

Review



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Signal detection and optimal acceptance thresholds in avian brood parasite–host systems: implications for egg rejection

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Signal detection theory addresses the challenge of successfully identifying informative signals in noisy information contexts, allowing optimal behavioural decisions in diverse ecological contexts. The optimal acceptance threshold hypothesis proposed by Reeve (Reeve 1989 *Am. Nat.* **133**, 407–435. (doi:10.1086/284926)) is an elegant theoretical model to predict the flexibility of acceptance thresholds for conspecific discrimination. This model has provided a robust framework used to explore recognition systems in a broad range of contexts such as animal communication, nest-mate discrimination or anti-parasitic host responses. In this review, we discuss key concepts related to the optimal acceptance threshold hypothesis applied to egg rejection decisions in avian brood parasite–host interactions. We explore those factors determining signal detectability in parasitized nests and how hosts adjust their rejection decisions to both the risk of parasitism and the potential costs associated with egg rejection. In addition, we discuss recent results that challenge some traditional assumptions of the optimal acceptance threshold hypothesis and provide a novel perspective to explore rejection decisions, such as the existence of single-threshold decision rules or acceptance decisions. An integrative view combining current evidence with traditional theory is needed to further advance the comprehension of optimal acceptance thresholds.

This article is part of the theme issue ‘Signal detection theory in recognition systems: from evolving models to experimental tests’.

1. Introduction

Throughout their lives, individuals face diverse challenges that require the identification of signals in random and noisy information contexts in which rapid responses and accurate decisions are often crucial for individual reproduction and survival [1]. Optimal decision making is especially important in those contexts in which costs of errors are expected high, such as avoiding predation [2] or prey choice tasks [3]. Signal detection theory (SDT) provides an elegant framework to study how individuals meet the challenge of identifying signals in noise (i.e. random patterns affecting a receiver’s performance [4]) and has been widely used to explore the decision-making process through which animals distinguish desirable from undesirable stimuli [5]. Such recognition systems are defined by three essential components: the nature of the cues used by individuals to acquire a signal (the production component), the mechanisms that allow the processing of recognition cues and that differentiate signals from noise (the perception component) and the coordination for the behavioural response (the action component) [4,5]. In essence, SDT assumes that an optimal individual performance depends on the payoffs of four mutually exclusive outcomes: correct detection, false alarm, missed detection and correct rejection [4], where the probabilities of each of these potential outcomes occurring are determined by both the signal detectability and the individuals’ threshold to respond [4]. SDT has been widely used by ecologists during past decades and has been decisive in further advancing our understanding of sensory thresholds in diverse fields such as animal communication (e.g.

recognition of mate or offspring calls) [6] or signal discrimination by pollinators [7].

In the light of SDT, Reeve [5] developed the optimal acceptance threshold (OAT) hypothesis to predict optimal decisions in the context of conspecific recognition. Besides the production component (i.e. the nature of the stimulus used by an individual to differentiate stimulus) and the perception component (i.e. the internal template to which individuals compare the perceived cues in order to classify recipients), Reeve's model introduced an action component to predict optimal, or evolutionarily stable, acceptance thresholds above which the stimulus would be rejected. Acceptance thresholds are determined by the degree of dissimilarity between an individual internal template and the perceived stimulus. The OAT hypothesis has been used in a range of recognition systems, such as nest-mate recognition in eusocial wasps [8], same-sex sexual behaviour in insects [9] and egg rejection behaviour in brood parasite–host systems [10].

Despite having been studied in a variety of taxa, from fishes to insects, birds have become a pivotal model for exploring coevolutionary relationships between brood parasites and their hosts [11]. Obligate avian brood parasites, which account for approximately 1% of birds [12], lay their eggs in the nests of other individuals and exploit the parental care that they provide to their offspring [13]. This reproductive strategy often is extremely costly for the host species since parasitic chicks frequently kill or evict all host offspring, or they are better at competing for food [12,14,15]. In response, many hosts have evolved successive lines of defences comprising strategies operating at all stages of the reproductive cycle, prominent among which are nest defence, egg and chick rejection or reluctance to feed parasitic fledglings [15,16]. Anti-parasitic defences in turn select for the evolution of sophisticated parasite counter-defences, leading to a sequence that may result in coevolutionary processes [14,16–18].

Coevolutionary interactions between brood parasites and their hosts are, to some extent, a battle for egg mimicry in which hosts must do their best to successfully detect and respond to parasitic eggs. Recognition and rejection of parasitic eggs are probably the most effective and widespread defences used by hosts to mitigate the pernicious consequences of brood parasitism [12,14,15,19], which often selects for egg mimicry on the part of brood parasites [20]. At this point, the coevolutionary arms race becomes even more complex, as both brood parasites and hosts are able to evolve polymorphic eggs in order to evade egg rejection and egg mimicry, respectively [21–24]. The astonishing inter- and intraspecific variation existing in anti-parasitic host responses has motivated extensive research on the egg rejection behaviour during the past decades. As a result, egg rejection has been well studied in many brood parasite–host systems [15], where flexible defences have been found to be crucial for hosts to maximize their fitness [25].

The signal detection model and the OAT hypothesis provide a useful framework to study rejection decisions in the context of avian brood parasitism [10,26–28]. In this review, we address some key concepts in relation to the OAT hypothesis and egg rejection decisions, such as signal detectability or the role of flexible acceptance thresholds. Moreover, we provide some insights into current advances in the study of host cognitive performance, as well as the largely neglected role of egg acceptance decisions.

2. Signal detectability

An optimal host performance requires that parasitized individuals successfully acquire and process information to realize the presence of a foreign egg in their nests [29]. The cognitive process underlying egg recognition is determined by two essential components: the nature of the cognitive stimulus involved in the recognition process and the cognitive abilities showed by the actor [25]; that is, the production and the perception components according to the OAT model [5]. At the proximate level, host cognitive abilities have been found to have a strong genetic basis, which determines the frequencies of potential 'rejecters' and 'acceptors' within host populations [30,31]. However, hosts can rely on different cognitive decision rules to identify foreign eggs within their clutches. These cognitive mechanisms have been well studied during the past decades in light of the pioneering studies conducted by Stephen Rothstein, who initially proposed two alternative scenarios for egg rejection decisions [32,33]. Hosts may reject the most dissimilar eggs by comparing them to the other eggs in the clutch (discordance mechanisms) or, alternatively, recognize foreign eggs by comparing their visual features to an innate or learned template of their own eggs' appearance (template-based mechanism or 'true recognition'). Whereas discordance mechanisms have been proved to be important for some hosts species, empirical evidence suggests that most hosts rely on template-based mechanisms for egg recognition [34–36]. However, hosts can maximize information about parasitic cues by combining template-based and discordance mechanisms [37]. As predicted by the OAT hypothesis, as uncertainty increases (e. g. higher ratio of parasitic to host eggs), egg rejection probabilities decrease and greater differences in egg appearance are needed by hosts to reach rejection decisions, which might result in rejection errors [37,38].

Besides such a cognitive basis, successful anti-parasitic host responses first require that signals (e. g. the parasitic egg) are detectable in a noisy environment (e. g. the clutch). In the framework of SDT, signal detectability can be understood as the distance between the peaks of the probability distributions for parasite and host egg appearance (figure 1), where the degree of overlap in parasite and host egg appearance represents stimuli dissimilarity (the production component, in terms of Reeve [5]). Thus, when signal detectability is weak (e.g. highly mimetic parasitic eggs), the risk of incurring both acceptance and rejection errors increases, such that finely tuned cognitive abilities are required on the part of hosts in order to make successful rejection decisions [25]. The OAT hypothesis predicts that parasitized individuals should respond to variations in the degree of dissimilarity between own and parasitic eggs [5], which has been supported by numerous studies showing that rejection probability increases as parasitic eggs look more different from the host's eggs (e.g. [34,39–41]).

In response to egg rejection, some brood parasites have evolved astonishing egg mimicry aimed at reducing detectability, with better matching when hosts show strong rejection abilities [20,42]. This strategy may be counteracted by hosts by reducing differences in appearance between eggs in a single clutch [43]. Lower intraclutch variation would make it easier for hosts to detect odd eggs, especially under discordance mechanisms, while high intraclutch variation would make egg recognition difficult under template-based mechanisms as greater perceived phenotypic variability in the own eggs would likely increase the probability that the foreign

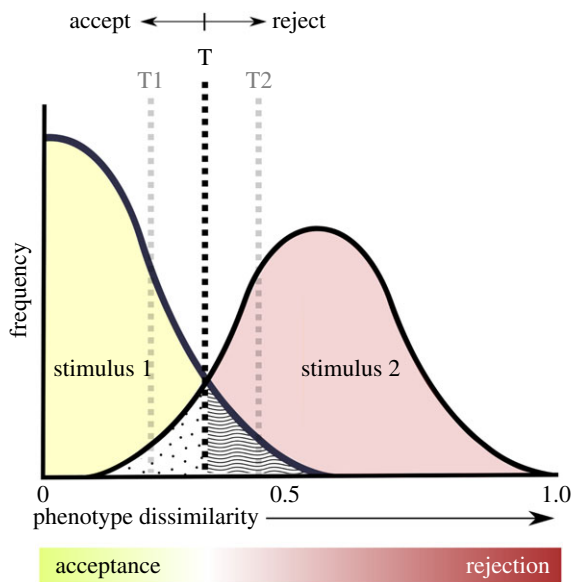


Figure 1. Frequency distributions of dissimilarity in egg appearance between hosts and brood parasites. Stimulus 1 represents eggs that should not be rejected by the host (i.e. host's own eggs), while stimulus 2 represents eggs that should be rejected (i.e. parasitic eggs). T (black dotted vertical line) represents the optimal threshold above which parasitic eggs will be rejected. The area to the right of the acceptance threshold represents rejection decisions, in which the wavy area corresponds to rejection errors and the red area represents correct rejection decisions. To the left of the threshold, both acceptance errors (i.e. recognition errors) and acceptance decisions are represented by the dotted area. T1 and T2 represent a more restrictive or permissive threshold, respectively. (Online version in colour.)

egg's appearance overlaps host eggs' appearance [28]. Reduced intraclutch variation has been found to play an important role in several common cuckoo (*Cuculus canorus*) hosts. For example, both reed warblers (*Acrocephalus scirpaceus*) [44] and great reed warblers (*Acrocephalus arundinaceus*) [45] eject non-mimetic eggs at higher rates in those nests showing lower intraclutch variation. Despite this, experimental evidence supporting the evolution of reduced intraclutch variation is mixed, and several studies have pointed out that intraclutch variation has less influence on rejection decisions than previously thought [46,47].

In most cases, eggshell coloration and patterns provide reliable sources of information determining rejection decisions [42,48,49]. According to the OAT hypothesis' predictions, most studies assume that host rejection decisions are based on the absolute appearance dissimilarity between parasite and host eggs (reviewed in [50]). This cognitive decision rule involves the existence of 'multiple thresholds' settled on each extreme of the parasitic egg's phenotypic range [38,50]. However, because of pigmentary constrictions, eggshell coloration often ranges from blue-green to brown through the avian colour space [51]. Recent studies using experimental eggs within a gradient of natural variations in eggshell appearance have provided novel results that challenge traditional assumptions on the perceptual decision rules used by hosts. Hanley *et al.* [50] found that some species of *Turdus* thrushes in Europe and North America directed their rejection decisions towards specific eggshell colours (brownier eggshells) instead of responding to absolute colour dissimilarity between parasitic and host eggs. Contrary to the traditional view, these results demonstrate that

rejection decisions may be biased toward one extreme of the phenotypic range ('single-threshold' decision rule), preventing host responses from being predicted by absolute perceptual differences between host and parasite egg appearance. Although it remains to be further explored, current evidence suggests that rejection decisions based on a single threshold might be widespread among host species. For instance, great reed warblers have been found to use differences across a natural blue-green to brown colour gradient to respond towards cuckoo parasitism [52]. A similar decision rule has also been documented in the chalk-browed mockingbird (*Mimus saturninus*), a common host of the shiny cowbird (*Molothrus bonariensis*) whose rejection decisions, while modulated by the eggshell spotting patterns, are biased towards brown eggs over blue-green eggs along a gradient of natural eggshell coloration [38]. Finally, recent research has shown that single-threshold decision rules are also used by common redstarts (*Phoenicurus phoenicurus*), a cavity-nesting host exploited by the common cuckoo [53]. Colour categorization, essential in diverse ecological contexts [3,54], has been proposed to underly decision rules associated with single-acceptance thresholds [38,50]. Hence, although the traditional hypothesis constitutes a valid and valuable framework to explore rejection decisions, an integrative perspective is needed to further comprehend the visual and cognitive processes guiding rejection decisions.

3. Flexible acceptance thresholds

The OAT hypothesis was initially developed to predict flexible adjustments in individual acceptance threshold to respond to variable recognition contexts [5]. Flexible responses towards parasitic eggs were predicted by theoretical models [26,27,55,56] and later found in several brood parasite–host systems (reviewed in [25]). Hosts would benefit from flexible thresholds by maximizing the fitness payoffs between the benefits of egg rejection and the costs associated with erroneously rejecting own eggs (figure 1). If the host's acceptance threshold is too permissive, the probability of acceptance errors will increase; instead, if the threshold is too restrictive, then the probabilities of incurring rejection errors would increase [5]. In order to optimize their individual performance, hosts are expected to adjust their acceptance thresholds according to the environmental context, so thresholds would become more restrictive as recognition errors and the risk of parasitism increase [5,57].

Learning is an essential component of animal cognition that has proven crucial for individual decision making [58], so hosts are expected to modify their thresholds in accordance to their individual prior experience with brood parasitism [27,56]. Hauber *et al.* [10] experimentally demonstrated that great reed warblers can vary their rejection decisions based on prior experience with parasitic eggs. In their study, the authors found that warblers ejected near-mimetic parasitic eggs at higher rates when they were previously exposed to experimental non-mimetic eggs, while naïve hosts without previous experience with parasitic eggs typically accepted near-mimetic eggs experimentally introduced into their nests. These results demonstrate that individual experience with brood parasitism leads to shifts in thresholds even within a single breeding attempt so that they become more restrictive when parasitism predictability

is high. Even in those cases in which consistency in egg rejection is high, prior experience with brood parasitism can yet impact rejection decisions as some hosts might reduce their ejection latency in subsequent events of parasitism, which confirms the importance of the learning component [59].

The host's ability to adjust their rejection decision to previous experience may, however, be used by brood parasites to force more permissive acceptance thresholds. For instance, experimental studies have demonstrated that hosts accept parasitic eggs in order to avoid the retaliation behaviour exhibited by some brood parasites. By systematically punishing rejecter hosts (i.e. predating those host clutches in which the parasitic egg disappeared), the great spotted cuckoo (*Clamator glandarius*) induces changes in magpies' (*Pica pica*) rejection decisions (i.e. increasing egg acceptance) during subsequent parasitism events [60–62]. This mafia-like strategy has also been described in a phylogenetically distant brood parasite, the brown-headed cowbird (*Molothrus ater*), which victimizes prothonotary warblers (*Protonotaria citrea*), a small passerine that reduces rejection decisions in response to previous interaction with the parasite [63].

Similarly to previous experience with brood parasitism, the presence of brood parasites near the host nest has been found to increase the probability of egg rejection [64–68]. Adjustments in acceptance thresholds occur in response to spatial variations in parasitism pressures and enable hosts to minimize the costs associated with egg rejection [25]. For instance, reed warblers have been found to respond differently to brood parasitism depending on the local risk of parasitism in different populations that are not genetically isolated [69,70], even when the parasitic eggs are detected [71]. In addition to geographical variations in brood parasitism, rapid changes in parasitism pressure across the breeding season or over a few years may lead to shifts in acceptance thresholds, giving hosts an optimal performance under a variable risk of parasitism [72–74]. Of course, an accurate assessment of the available cues will be needed for hosts to successfully track changes in the current risk of parasitism [25].

Flexible adjustments in acceptance thresholds probably have a strong endocrine basis as circulating levels of certain hormones, such as testosterone, corticosterone or prolactin, are expected to play key roles in parental decisions related to egg rejection [75]. Indeed, brood parasitism has been found to affect hosts' levels of both corticosterone and prolactin, as well as their energetic state [76], which could significantly affect thresholds for egg rejection. The study of the host physiology would therefore provide valuable information on the proximate mechanisms underlying flexible responses towards brood parasitism.

Besides the existence of flexible acceptance thresholds, as well as shifts in fixed thresholds over evolutionary time, temporal variations in hosts' responses to brood parasitism might also reflect changes in the perception component. In this regard, Liebert & Starks [57] highlighted the need to distinguish between flexible thresholds (i.e. context-dependent changes in acceptance thresholds' permissiveness) and flexible templates (i.e. updatable templates that can change by incorporating new information). Individual experience with own eggs during the first breeding attempt enables hosts to learn their own eggs' appearance and to establish an internal template for egg recognition, which are crucial to achieve optimal rejection decisions under imprinting-like

mechanisms (i.e. true recognition) [32,34,77]. This is the case in great reed warblers, where young breeders were more prone to accept parasitic eggs compared to experienced females [39,78]. But template-based mechanisms can also be costly if naïve individuals imprint on parasitic eggs during the first breeding attempt, a misimprinting process that can be used by some parasites to defeat egg recognition and force egg acceptance in future parasitism events [79]. However, recent experimental evidence suggests that learning may occur beyond the first breeding attempt so that updated recognition templates may be acquired at each subsequent breeding attempt [80], a mechanism that is widespread among host species [28,34,39]. Such updatable templates, along with flexible acceptance thresholds, provide hosts with the most dynamic type of responses towards brood parasitism and may be crucial to reach optimal rejection decisions.

4. A focus on acceptance decisions

Egg recognition (i.e. the cognitive process through which hosts identify a foreign egg as a parasitic egg [29]) is expected to result in rejection decisions enabling hosts to mitigate the costs of brood parasitism and maximize individual fitness [12]. But does egg rejection necessarily follow egg recognition? Instead of exploring the perception component of recognition systems, most egg rejection studies have focused on the action component, which prevents us from reaching accurate conclusions about egg recognition. Rejection rates have been widely used to infer recognition abilities in most brood parasite–host systems (e.g. [19,23,34,81–84]), so the absence of response (i.e. egg acceptance) has often been interpreted as a lack of recognition. This assumption is valid in many cases. For example, some birds exploited by brood parasites, as is the case for some cowbird hosts in North America, show a low rejection rate because the recent contact with the parasite has prevented the evolution of suitable recognition abilities [85]. On the other hand, recognition abilities are not expected to evolve in those cases in which egg acceptance is adaptive [26] and, when they evolve, highly mimetic eggs are more likely to be accepted as they are more difficult for hosts to detect [86,87]. Despite this, some studies have pointed out that the absence of response does not necessarily imply the absence of recognition (see below), so it is possible that some acceptances are not acceptance errors, but acceptance decisions.

The OAT hypothesis predicts that individual decisions will be determined by the location of the threshold [4]. Certain environmental factors (e.g. low risk of parasitism) are expected to result in more permissive thresholds leading to the acceptance of eggs that would be ejected under a different context. Although the OAT hypothesis provides a strong model for the study of flexible rejection decisions that considers the occurrence of acceptance errors, current evidence suggests that, in some cases, the absence of response to parasitic eggs might reflect acceptance decisions instead of recognition failures. The detailed study of the different stages guiding the egg rejection process (i.e. judgement, decision and action) has led to a better comprehension of host decision making and has shed light on the relationships between egg recognition and rejection decisions [25]. The existence of flexible acceptance thresholds implies that egg acceptance, often considered evidence of acceptance errors

(dotted area in figure 1), is not necessarily a consequence of recognition failures, but may instead reflect acceptance decisions as hosts may recognize more eggs than they reject [28,71,86,88–90]. Egg acceptance may be motivated by the high potential costs of egg rejection in contexts of low risk of parasitism [86,89], especially in those cases where physical constraints linked to egg characteristics increase potential costs [90]. For example, some egg characteristics, such as egg size or weight, have been found to specifically affect the action stage of the egg rejection process, leading to the acceptance of experimental eggs that were recognized as foreign eggs [86,90]. In other cases, a decrease in brood parasitism pressures, or the retaliatory behaviour showed by some brood parasites, may lead hosts to accept parasitic eggs [25]. These results suggest that some hosts may not be willing to assume the potential costs of egg rejection under certain circumstances (e.g. low risk of parasitism), therefore resulting in acceptance decisions.

5. How to evaluate host cognitive performance?

From a signal detection perspective, an optimal cognitive performance implies that hosts are able to match the perceived cues against the internal recognition template in order to classify the focal stimulus. Potential acceptance decisions prevent hosts' recognition abilities from being inferred from rejection rates, raising the need for cognitive abilities (i.e. the perceptual component) to be assessed separately from host responses (i.e. the action component) [25,29]. However, the exhaustive study of the perceptual component in rejection decisions poses an important challenge for behavioural ecologists as individual sensory perception and cognitive performance cannot be directly observed. By filming the host behaviour at the nest, behavioural ecologists have advanced the study of the proximate mechanisms underlying rejection decisions while minimizing disturbance to birds (table 1), which has improved our knowledge on the link between recognition abilities and rejection behaviour.

Clutch inspection behaviour has been used to infer cognitive performance in different brood parasite–host systems (table 1), arguing that the time spent by hosts looking at parasitized clutches is a useful proxy of their recognition abilities [92]. Guigueno & Sealy [88] found that both accepter and rejecter yellow warblers (*Setophaga petechia*) significantly increased their inspection time in response to both brown-headed cowbird and non-mimetic experimental eggs added to their nests, with egg rejection probability increasing as warblers spent more time inspecting their clutches. Increased inspection behaviour in response to experimental parasitism has also been evidenced in several cuckoo hosts [87,97]. But could these long inspection times indicate that more time is needed to perceive the presence of parasitic eggs in their nest? Some cuckoo hosts inspecting their clutches for longer periods often show a lower ejection latency compared to those individuals that spent less time in clutch inspection tasks, which confirms the link between clutch inspection and egg recognition since individuals would need time to process visual stimuli associated with the presence of parasitic eggs [89,92,93]. However, beyond the perceptual component, increased inspection time might also reflect that hosts inspecting their clutches for a longer period of time need more time to reach rejection decisions [86,89]. In line with this, recent studies with the

Eurasian blackbird (*Turdus merula*) have found that females that spend more time inspecting their clutches delay [86] and reduce [97] rejection decisions compared to those individuals that engage more briefly with clutch inspection tasks.

Other studies have focused on those tactile mechanisms that allow hosts to gather additional information about egg identity and assess the potential costs linked to egg ejection [29,86,89,90]. Pecking behaviour, which has often been interpreted as puncture trials preceding failed ejection attempts [93,94], is directed exclusively to experimental eggs and constitutes a clear demonstration of egg recognition in egg-puncturing species [89,94], nest-deserter species [99] and grasp ejectors [99]. Likewise, egg-touching behaviour during the first visual contact with parasitic eggs has been considered a genuine response of hosts towards parasitic eggs [97], suggesting that egg recognition may occur immediately after the first arrival to the parasitized nest [86,87,90,97]. Such egg touches mainly occur as a response to experimental parasitism, being almost completely absent in control nests in which this behaviour probably corresponds to bird behaviours not directly related to egg recognition (e.g. probing behaviour) [86,90]. Although erroneous attributions could also be expected in experimental nests at similar rates, they likely involve a very small proportion of the touching behaviour found in these nests, where the number of touches is mainly predicted by egg mimicry [86]. Moreover, hosts do not increase the number of touches after the experimental introduction of a conspecific egg (i.e. highly mimetic eggs) in their nests [87], which unequivocally demonstrates the link between touching behaviour and egg recognition.

Recent research has revealed that the gathering and integration of available information are not limited to the onset of incubation, but cues necessary for rejection decisions are perceived at different time points of the nest attendance period [100]. Despite this, the link between the egg-touching behaviour and egg recognition is uncertain during incubation, and egg rejection experiments have provided mixed results. In Eurasian blackbirds, the presence of highly non-mimetic eggs leads hosts to reduce incubation touches [61], while slightly non-mimetic eggs result in an increased touching behaviour during incubation [68]. Moreover, incubation touches can be predicted by the individual behaviour before the experimental parasitism [69]. These results suggest that incubation touches do not reflect a genuine response to brood parasitism; instead, this behaviour is probably related to those tasks inherent to incubation requirements, such as egg turning [101,102], which means that they are not a good proxy of egg recognition. Further research on the timing of cue acquisition is needed to fully understand the perceptual component allowing hosts to set optimal thresholds.

Besides behavioural responses to brood parasitism, new methodologies open up additional possibilities for the study of sensory and cognitive processes associated with the detection of parasitic eggs, such as potential changes in brain activity and neural function during egg recognition [103] or the link between brain lateralization and visual processing in egg recognition contexts [104]. Similarly, potential endocrine variations linked brood parasitism [75,76] can be used to elucidate the host ability to identify foreign eggs, as well as the effects of physiological changes in the cognitive performance of hosts [105]. Still little explored, these questions pose future research avenues that must be addressed in avian brood parasite–host systems.

Table 1. Review of the egg-rejection studies assessing hosts' egg recognition abilities separately from rejection decisions.

host species	brood parasite	egg mimicry	egg type	video-recording	experimental approach	acceptance decisions	reference
<i>Acrocephalus arundinaceus</i>	<i>Cuculus canorus</i>	mimetic	real	yes	pecking/clutch inspection	yes	[91]
<i>Acrocephalus arundinaceus</i>	<i>Cuculus canorus</i>	non-mimetic	real	yes	clutch inspection	no	[92]
<i>Acrocephalus palustris</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	real	yes	pecking behaviour	no	[93]
<i>Acrocephalus scirpaceus</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	artificial	no	pecking behaviour	yes	[71]
<i>Cercotrichas galactotes</i>	<i>Cuculus canorus</i>	non-mimetic	artificial/real	yes	pecking/clutch inspection	yes	[89]
<i>Cercotrichas galactotes</i>	<i>Cuculus canorus</i>	non-mimetic	artificial	yes	pecking behaviour	yes	[73]
<i>Hippolais pallida</i>	<i>Cuculus canorus</i>	non-mimetic	artificial/real	yes	pecking/clutch inspection	no	[94]
<i>Phylloscopus bonelli</i>	<i>Cuculus canorus</i>	non-mimetic	artificial	yes	touching behaviour	no	[95]
<i>Setophaga petechia</i>	<i>Molothrus ater</i>	near-mimetic/non-mimetic	artificial/real	yes	probing/clutch inspection	yes	[88]
<i>Sylvia atricapilla</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	artificial/real	yes	pecking behaviour	no	[96]
<i>Sylvia cantillans</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	artificial/real	yes	pecking behaviour	no	[96]
<i>Turdus merula</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	artificial	yes	pecking behaviour	no	[96]
<i>Turdus merula</i>	<i>Cuculus canorus</i>	non-mimetic	real	yes	touching behaviour	yes	[90]
<i>Turdus merula</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	real	yes	touching/clutch inspection	no	[87]
<i>Turdus merula</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	real	yes	touching behaviour	yes	[86]
<i>Turdus merula</i>	<i>Cuculus canorus</i>	mimetic	real	yes	pecking/clutch inspection	yes	[97]
<i>Turdus merula</i>	<i>Cuculus canorus</i>	mimetic/non-mimetic	real	yes	touching behaviour	no	[98]

6. Concluding remarks

During the past thirty years, the OAT hypothesis has provided a valuable framework for the study of egg rejection decisions. The original model proposed by Reeve [5] predicts flexibility in acceptance thresholds and is widely used to explore adjustment in the host responses to parasitic eggs. Hosts have been demonstrated to modify their rejection decisions according to both the reliability of recognition cues, previous experience with brood parasitism and the current risk of being parasitized. Recent research has provided important insights on both the cognitive basis and the conditional component of rejection decisions. Future studies must therefore integrate new discoveries with the traditional hypothesis to fully understand those

factors underlying rejection of parasitic eggs and its consequences for the coevolutionary interactions between brood parasites and their hosts.

Data accessibility. This article has no additional data.

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