerine families		References
Dead nestlings	Tyrannidae	Fringillidae	Guigueno and Sealy (2012) Kirkpatrick et al. (2009)
	Vireonidae	Parulidae	
	Troglodytidae	Icteridae	
	Mimidae	Calcariidae	
	Sturnidae	Emberizidae	
	Turdidae		

faecal sacs far enough from the nest to avoid attracting predators (but see Ibáñez-Álamo et al. 2014b), as predation has been shown experimentally to increase when the distance between eggs and faeces decreased (Petit et al. 1989). In addition, water pipits (*Anthus spinoletta*; Hendricks 1987) and northern wheatears (*Oenanthe oenanthe*; Brooke 1981) flew significantly farther from the nest when they carried a faecal sac than when they did not. Apparently, faecal sacs do not attract invertebrate parasites (Ibáñez-Álamo et al. 2016), but a potential antimicrobial function of the sacs suggests that their removal protects the nestlings and parents from harmful microorganisms (Ibáñez-Álamo et al. 2014a). In sum, removal of faecal sacs involves cooperation between nestlings and parents to keep the nest clean, potentially avoiding the attraction of predators and reduces exposure to harmful microorganisms.

21.2.2 Invertebrates

Passerines may also remove invertebrates from their nests and nestlings, which was reported in 11 families (Table 21.1). Invertebrates removed from the nest include blowflies (*Protophthora* spp.) (Hurtrez-Boussès et al. 2000) and hen fleas (*Ceratophyllus gallinae*) (Christie et al. 1996). Removal of invertebrates was highest in a species with the highest infestations levels (Cantarero et al. 2013). Invertebrate load may be so great that adults forage and sleep less to increase nest sanitation, which may reduce their survival after the breeding period (Christie et al. 1996; Tripet et al. 2002). As such, this high cost suggests that ridding nests of invertebrates is of paramount importance.

21.2.3 Eggshells

We reported eggshell removal from 12 passerine families (Table 21.1). It is beneficial for parents to remove eggshells from their nests as it prevents egg capping (i.e. eggshell adhering to intact, unhatched eggs) and injury to the hatched chicks, in addition to potentially reducing attraction of the nests to predators and invertebrate parasites. As with faecal sacs, eggshells may be eaten piecemeal at the nest or carried away by the parents before being dropped (Nethersole-Thompson and

Nethersole-Thompson 1942; Smith 1950; Winkler 2004; Guigueno and Sealy 2012). Because embryos extract about 80% of their skeletal calcium from the eggshell, the remaining shell probably provides limited nutrition (Simkiss 1961; Jones 1976), although eggshells may be used as grit (Nethersole-Thompson and Nethersole-Thompson 1942). Although other types of nest sanitation, namely, faecal sac removal, is “practically confined” to passerines and their allies, eggshell removal is frequently observed in other groups, such as gulls (Nethersole-Thompson and Nethersole-Thompson 1942; Tinbergen et al. 1962). Related to eggshell removal, passerines also remove broken eggs, but this declines abruptly during hatching, possibly so that parents do not remove their own pipped egg (Kemal and Rothstein 1988; Mallory et al. 2000; McMaster and Sealy 1997). As such, the removal of broken eggs is a type of nest sanitation behaviour that differs from other types because normally the removal of objects does not decline around pipping. In addition to laying their egg in hosts nests, some brood parasites, such as great spotted cuckoos (*Clamator glandarius*) and shiny cowbirds (*Molothrus bonariensis*), may puncture eggs already present in the nest (Soler et al. 1997, 1999; Gloag et al. 2012). The hosts, in turn, remove these punctured eggs (Soler et al. 1997, 1999; Gloag et al. 2012). In sum, although the removal of eggshells may provide only limited nutritional benefit when ingested, it seems to be a form of nest sanitation that is more widespread, occurring in non-passerines.

21.2.4 Dead Nestlings

The removal of dead nestlings was recorded in 11 families (Table 21.1). Removing dead nestlings eliminates the subsequent production of scents and bacteria associated with decomposition that could attract predators and invertebrate parasites. Dead nestlings are normally carried and dropped away from the nest. Brewer’s blackbirds (*Euphagus cyanocephalus*) disposed of dead nestlings in areas normally used to drop faecal sacs (Welty 1982). Kirkpatrick et al. (2009) observed removal of entire broods of dead nestlings by yellow-eyed juncos (*Junco phaeonotus*) and red-faced warblers (*Cardellina rubrifrons*), which apparently had starved due to inclement weather. In these cases, empty nests do not necessarily indicate a predation event (Kirkpatrick et al. 2009). A partial predation event in which some dead chicks are left behind could also elicit their subsequent removal from the nest by the parents, leaving the nest empty and appearing as though the brood was completely depredated. In sum, some or all of the chicks may be removed from a nest if they are dead and carried away before being dropped.

21.2.5 Feathers, Vegetation and Uneaten Food

The removal of feathers, vegetation such as twigs and leaves, and uneaten food has been reported less frequently, but this type of behaviour was recorded in seven families (Table 21.1).

21.3 Nest Sanitation Hypothesis

As stated above, nest sanitation may reduce predation (and presumably disease), thereby increasing fitness. Removing foreign eggs also increases the host's fitness in the context of brood parasitism. There are at least three hypotheses related to the evolution of nest sanitation and egg rejection that could be expected: (1) There is no interaction between nest sanitation and egg rejection (i.e. they develop independently from each other); (2) nest sanitation is a preliminary stage for egg rejection, and well-developed nest sanitation behaviour results in the ability of hosts to reject parasitic eggs; and (3) egg rejection behaviour may affect nest sanitation as a side effect. The most plausible version may be (2) (but see Luro and Hauber 2017), although (2) and (3) are not mutually exclusive and little research has been conducted on (3). Many passerines demonstrate nest sanitation outside the context of brood parasitism, and, clearly, nest sanitation predates anti-parasitic defences in passerine birds. Consequently, nest sanitation behaviour may be a preadaptation for the evolution of egg rejection behaviour in hosts of avian brood parasites (hypothesis (2); Moskát et al. 2003; Guigueno and Sealy 2009). As proposed by Moskát et al. (2003), there are testable predictions associated with the nest sanitation hypothesis. First, the more an object departs from the shape of an egg, the more likely it will be rejected. Second, the frequency of rejection will be constant across pre-nestling stages (e.g. egg laying and incubation) because debris would be expected to occur at a similar frequency across them (Moskát et al. 2003; Guigueno and Sealy 2009, 2012). In sum, egg rejection by hosts of brood parasites is likely to evolve first by hosts rejecting all non-egg-shaped objects and second via the evolution of egg recognition (Moskát et al. 2003).

21.4 Non-egg-Shaped Objects Added to Nests in Experimental Contexts

Various types of non-egg-shaped objects have been experimentally added to nests of passerines (Table 21.2). Eight families have been included in such studies: Corvidae, Hirundinidae, Mimidae, Turdidae, Passeridae, Acrocephalidae, Parulidae and Icteridae (Table 21.2). Examples of object shapes include cubes, rectangles, stars, discs/other flat objects, cylinders and dumbbells (two partial spheres glued together at their flat ends) (Fig. 21.1; Table 21.2). The non-egg-shaped objects included in the experiments were all artificial except for peanut shells (Yang et al. 2015a, b), reed stems (Bártol et al. 2003), pine cone bract scale (Peer 2017) and Douglas fir leaf clipping (Luro and Hauber 2017) (Table 21.2).

Across studies, non-egg-shaped objects were rejected more frequently than round or egg-shaped objects (Table 21.2). Non-egg-shaped objects were rejected by ejection, burial or nest desertion at 6–100% of nests, whereas egg-shaped or round objects added to nests in the same studies were rejected at 0–69% of nests (Álvarez et al. 1976; Ortega and Cruz 1988; Ortega et al. 1993; Bártol et al. 2003; Hoover 2003; Moskát et al. 2003; Underwood and Sealy 2006; Guigueno and

Table 21.2 Non-egg-shaped objects experimentally added to nests of brood-parasitic hosts during the pre-nesting stages

Species	Non-egg-shaped object	% rejected (total <i>n</i>)	% egg-shaped or round object rejected (total <i>n</i>)	Reference
Eurasian magpie (<i>Pica pica</i>)	Cubes	Cubes (<i>n</i> = 16) rejected significantly faster than oval models (<i>n</i> = 18) and real eggs (<i>n</i> = 20)		Álvarez et al. (1976)
Barn swallow (<i>Hirundo rustica</i>)	Half peanut shell	100 (25)	34 (62)	Yang et al. (2015a)
Barn swallow (<i>Hirundo rustica</i>)	Stick model	80 (60)	48 (62)	Yang et al. (2015b)
	Coin model	74 (50)		
	Half peanut shell	93 (28)		
Red-rumped swallow (<i>Cecropis daurica</i>)	Stick model	20 (15)	0 (14)	Yang et al. (2015b)
	Half peanut shell	15 (13)		
Grey catbird (<i>Dumetella carolinensis</i>)	Cylinders, rectangles, cubes	58 (42)	21 (42)	Underwood and Sealy (2006)
American robin (<i>Turdus migratorius</i>)	Cylinders, rectangles, cubes	60 (42)	37 (43)	Underwood and Sealy (2006)
	Douglas fir leaf clipping	97 (32)	65 (35)	Luro and Hauber (2017)
Eurasian Tree sparrow (<i>Passer montanus</i>)	Flat cut-out models (egg and square shaped)	81.7 (60 ^a)	36.8 (19)	Poláček et al. (2013)
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	Reed stems	88 (16)	Not measured	Bártol et al. (2003)
	Coins	91 (33)		
	Sticks	96 (50)	69 (51)	Moskát et al. (2003)
	Discs	91 (44)		
Yellow warbler (<i>Setophaga petechia</i>)	Stars	27 (139)	11 (200)	Guigueno and Sealy (2009)
	Dumbbells	6 (148)		
Prothonotary warbler (<i>Protonotaria citrea</i>)	Dice	45 (20)	40 (40)	Hoover (2003)

Red-winged blackbird (<i>Agelaius phoeniceus</i>)	Flagging tape	100 (23)	0 (53)	Peer (2017)
	Pine cone bract scale	100 (10)		
	Bead with hole	77 (26)	22 ^b (89)	Ortega et al. (1993)
	Dowel (cylinder)	9 (23)		
	Star	95 (22)		
Yellow-headed blackbird (<i>Xanthocephalus xanthocephalus</i>)	Various non-egg-shaped objects (beads, pom-poms, oblong, stars)	98 (44)	21 (195)	Ortega and Cruz (1988)
	Various non-egg-shaped objects (beads, pom-poms, oblong, stars)	100 (6)	7 (83)	Ortega and Cruz (1988)

^a60 nests each tested with two objects

^bRound beads with hole filled in

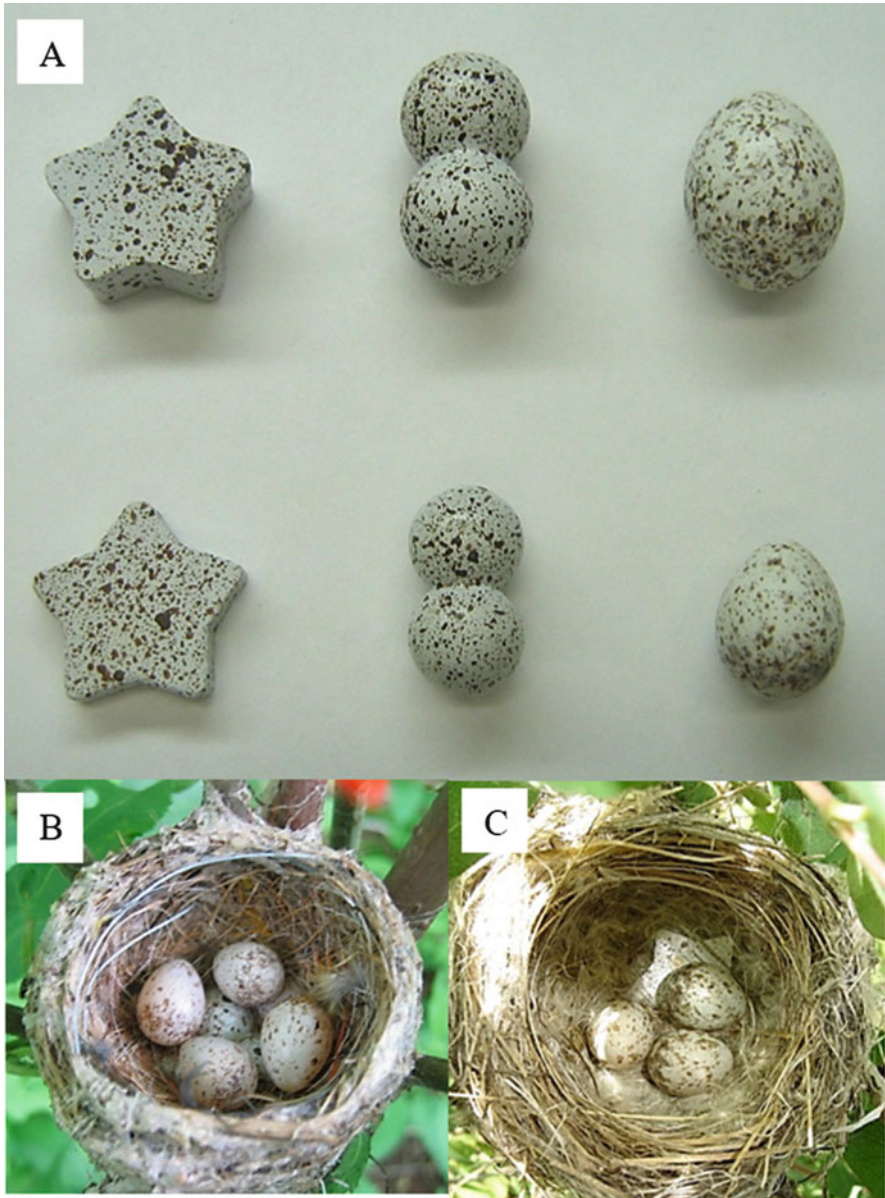


Fig. 21.1 (a) Examples of non-egg-shaped objects added to the nests of a host of a brood parasite. These objects were added to the nests of yellow warblers, with larger objects on the top row and smaller objects on the bottom row (Guigueno and Sealy 2009). From left to right: Stars, dumbbells and real eggs (brown-headed cowbird egg on top, yellow warbler egg at bottom). (b) A large dumbbell buried with two warbler eggs, with a new clutch of four eggs laid on top. (c) A small star selectively buried, with the warbler eggs untouched

Sealy 2009; Poláček et al. 2013; Yang et al. 2015a; Luro and Hauber 2017; Peer 2017; Table 21.2). We counted each species in each study as a data point (i.e. two species in one study plus one species in another study as three data points). Out of the 15 data points in which the responses to non-egg-shaped objects and round or egg-shaped objects were measured simultaneously within the same study, all 15 data points indicated that all or some of the non-egg-shaped objects for each data point were rejected more frequently and/or more quickly than round or egg-shaped objects (Table 21.2). Only two data points recorded that other types of non-egg-shaped objects were not rejected more frequently than round or egg-shaped objects (Ortega et al. 1993; Guigueno and Sealy 2009). Objects diverge from the shape of an egg as the number of edges increases (Guigueno and Sealy 2009). For example, star-shaped objects are less similar to the shape of an egg than a cylinder or a dumbbell (Fig. 21.1a). Guigueno and Sealy (2009) reported that dumbbells, which may have appeared and felt like two host eggs, were not rejected more frequently than a cowbird egg, unlike stars (Fig. 21.1a). Similarly, Ortega et al. (1993) reported that cylinders were not rejected more frequently than round beads with holes filled in, unlike stars and beads with holes. The more an object resembles debris, therefore, the more likely, it seems, that it is to be rejected.

Rejection of non-egg-shaped objects remained constant between pre-incubation, when the risk of parasitism was high, and incubation, when the risk of parasitism was lower, if the cost of rejection also remained the same. Eurasian magpies (*Pica pica*), grey catbirds (*Dumetella carolinensis*), American robins (*Turdus migratorius*) and Eurasian tree sparrows (*Passer montanus*), whose bills were large enough relative to the size of non-egg-shaped objects, removed them by ejection but rejected the objects at similar frequencies between nesting stages (Álvarez et al. 1976; Underwood and Sealy 2006; Poláček et al. 2013). Great reed warblers and yellow warblers, however, resorted to alternate forms of rejection, depending on the object (Moskát et al. 2003; Guigueno and Sealy 2009). Both small (warbler egg volume) and large (double the volume of a warbler egg) non-egg-shaped objects were added to the nests of yellow warblers (Guigueno and Sealy 2009). Small objects were ejected or buried on their own (i.e. no warbler eggs were buried in the process; Fig. 21.1c), whereas large objects were buried with warbler eggs, which normally occurs when cowbird eggs are buried (Fig. 21.1b; Guigueno and Sealy 2009). As such, rejection of large objects was costlier than rejection of small objects, both in time and energy required to lay a new clutch. It follows that small objects were rejected at a similar frequency in pre-incubation and incubation stages, whereas large objects were rejected more frequently in pre-incubation (Guigueno and Sealy 2009). Similarly, there was no difference in the rejection frequency between pre-incubation and incubation in great reed warblers, but ejection replaced nest desertion in incubation when the clutch was complete (Moskát et al. 2003). Abandoning the entire clutch in incubation is costlier than abandoning one or two eggs in pre-incubation (Guigueno and Sealy 2010). In sum, the removal of non-egg-shaped objects is stable across pre-hatching stages, unless precluded by rejection costs, which is consistent with the nest sanitation hypothesis.

Egg ejection may be elicited by the process of keeping nests clean. Barn swallows (*Hirundo rustica*), which are intermediate egg rejecters, were more likely to reject a non-mimetic model egg if a half peanut shell was added to the nest at the same time (Yang et al. 2015a). Similarly, the frequency of egg rejection tended to increase with the increase in rejection frequency of non-egg-shaped objects across different barn swallow populations (Yang et al. 2015b). Red-rumped swallows (*Cecropis daurica*), which accept non-mimetic eggs, rejected non-egg-shaped objects less frequently than barn swallows, which suggests brood parasitism may in turn increase the rejection frequency of non-egg-shaped objects (Yang et al. 2015b). In contrast to Yang et al. (2015a), red-winged blackbirds (*Agelaius phoeniceus*) were *not* more likely to reject a model cowbird egg, with its maculation but different background colour, if the model egg was simultaneously added to the nest with flagging tape or a pine cone bract scale (Peer 2017). Similarly, having American robins remove a Douglas fir leaf clipping from their nests did not influence whether they removed a model cowbird egg from their (Luro and Hauber 2017). Possibly, the half peanut shell used by Yang et al. (2015a) elicited a stronger sanitation response because it was more voluminous and roughly shaped than the tape or bract scale used by Peer (2017) or the fir leaf clipping in Luro and Hauber (2017), which then influenced subsequent egg rejection. In addition, the model egg added to barn swallow nests was immaculate blue, whereas barn swallow eggs are spotted against a white background. Barn swallows may have received a more salient visual cue than red-winged blackbirds or American robins in removing the model egg. All things considered, nest sanitation may elicit egg rejection.

Concluding Remarks and Future Directions

Costs and benefits of keeping a nest clean merit further study. For example, we know little of the costs of ingestion of faecal sacs versus carrying them away and whether these costs change over the nestling stage as the faecal sacs get larger, in the context of adult survival and reproduction. Identifying species with marked differences in nest sanitation behaviour, such as house finches (*Haemorrhous mexicanus*), which do not clean their nests, and understanding the nature of these differences will allow us to more clearly test the importance of nests sanitation in the context of brood parasitism.

Nest sanitation seems to be complex, containing several different behavioural elements. Some of these elements are similar to each other (i.e. removing a twig versus a leaf from a nest) or completely different (i.e. removing faecal sacs versus invertebrate parasites). Future studies should take into consideration these differences, in respect to nesting stages (laying, incubation and nestlings).

Results from experiments with non-egg-shaped objects support the hypothesis that nest sanitation is a preadaptation for the evolution of egg rejection in hosts of brood parasites. Debris-like objects were rejected more frequently

(continued)

than egg-like objects, and rejection remained constant across egg laying and incubation. Nevertheless, answers to some questions are unclear, such as what is the degree to which nest sanitation influences egg rejection versus brood parasitism? Studies examining the responses of non-egg-shaped objects in parasitized versus unparasitized populations of the same host species may enhance our understanding of the potential side effect of brood parasitism on nest sanitation behaviour. Likewise, more studies addressing whether nest sanitation elicits egg rejection at the same nests, which use robust phylogenetic comparisons, are needed as they simultaneously test whether nest sanitation influences egg rejection in the same individual. Lastly, studies examining the responses of hosts to non-egg-shaped objects throughout the nesting stages (egg laying, incubation and nestling) will determine whether rejection of these objects is more pronounced when nest sanitation in a non-experimental context is increased at the nestling stage via the removal of faecal sacs. Although some evidence exists for the hypothesis that nest sanitation is a preadaptation for egg rejection in hosts of brood parasites, such future studies are essential to more clearly understand its potential role.

Acknowledgements We thank the reviewers, Csaba Moskát, Manolo Soler and Canchao Yang for constructive comments on the earlier drafts of this chapter.

References

- Álvarez F, de Reyna LA, Segura M (1976) Experimental brood parasitism of the magpie (*Pica pica*). *Anim Behav* 24:907–916
- Bártol I, Moskát C, Karcza Z, Kisbenedek T (2003) Great reed warblers bury artificial objects, not only cuckoo eggs. *Acta Zool Acad Sci H* 49:111–114
- Blair RH, Tucker BW (1941) Nest sanitation. *Br Birds* 34:206–215, 226–235, 250–255
- Bolopo D, Canestrari D, Marcos JM, Baglione V (2015) Nest sanitation in cooperatively breeding carrion crows. *Auk* 132:604–612
- Brooke M d L (1981) How an adult wheatear (*Oenanthe oenanthe*) uses its territory when feeding nestlings. *J Anim Ecol* 50:683–696
- Cantarero A, López-Arrabé J, Rodríguez-García V, González-Braojos S, Redondo AJ, Moreno J (2013) Factors affecting the presence and abundance of generalist ectoparasites in nests of three sympatric hole-nesting bird species. *Acta Ornithol* 48:39–54
- Christie P, Richner H, Oppliger A (1996) Of great tits and fleas: sleep baby sleep. *Anim Behav* 52:1087–1092
- Gloag R, Fiorini VD, Reboreda JC, Kacelnik A (2012) Brood parasite eggs enhance egg survivorship in a multiply parasitized host. *Proc R Soc B Biol Sci* 279:1831–1839
- Guigueno MF, Sealy SG (2009) Nest sanitation plays a role in egg burial by yellow warblers. *Ethology* 115:247–256
- Guigueno MF, Sealy SG (2010) Clutch abandonment by parasitized yellow warblers: egg burial or nest desertion? *Condor* 112:399–406

- Guigueno MF, Sealy SG (2011) Aggression towards egg-removing cowbird elicits clutch abandonment in parasitized yellow warblers, *Dendroica petechia*. *Anim Behav* 81:211–218
- 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, Westphal AM (2014) Rejection of parasitic eggs in passerine hosts: size matters more for a non-ejecter. *Auk* 131:583–594
- Hendricks P (1987) Foraging patterns of water pipits (*Anthus spinoletta*) with nestlings. *Can J Zool* 65:1522–1529
- Hoover JP (2003) Experiments and observations of prothonotary warblers indicate a lack of adaptive responses to brood parasitism. *Anim Behav* 65:935–944
- Hosoi SA, Rothstein SI (2000) Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Anim Behav* 59:823–840
- Hurd PL, Weatherfaed PJ, McRac SB (1991) Parental consumption of nestling feces: good food or sound economics? *Behav Ecol* 2:69–76
- Hurtrez-Boussès S, Renaud F, Blondel J, Perret P, Galan MJ (2000) Effects of ectoparasites of young on parents' behaviour in a Mediterranean population of blue tits. *J Avian Biol* 31:266–269
- Ibáñez-Álamo JD, Ruiz-Rodríguez M, Soler JJ (2014a) The mucous covering of fecal sacs prevents birds from infection with enteric bacteria. *J Avian Biol* 45:354–358
- Ibáñez-Álamo JD, Ruiz-Raya F, Roncalli G, Soler M (2014b) Is nest predation an important selective pressure determining fecal sac removal? The effect of olfactory cues. *J Ornithol* 155:491–496
- Ibáñez-Álamo JD, Ruiz-Raya F, Rodríguez L, Soler M (2016) Fecal sacs attract insects to the nest and provoke an activation of the immune system of nestlings. *Front Zool* 13:3
- Jones PJ (1976) The utilization of calcareous grit by laying *Quelea quelea*. *Ibis* 118:575–576
- Kemal RE, Rothstein SI (1988) Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. *Anim Behav* 36:175–183
- Kirkpatrick C, Conway CJ, Ali MH (2009) Sanitation of entire broods of dead nestlings may bias cause-specific nest failure rates. *Ibis* 151:207–211
- Lotem A, Nakamura H, Zahavi A (1995) Constraints on egg discrimination and cuckoo-host co-evolution. *Anim Behav* 49:1185–1209
- 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
- Mallory ML, Rendell WB, Robertson RJ (2000) Responses of birds to broken eggs in their nests. *Condor* 102:673–675
- Markman S, Yom-Tov Y, Wright J (1996) The effect of male removal on female parental care in the orange-tufted sunbird. *Anim Behav* 52:437–444
- McGowan KJ (1995) A test of whether economy or nutrition determines fecal sac ingestion in nesting corvids. *Condor* 97:50–56
- McMaster DG, Sealy SG (1997) Red-winged blackbirds (*Agelaius phoeniceus*) accept prematurely hatching brown-headed cowbirds (*Molothrus ater*). *Bird Behav* 12:67–70
- Mico MA (1998) Yellow warbler nests: structure, building materials and cowbird parasitism. MSc thesis, University of Manitoba, Winnipeg, 89 pp
- Moksnes A, Røskaft E (1989) Adaptations of meadow pipits to parasitism by the common cuckoo. *Behav Ecol Sociobiol* 24:25–30
- Morton ML (1979) Fecal sac ingestion in the mountain white-crowned sparrow. *Condor* 81:72–77
- Moskát C, Honza M (2002) European cuckoo *Cuculus canorus* parasitism and host's rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus arundinaceus* population. *Ibis* 144:614–622
- Moskát C, Székely T, Kisbenedek T et al (2003) The importance of nest cleaning in egg rejection behaviour of great reed warblers *Acrocephalus arundinaceus*. *J Avian Biol* 34:16–19
- Nethersole-Thompson C, Nethersole-Thompson D (1942) Egg-shell disposal by birds. *Br Birds* 35:162–169

- Ortega CP, Cruz A (1988) Mechanisms of egg acceptance by marsh-dwelling blackbirds. *Condor* 90:349–358
- Ortega JC, Ortega CP, Cruz A (1993) Does brown-headed cowbird egg coloration influence red-winged blackbird responses towards nest contents? *Condor* 95:217–219
- Peer BD (2017) Nest sanitation does not elicit rejection in a brown-headed cowbird host. *Anim Cogn* 20:371–374
- 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
- Quan RC, Li H, Wang B, Goodale E (2015) The relationship between defecation and feeding in nestling birds: observational and experimental evidence. *Front Zool* 12:21
- Sealy SG (1995) Burial of cowbird eggs by parasitized yellow warblers: an empirical and experimental study. *Anim Behav* 49:877–889
- Simkiss K (1961) Calcium metabolism and avian reproduction. *Biol Rev* 36:321–359
- Skutch AF (1976) Parent birds and their young. University of Texas Press, Austin
- Smith S (1950) The yellow wagtail. Collins, London
- Soler M, Soler JJ, Martínez JG (1997) Great spotted cuckoos improve their reproductive success by damaging magpie host eggs. *Anim Behav* 54:1227–1233
- Soler M, Soler JJ, Pérez-Contreras T (1999) The cost of host egg damage caused by a brood parasite: experiments on great spotted cuckoos (*Clamator glandarius*) and magpies (*Pica pica*). *Behav Ecol Sociobiol* 46:381–386
- Tinbergen N, Broekhuysen GJ, Feekes F, Houghton JCW, Kruuk H, Szulc E (1962) Egg shell removal by the black-headed gull, *Larus ridibundus* L.; a behaviour component of camouflage. *Behaviour* 19:74–116
- Tripet F, Glaser M, Richner H (2002) Behavioural responses to ectoparasites: time-budget adjustments and what matters to blue tits *Parus caeruleus* infested by fleas. *Ibis* 144:461–469
- Underwood TJ, Sealy SG (2006) Influence of shape on egg discrimination in American robins and gray catbirds. *Ethology* 112:164–173
- Welty JC (1982) The life of birds. WB Saunders, Philadelphia
- Winkler DW (2004) Nests, eggs, and young: breeding biology of birds. In: Podulka S, Rohrbaugh RW Jr, Bonney R (eds) *Handbook of bird biology*, 2nd edn. Princeton University Press, Ithaca, pp 1–152
- Yang C, Chen M, Wang L, Liang W, Møller AP (2015a) Nest sanitation elicits egg discrimination in cuckoo hosts. *Anim Cogn* 18:1373–1377
- 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 Cogn* 18:355–360