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Disappearance of eggs from non-parasitized nests of brood parasite hosts – the evolutionary equilibrium hypothesis revisited

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ABSTRACT

The evolutionary equilibrium hypothesis was proposed to explain variation in egg rejection rates among individual hosts (intra- and interspecific) of avian brood parasites. Hosts may sometimes mistakenly reject own eggs when they are not parasitized, i.e. make recognition errors. Such errors would incur fitness costs and could counter evolution of host defences driven by costs of parasitism, i.e. creating equilibrium between acceptors and rejecters within particular host populations. Here, we report disappearance of host eggs from non-parasitized nests in populations of 7 European passerine species. Based on these data we calculate the magnitude of the balancing parasitism rate given that all eggs lost are due to recognition errors. Importantly, since eggs are known to disappear from nests for other reasons than erroneous host rejection, our data represent maximum estimates of such costs. Nonetheless, disappearance of eggs was rare events and incurred low costs compared to the high costs of parasitism. Hence, costs due to recognition errors are probably of minor importance as opposing selective pressure to evolution of egg rejection in most hosts. We cannot exclude the possibility that intermediate egg rejection rates in some host populations may be caused by spatiotemporal variation in occurrence of parasitism and gene flow, creating variable influence of opposing costs due to recognition errors and costs of parasitism.

KEYWORDS: Co-evolution; cuckoo; fitness cost; host defence; host-parasite interactions; disappearance of eggs

INTRODUCTION

In hosts of avian brood parasites, costs of parasitism impose strong selection for evolution of defensive traits because successful parasitism in many cases leads to total loss of host reproductive output. Therefore, many hosts have evolved fine-tuned egg rejection abilities, which in several cases have been countered by parasites evolving mimetic eggs (e.g. Payne, 1967; Brooke & Davies, 1988; Davies & Brooke, 1989a; Moksnes *et al.*, 1991; Antonov *et al.* 2006a; Starling *et al.* 2006; Spottiswoode & Stevens 2010; Stoddard & Stevens, 2010, 2011; Begum *et al.*, 2011). In some species, there is apparently no variation in rejection abilities either within or between populations, and rejection rates are more or less fixed at 100% (i.e. all individuals are capable of rejection) as long as the appearance of the parasitic egg is cognitively recognizable for the individuals in question (Stokke, Moksnes & Røskaft, 2005). However, even rejection rates of non-mimetic eggs are only moderate in several other host species, often showing prominent temporal and/or spatial variation (Brooke, Davies & Noble, 1998; Soler *et al.*, 1999; Stokke *et al.*, 2008), relying on additional cues other than egg appearance when deciding to reject parasitic eggs (i.e. conditional responses (Brooke *et al.*, 1998; Davies, 2000)). Such co-occurrence of acceptors and rejecters (either as fixed or flexible strategies) within a single host population is often explained by costs of making errors in recognition and rejection of foreign eggs, which could outweigh the benefits of egg rejection under specific circumstances (Rothstein, 1982a; Marchetti, 1992; Lotem, Nakamura & Zahavi, 1995; Davies, Brooke & Kacelnik, 1996; Takasu, 1998). Specifically, host individuals attuned to reject foreign eggs may mistakenly reject one of their own eggs in nests that are not parasitized (Stokke *et al.*, 2005; Røskaft *et al.*, 2002a). These costs obviously have fitness consequences because the resulting clutch size will be smaller than the optimal one. In theory, such errors are most likely to occur in hosts that have high variation in egg appearance within clutches (Davies & Brooke, 1989b; Lotem *et al.*, 1995; Stokke *et al.*, 2007), making it difficult for hosts to recognize and hence reject parasitic eggs. Thus, if parasitism rates are low or variable, the costs of making recognition errors could sometimes potentially be higher than the costs of parasitism. Such a scenario could result in equilibrium between acceptors and rejecters within particular host populations or, if costs due to recognition errors and rejection costs are high, even lead to acceptance being the optimal strategy (the evolutionary equilibrium hypothesis, Lotem & Nakamura, 1998).

However, the importance of recognition errors as an opposing selective force to egg rejection, at least in hosts of evicting parasites, has been questioned (Røskaft *et al.*, 2002a; Stokke *et al.*, 2002a). In brood parasites like honeyguides (Indicatoridae) and cuckoos (Cuculidae), the parasitic chick gets rid of all host eggs or young from the nest soon after hatching (Davies, 2000; Anderson *et al.*, 2009, Grim *et al.*, 2009; Spottiswoode & Koorevaar, 2012), enforcing high costs on host reproduction and hence strong selection for evolution of defences against parasitism, depending on the level of parasitism. Furthermore, estimating occurrence of recognition errors is not straightforward. It is well known that partial egg losses may be due to other causes than erroneous ejection of own eggs, like e.g. jostling or partial predation (e.g. Rothstein, 1982b; Lerkelund *et al.*, 1993). Hence, only constant monitoring of nests throughout the egg laying and incubation period can provide us with evidence for the occurrence of recognition errors. Without such monitoring, we cannot rule out the possibility that eggs may disappear for other reasons than erroneous host rejection and estimates of such costs are therefore in many cases likely to be higher than what is actually the case.

The objective of the present study is to report the disappearance of own eggs in actual and potential host species of common cuckoo *Cuculus canorus*. Based on these data, we estimate maximum costs of recognition errors and the parasitism rate that should balance these costs. We discuss our results in relation to current knowledge of co-evolutionary adaptations in cuckoos and their hosts.

MATERIAL AND METHODS

ESTIMATE OF PARASITISM RATE BALANCING MAXIMUM RECOGNITION ERRORS ESTIMATES

We acknowledge that the response to a parasitic egg may be conditional/plastic (Brooke *et al.*, 1998; Lindholm & Thomas, 2000; Soler, Martín-Vivaldi & Fernández-Morante, 2012). Furthermore, we realistically assume that host egg rejection behaviour has a genetic basis (Martín-Gálvez *et al.*, 2006). In the absence of parasitism, the frequency of rejecters in the population may decline due to recognition errors, but also due to other costs related to maintaining specific traits or due to stochasticity (Lahti, 2005, 2006). In populations experiencing parasitism above a certain threshold level, selection will likely lead to rejecters producing more offspring than acceptors because rejecters escape the costs of parasitism. We use the model presented by Davies & Brooke (1989b) to derive average reproductive success of acceptor and rejecter pairs (RS_{acceptor} and RS_{rejecter}) and the corresponding balancing parasitism rate, p^*. Let p be the parasitism rate (probability of a host nest being parasitized). Average reproductive success of acceptor pairs (both sexes are acceptors) is

$$RS_{\text{acceptor}} = F(1 - p) + c\,(F - 1)\;p$$

where F is the average host clutch size and c is the proportion of host young reared together with a parasitic chick ($0 \leq c \leq 1$). Typically, for evicting brood parasites like *Cuculus* cuckoos, $c = 0$ (but see Rutila, Latja & Koskela, 2002), but for non-evicting parasites, c can be larger. We assume that cuckoo females remove one host egg from the nest when parasitizing the nest (Davies, 2000), even though removal of more than one egg is not uncommon (Øien *et al.*, 1998). Average reproductive success of rejecter pairs (at least one breeding individual is rejecter), where all parasite eggs are rejected is

$$RS_{\text{rejecter}} = (F - \Delta F)(1 - p) + (F - \Delta F - 1)\, p$$

where ΔF denotes recognition errors expressed as the number of host eggs lost by rejecters. Since only rejecters are likely to commit recognition errors, we need to take egg rejection rates within the population into account when calculating ΔF as follows

ΔF = [Proportion of host eggs lost from unparasitized nests in population] [Mean clutch size in population] / [Egg rejection rate in population] (1)

At equilibrium, the average reproductive success, $RS_{\text{acceptor}} = RS_{\text{rejecter}}$, we obtain the parasitism rate, p^*, that balances the benefit of rejecting parasite eggs with the cost of rejecting own eggs in non-parasitized nests (recognition errors) as

$$p^* = \Delta F/(F - 1)/(1 - c)$$

In some species, host individuals show phenotypic plasticity in their responses against parasites (based on social cues; Campobello & Sealy (2011), based on personality, Avilés & Parejo (2011), based on perception of risk of parasitism, Welbergen & Davies (2009)) and parasitic eggs, and hosts will more likely reject eggs if they experience additional cues other than the egg itself, like for instance observing a cuckoo in the vicinity of the nest (Moksnes *et al.*, 2000). Furthermore, the ability of individuals to reject parasitic eggs usually depends on the contrast between own and foreign eggs, i.e. egg mimicry (Davies, 2000; Spottiswoode &

Stevens, 2010). Hence, from Eq. 1 we obtain four estimates of ΔF; assuming that 1) all (RE1), 2) 50% (RE2), 3) 25% (RE3) and 4) observed % (RE4) of individuals in the population are able to reject foreign eggs. The estimate RE4 is based on rejection of experimental non-mimetic eggs in the specific study population (Table 1). We acknowledge that these four estimates are only crude attempts to take phenotypic plasticity into account in our calculations, but firstly we want to keep our calculations as simple as possible, and secondly, we lacked reliable quantitative estimates of phenotypic plasticity. By calculating four estimates, at least some of the phenotypic plasticity present at the individual level in specific populations is taken into account.

EMPIRICAL DATA IN DISAPPEARANCE OF EGGS AND OTHER RELEVANT FACTORS

Data on disappearance of own eggs in non-parasitized nests were retrieved from own field studies in which nests were monitored throughout the egg laying and incubation periods. We retrieved 1) number of host eggs lost from unparasitized host nests in the specific population; 2) mean clutch size in the specific population (F); and 3) rejection rate of experimentally added, non-mimetic eggs within the study populations. In addition, we also retrieved 4) observed parasitism rate within each population (Table 1). The number of eggs lost in each population, termed “number of disappeared eggs”, was calculated as the number of eggs lost from non-parasitized nests / total number of non-parasitized nests (excluding nests that were naturally or experimentally parasitized). We only included nests with single host eggs lost, because disappearance of more than one egg could indicate partial predation rather than actual errors in recognition. Hence, in our marsh warbler *Acrocephalus palustris* population we omitted cases where three out of four eggs (N = 1), and four out of five eggs (N = 2) disappeared. In our corn bunting *Miliaria calandra* population we omitted cases where two out of three eggs (N = 1), three out of five eggs (N = 1), and four out of five eggs (N = 1) disappeared. We also omitted clutches where egg laying did not follow the “one egg per day” criterion. More specifically this refers to two extraordinary cases in the chaffinch *Fringilla coelebs* population, with an irregular egg laying sequence (Stokke *et al.*, 2002a). Furthermore, loss of all eggs in the clutch was considered to be caused by predation, and such nests were omitted from the calculations.

Nests were monitored daily from nest building until six days of incubation to allow estimates of disappearance of own eggs from non-parasitized nests. Eggs were marked with permanent ink in the sequence they were laid. Clutch size was estimated from completed, non-parasitized clutches. Nests used to calculate recognition errors and clutch size were different from those used to calculate rejection rate of experimentally added, non-mimetic eggs.

Disappearance of eggs from non-parasitized nests were estimated in 8 study populations (Table 1): (1) great reed warblers *Acrocephalus arundinaceus* in Apaj, Hungary (1998-2008), (2) great reed warblers in Embalse del Hondo, Alicante, Spain (XXXX-XXXX), (3) reed warblers *Acrocephalus scirpaceus* in Embalse del Hondo, Alicante, Spain (XXXX-XXXX), (4) marsh warblers in Zlatia, Bulgaria (2002-2009), (5) olivaceous warblers *Hippolais pallida* in Zlatia, Bulgaria (2001-2009), (6) chaffinches in Stjørdal, Norway (1999-2001), (7) bramblings *Fringilla montifringilla* in Tana, Norway (2003-2004), and (8) corn buntings in Zlatia, Bulgaria (2002-2009). All these species are known to be parasitized by common cuckoos to various extents (Moksnes & Røskaft, 1995). Data on clutch sizes, parasitism rates, and rejection rates of experimentally added, non-mimetic eggs were retrieved from the literature for the same populations from which we obtained data on disappearance of eggs (Moksnes *et al.*, 1991; Moksnes, Røskaft & Solli, 1994; Bártol *et al.*, 2002; Moskát & Honza, 2002; Stokke *et al.*, 2002a, 2004; Antonov *et al.*, 2006a,b, 2007a,b, 2009; Hauber,

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Moskát & Bàn, 2006; Moskát *et al.*, 2008a,b,c, 2009; Avilés *et al.*, 2009; Vikan *et al.*, 2009, 2010, 2011). A few data from unpublished studies were also included; in the Spanish reed warbler population (number 3 in the list above), rejection data of non-mimetic eggs refer to experimentally added eggs painted pale blue.

RESULTS

Disappearance of eggs from non-parasitized nests was most pronounced in great reed and reed warblers (7 - 7.4%). In the remaining species, eggs disappeared in only 0 - 0.9% of the nests (Table 1). Individuals in the populations included in our analyses experienced 0 to 16.7% loss of own eggs in non-parasitized nests depending on how we consider rejection abilities (Table 1). Calculations of parasitism rates that would balance the costs of recognition errors (provided that all eggs lost were due to erroneous egg rejection) show considerable variation among species (Table 1, range 0 – 23.3%). Since only rejecters are assumed to erroneously reject own eggs, and our estimate of recognition errors is one fixed value per population, the cost of recognition errors and the corresponding balancing parasitism rate will be higher when fewer individuals are classified as rejecters (Equation 1). Hence, within particular populations, estimates of recognition errors and balancing parasitism rates will generally be higher when considering rejection of mimetic eggs than non-mimetic eggs, since the rejection rate for mimetic eggs in the population is generally lower than for non-mimetic eggs. If we assume that all individuals have the ability to reject eggs (100% rejection rate), estimates of both recognition errors and balancing parasitism rate can be regarded as minimum estimates.

The balancing parasitism rates are generally in the magnitude of 0 – 1.2%, except in great reed and reed warblers where it may reach 7.7 and 23.3% respectively, depending on calculation of the proportion of individuals that are able to reject parasitic eggs. In seven of the eight study populations, observed parasitism rates are equal to or higher than those required to balance the costs of making recognition errors, indicating that egg rejection abilities should evolve and be maintained, which is in accordance with the high rejection rates of non-mimetic eggs generally found in this study. Hence, recognition errors should not be important as opposing selection pressure in these populations. The only exception among these seven populations is the corn bunting, which experience a rather high parasitism rate but still only reject non-mimetic eggs at an intermediate level. The remaining population, Spanish reed warblers, experience a parasitism rate that is lower than the ones required maintaining rejection behaviour with all four estimates of recognition errors (Table 1).

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DISCUSSION

Perceptual errors may cause costs that could oppose evolution or maintenance of apparently optimal adaptations like those involved in co-evolutionary arms races. Such costs may act as opposing selective pressures against evolution of host defences against brood parasitism, as outlined in the evolutionary equilibrium hypothesis (Rothstein, 1982a; Lotem *et al.*, 1995; Davies *et al.*, 1996). Here we have shown that the magnitudes of such errors are in general low across eight different host populations, even with our overestimated rates of recognition errors. Furthermore, our estimates of recognition errors are comparable to those obtained from other species (Marchetti, 1992, 2000; Lotem *et al.*, 1995).

Several European passerines regarded as suitable cuckoo hosts show strong rejection of experimentally added eggs (Davies & Brooke, 1989a; Moksnes *et al.*, 1991; Moskát, Szentpéteri & Barta, 2002; Honza *et al.*, 2004; Lovászi & Moskát, 2004; Procházka & Honza, 2004; Rutila *et al.*, 2006; Samaš *et al.*, 2011; Table 1). Such species are often characterized by having a low intraclutch variation in egg appearance (Øien, Moksnes & Røskaft, 1995; Soler

& Møller, 1996; Stokke, Moksnes & Røskaft, 2002b), reducing the risk of making recognition errors and enhancing rejection of even moderately mimetic parasitic eggs (Stokke *et al.*, 2007; Moskát *et al.*, 2008a). Furthermore, several species may retain rejection behaviour in the absence of parasitism over very long time periods (Underwood, Sealy & McLaren, 2004; Lahti, 2006), and even after speciation events (Bolen, Rothstein & Trost, 2000; Rothstein, 2001; Peer & Sealy, 2004a) indicating that opposing selective pressures to egg rejection, like recognition errors, are negligible in these species. Even with the existence of recognition errors, rejection behaviour may be retained without apparent interspecific parasitism due to several reasons. Firstly, there may be unaccounted benefits to egg rejection behaviour, such as resistance to intraspecific brood parasitism, that maintain rejection behaviour and even cause it to increase in frequency (Grim *et al.*, 2011, Samaš *et al.*, 2011). Secondly, interspecific parasitism may still occur at a low rate without researchers being able to detect it. Hence, parasitism by cuckoos laying non-mimetic eggs (i.e. from a gens with another main host) may happen from time to time, but since such eggs would be ejected quickly the host population appears to be non-parasitized. Such “accidental” layings are not uncommon (Čapek, 1896; Chance, 1940), and the rate of which such events are occurring may be sufficient to retain rejection rates as apparent from the balancing parasitism rates reported in our study. For instance, Moksnes & Røskaft (1995) found 76 cuckoo eggs in chaffinches stored in European museums, and out of 58,000 cases of cuckoo parasitism from Europe collected by B.G. Stokke, 325 cases were recorded in chaffinch nests scattered all over Europe (unpublished data). The balancing parasitism rates estimated for chaffinches and bramblings in the present study are equal to zero, indicating that occasional parasitism by cuckoos is sufficient to retain high rates of egg rejection. Third, the retention of egg rejection in these species may be caused by immigration of rejecters from other populations that suffer high parasitism rates (Soler *et al.*, 2001). Hence, there are reports of chaffinches being utilized regularly by cuckoos in the European parts of Russia (Malchevsky, 1960), and bramblings are favoured hosts in parts of Fennoscandia (Vikan *et al.*, 2011).

On the other hand, our results also indicate that perceptual errors may be influential for the evolution of egg rejection in some cases. Hence, one of our study populations experience parasitism rates lower than the balancing parasitism rates. Reed warblers in Spain experience a parasitism rate of 2.0%, which is slightly lower than the calculated balancing parasitism rate (2.9 - 23.3%). In this population, egg rejection abilities should therefore deteriorate with time, based on our current estimates of recognition errors, provided that there is no immigration of rejecters from other populations, or as long as there are no large fluctuations in parasitism rate among years. Several studies have focused on the influence of recognition errors in reed warblers, although support for the importance of errors has been ambiguous (e.g. Davies & Brooke, 1988; Davies *et al.*, 1996; Røskaft *et al.*, 2002a; Čapek *et al.*, 2010). This species shows marked spatial variation in egg rejection related to parasitism pressure in the specific population (Lindholm & Thomas, 2000; Stokke *et al.*, 2008), indicating that there could be opposing selective pressures working against egg rejection in populations experiencing no or low parasitism. Alternatively, temporal variation in parasitism (Brooke *et al.*, 1998) may also lead to the same pattern with fluctuations in selective pressures depending on the current costs of parasitism. Furthermore, reed warblers have substantial intraclutch variation in egg appearance (Stokke *et al.*, 1999, 2002b) and are parasitized by cuckoos laying mimetic eggs (Davies & Brooke, 1988), making recognition of parasitic eggs error prone. In such cases, hosts may rely on conditional stimuli in perceiving the risk of parasitism (Rothstein, 1982a; Davies & Brooke, 1988, 1998; Stokke *et al.*, 2005, 2007). Hence, reed warblers are more likely to reject parasitic eggs when they observe a cuckoo close to the nest, indicating increased risk of parasitism (Davies & Brooke, 1988; Moksnes, Røskaft & Korsnes, 1993; Moksnes *et al.*, 2000). However, a recent study disclosed that the presence of a cuckoo does not necessarily lead to increased risk of making recognition errors (Čapek *et al.*, 2010). Careful investigations of reed warbler nests by utilizing video recordings should be undertaken to determine unambiguously if disappearance of eggs is due to erroneous rejection of own eggs.

Gene flow, not considered directly in the present study, may potentially slow down the process of evolving optimally expressed traits in particular populations or lead to local mal-adaptation (Nuismer, Thompson & Gomulkiewicz, 1999). Influx of rejecter or acceptor alleles may therefore influence expression of egg rejection in local populations. However, this critically depends on spatiotemporal variation in selection regimes (Duffy & Forde, 2009), like cuckoo parasitism and costs due to recognition errors, although at present such data are unavailable. Gene flow could also increase the frequency of rejecter alleles in non-parasitized or weakly parasitized populations (e.g. Røskaft *et al.*, 2002b, 2006; Moskát *et al.*, 2008b), thus causing errors to increase. Interestingly, there is low genetic differentiation among reed warbler populations in Europe, showing evidence of extensive gene flow among populations (Procházka *et al.*, 2011). The intermediate rejection of non-mimetic eggs in reed warblers and possibly in corn buntings may therefore be caused by a combined effect of costs of making recognition errors, gene flow and spatiotemporal variation in occurrence of parasitism creating a mosaic of situations in which the opposing costs vary in relative magnitude. Interestingly, the few studies available on corn buntings, indicate similar spatial variation in parasitism as in reed warblers. Hence, in Italy only 1.4% (N = 208) corn bunting nests were parasitized (Campobello & Sealy, 2009), which is profoundly different from the relatively high parasitism rate at our Bulgarian study site.

It is important to acknowledge that recognition errors are probably rarer events than estimated in the present study, because eggs may disappear from nests for many other reasons like e.g. jostling or partial predation (e.g. Rothstein, 1982b; Lerkelund *et al.*, 1993; Moksnes *et al.*, 2000; Røskaft *et al.*, 2002a). For instance, Moksnes *et al.* (2000) and Røskaft *et al.* (2002a) reported that cuckoos visited and partially depredated 12% of reed warbler nests without actually parasitizing them (see also Wyllie, 1975). Furthermore, cuckoos often remove one or two host eggs just prior to laying their own egg (Wyllie, 1975, 1981). If the host then rapidly ejects the parasitic egg, the loss of it's own egg(s) will appear to be self-inflicted to the observer even when this was not actually the case. Even with daily monitoring of nests such mistakes may take place.

In our approach, we focused only on hosts of cuckoos *Cuculus* spp. However, the same argument can be used for other brood parasitic systems. One important point to consider is calculations of the cost of parasitism. In the North American brown-headed cowbird *Molothrus ater*, the parasite chick does not evict host chicks leading to a lower cost of parasitism in most cases, but not always ($0 \leq c \leq 1$). We show that the balancing parasitism rate p^* increases as c increases and hence even smaller costs due to recognition errors oppose the evolution of rejection behaviour. Furthermore, even rejection costs, such as damage of own eggs when trying to reject the parasitic egg, can be important for opposing egg rejection in such hosts (Rohwer & Spaw, 1988; Røskaft & Moksnes, 1998) in contrast to cuckoo hosts where such costs are of minor importance (Stokke *et al.*, 2005, but see Antonov *et al.*, 2009). In addition, North American passerines in general have a higher intraclutch variation in egg appearance than comparable species in Europe, which may increase the risk of committing recognition errors (Stokke *et al.*, 2002b). However, in many cases the brown-headed cowbird egg is non-mimetic, many hosts experience very high parasitism rates, and especially smaller hosts also suffer high costs when raising a cowbird chick (Kilner, 2003). Therefore, lag in the evolution of egg rejection (perhaps due to lack of genetic background) is still the most plausible explanation for the lack of egg rejection in most hosts parasitized by cowbirds (Peer & Sealy, 2004b). However, other causes than recognition errors may cause apparently suboptimal rejection rates. For instance, costs of desertion due to nest site limitation (hole nesters), parasite mafia behaviour or few re-nesting opportunities may lead to acceptance of parasitic eggs (e.g. Soler *et al.*, 1995; Avilés, Rutila & Møller, 2005; Hoover & Robinson, 2007; Krüger, 2007, 2011).

By using empirical data on disappearance of own eggs from non-parasitized nests, we have shown that costs opposing evolution of egg rejection in hosts of avian brood parasites may exist but are in general small. Importantly, our estimates are most probably overestimates of true recognition errors, indicating that such costs in general are minute compared to the high costs of parasitism. Recognition errors seem most likely in species with specific characteristics like a high intraclutch variation in egg appearance, intermediate and variable rejection rate, spatiotemporal variation in occurrence of parasitism, and parasitism by brood parasites laying eggs that at least to some extent mimic host eggs, like in reed warblers and perhaps corn buntings. Future studies on the importance of recognition errors should focus on long-term studies of such "intermediate" rejecters at a spatiotemporal scale including several populations thus taking gene flow into account, while also considering phenotypic plasticity in host anti-parasite behaviour. By this approach, we should be able to obtain reliable estimates of variation in recognition errors, rejection rates and parasitism rates and address the importance of the various costs for the evolution of egg rejection. Finally, use of video cameras (e.g. Weidinger, 2010) would disclose the proportion of eggs that are actually lost by erroneous ejection of own eggs and not to other factors such as jostling or partial predation.

Our findings should be of importance for evaluating hypotheses set forward to explain variation in expression of defences in hosts. Further research should focus on clarifying how recognition errors promote selection for low intraclutch variation, an important antiparasite defence in hosts of brood parasites, as host eggs with extreme appearance are expected to be identified as parasitic eggs. We also suggest future research looking at how frequency of recognition errors might be characteristic for specific stages of the arms race between hosts and brood parasites.

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Table 1. Data used to calculate the balancing parasitism rate (%) required for opposing maximum estimates of costs due to recognition errors. The frequency of recognition errors is estimated as the proportion of own eggs lost out of all eggs laid ((ΔF/F)*100)) in non-parasitized nests assuming that 1) all (RE1), 50% (RE2), 3) 25% (RE3) of the individuals are capable of rejecting eggs. As a fourth estimate (RE4) we also consider the proportion of individuals in the population that are able to reject experimental non-mimetic eggs (see Equation 1 for calculation). *Individuals that recognized and pecked foreign eggs. **Rejection rate of non-mimetic eggs in Hungarian population used. Numbers in brackets refer to number of nests. See Methods for more details.

Species	Locality	Number of disappeared eggs	RE1 (%)	RE2 (%)	RE3 (%)	RE4 (%)	Parasitism rate (%)	Rejection rate, RE4 (%)	Clutch size	Balancing parasitism, RE1	Balancing parasitism, RE2	Balancing parasitism, RE3	Balancing parasitism, RE4
Acrocephalus arundinaceus	Hungary	4 (54)	1.53 (54)	3.07 (54)	6.13 (54)	1.61 (54)	59.4 (546)	95.2 (58)	4.83 (137)	1.9	3.9	7.7	2.0
A. arundinaceus	Spain	6 (86)	1.50 (86)	3.01 (86)	6.01 (86)	1.58(86)**	12.1 (116)	NA	4.64 (59)	1.9	3.8	7.7	2.0**
A. scirpaceus	Spain	17 (229)	2.09 (229)	4.18 (229)	8.36 (229)	16.73 (229)	2.0 (402)	12.5 (16)	3.55 (273)	2.9	5.8	11.6	23.3
A. palustris	Bulgaria	1 (157)	0.14 (157)	0.27 (157)	0.54 (157)	0.15 (157)	28.3 (532)	88.2 (17)	4.68 (159)	0.2	0.3	0.7	0.2
Hippolais pallida	Bulgaria	1 (113)	0.23 (113)	0.46 (113)	0.92 (113)	0.25 (113)	26.6 (128)	91.3 (23)*	3.85 (113)	0.3	0.6	1.2	0.3
Fringilla coelebs	Norway	0 (38)	0.00 (38)	0.00 (38)	0.00 (38)	0.00 (38)	0.0 (220)	87.0 (152)	4.75 (92)	0.0	0.0	0.0	0.0
F. montifringilla	Norway	0 (57)	0.00 (57)	0.00 (57)	0.00 (57)	0.00 (57)	0.0 (250)	78.4 (37)	6.02 (189)	0.0	0.0	0.0	0.0
Miliaria calandra	Bulgaria	1 (118)	0.17 (118)	0.34 (118)	0.69 (118)	0.30 (118)	14.6 (356)	56.5 (108)	4.93 (119)	0.2	0.4	0.9	0.4