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BROOD PARASITE-HOST COEVOLUTION IN AMERICA VERSUS EUROPE: EGG REJECTION IN LARGE-SIZED HOST SPECIES

COEVOLUCIÓN ENTRE PARÁSITOS DE CRÍA Y SUS HOSPEDADORES EN AMÉRICA VERSUS EUROPA: EXPULSIÓN DE HUEVOS EN LAS ESPECIES DE MAYOR TAMAÑO

Manuel SOLER[1] *

SUMMARY.—The hosts of brood parasites have evolved egg-discrimination ability as a defence that allows them to reject parasitic eggs laid in their nests. Twenty-five years ago, Stephen Rothstein emphasised that rejection rates differed markedly between potential host species in Europe and America. The much more complete information available today supports Rothstein's conclusions, but also allows new ones, especially when considering host size. For instance, successful resistance, one of the three potential long-term outcomes of brood parasite-host coevolution, is considerably more frequent in small-sized European host species and in medium-sized and large-sized Nearctic host species, while this evolutionary outcome is rare among Neotropical hosts regardless of their size. These results have never before been discussed, despite the differences being spectacular: 17 out of 19 small hosts presenting successful resistance are from Europe and 16 out of 17 medium-sized and 11 out of 13 large hosts presenting successful resistance are from North America. Interestingly, many large Nearctic hosts with a rejection rate close to 100% are corvids. The high rejection capacity shown by large Nearctic potential hosts probably evolved as a response to a highly virulent extinct brood parasite, either a large extinct cowbird or an extinct cuckoo species, which went extinct after losing the arms race against its large hosts.

Key words: brood parasitism, coevolution, *Cuculus canorus*, egg rejection, *Molothrus*, successful resistance.

RESUMEN.—En las especies hospedadoras de los parásitos de cría ha evolucionado la habilidad de reconocer huevos como una defensa que les permite expulsar los huevos parásitos que hayan sido puestos en sus nidos. Hace 25 años, Stephen Rothstein destacó que la proporción de tasas de expulsión de huevos eran muy diferentes cuando se comparaban las especies hospedadoras potenciales de Europa con las de América. Actualmente se dispone de una información mucho más completa que apoya las conclusiones de Rothstein, pero que, además, permite destacar algunas nuevas, especialmente cuando se tiene en cuenta el tamaño de la especie hospedadora. Por ejemplo, "resistencia exitosa" (uno de los tres resultados potenciales a largo plazo de la coevolución existente entre parásitos de cría y sus

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hospedadores) es considerablemente más frecuente en las especies hospedadoras europeas de pequeño tamaño y en las especies hospedadoras neárticas de mediano y gran tamaño, mientras que este resultado evolutivo es raro entre las especies hospedadoras neotropicales independientemente de su tamaño. Estos resultados no se han discutido nunca antes a pesar de que las diferencias son muy llamativas: 17 de 19 especies hospedadoras de pequeño tamaño que presentan resistencia exitosa son europeas y 16 de 17 de mediano tamaño y 11 de 13 de las de mayor tamaño son de Norteamérica. Es de destacar que muchas de las especies hospedadoras neárticas de mayor tamaño que presentan una tasa de expulsión de huevos próxima al 100% son córvidos. Probablemente, la elevada capacidad de reconocer y expulsar huevos mostrada por las especies neárticas de gran tamaño potencialmente hospedadoras evolucionó como respuesta a un parásito de cría muy virulento que pudo haber sido un tordo (*Molothrus* spp.), o un cuco de tamaño grande que se extinguió tras perder su carrera de armamentos coevolutiva con estas especies hospedadoras de tamaño grande.

Palabras clave: coevolución, *Cuculus canorus*, *Molothrus*, parasitismo de cría, rechazo de huevos, resistencia exitosa.

Introduction

Brood parasitism is a prevalent breeding strategy in birds, with about 1% of all species being obligate brood parasites (Davies, 2000). These species, being able to reproduce only by laying eggs in the nests of other species (the hosts), rely on these unrelated foster parents to care for the parasitic young (Johnsgard, 1997; Davies, 2000). This type of parental-care parasitism (Roldán and Soler, 2011) reduces the fitness of the hosts to a variable extent, providing selective pressures on hosts to evolve defences against brood parasites, which in turn would select for the evolution of counter-defences in brood parasites, leading to selection for improved host defences, further parasitic adaptations, and so on (Rothstein, 1990; Davies, 2000). This escalation in defences and counter-defences both by hosts and by parasites, gives rise to a coevolutionary arms race (Dawkins and Krebs, 1979).

The most common and effective host defence against brood parasitism is recognition and subsequent rejection of parasitic eggs (Rohwer and Spaw, 1988; Rothstein, 1990; Davies, 2000). Egg rejection may be costly because hosts may sometimes eject one of their own eggs (recognition errors; Davies and Brooke, 1988; Marchetti, 1992; Davies *et al*., 1996) and/or may also damage their own eggs while trying to eject the parasitic egg (ejection costs; Davies and Brooke, 1988; Rohwer and Spaw, 1988; Marchetti, 1992; Røskaft *et al*., 1993). Rejection costs are especially critical when small-sized host species in which ejection behaviour has not evolved desert their nests as a response to parasitism (Hoover, 2003; Servedio and Hauber, 2006). It is widely accepted that recognition errors as well as ejection costs would select against the maintenance of egg discrimination in the absence of brood parasitism (Rothstein, 1990; Brooke *et al*., 1998; Davies, 2000, 2011). However, it has recently been emphasised that rejection behaviour persists in many host species despite rejection costs and recognition errors (Bolen *et al*., 2000; Rothstein, 2001; Underwood *et al*., 2004; Peer *et al*., 2007; Martín-Vivaldi *et al*., 2012; Medina and Langmore, 2015). In fact, it has been shown that successful resistance, i.e. a rejection rate of about 100% in species that are not currently used as hosts by brood parasites, is a more frequent long-term coevolutionary outcome in the relationships between brood parasites and their hosts than previously suspected (Soler, 2014), meaning that rejection behaviour has insignificant costs in these host species.

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Aims and methodology

This article synthesises data on egg rejection by potential host species of brood parasites on different continents. This comparison was first done by Rothstein, 1990, 1992) but an updated review is needed since much more experimental data is now available. Furthermore, the main aim of the present paper is to examine differences in rejection rates among hosts of the three geographical areas taking into account the sizes of the species involved, which has significant evolutionary implications.

The data used in this review (see table S1 in Supplementary Electronic Material, and table 1) are based on the Appendix in Soler (2014) to which new information and species have been added. The body mass of all species has been taken from the *Handbook of the Birds of the World* (del Hoyo *et al*., 2003-2011). The mass of the cattle tyrant *Machetornis rixosa*, which is not provided in the above-mentioned handbook, was taken from Dunning (1993). Host status was determined from the cited references for each species or from Friedmann *et al*. (1977) and/or Davies (2000). For cowbird host status, if not mentioned in the original paper and if that species is not included in Friedmann *et al*. (1977), the species is considered a non-host. The reported rejection rate both in the Supplementary Electronic Material and fig. 1 is that corresponding to non-mimetic eggs (or models), according to the criterion of authors in each paper. Sporadic nest desertions (1-3 nests) in egg-recognition experiments with low sample sizes were not considered as rejections because, without an appropriate control, these desertions could be due to other factors unrelated to experimental parasitism (Soler *et al*., 2011). Most rejection rates of non-mimetic eggs of European hosts of the common cuckoo were taken from Martín-Vivaldi *et al*. (2012). When considering the effect of host size, I have considered 'small' to indicate a mass of less than 30 g, 'medium' to be a mass of 30-75 g, and 'large' to be more than 75 g. For coevolutionary outcomes, following Soler (2014), a lack of rejection was considered to apply when the rejection rate was 10% or less, successful resistance when egg rejection was 90% or more, and intermediate rejection rate for percentages in between.

Brood parasites in Europe and America

Interspecific avian brood parasitism has evolved independently seven times in birds (Sorenson and Payne, 2002). Brood parasites are distributed throughout all continents, being especially frequent in Africa but also in South-east Asia and Australia (Davies, 2000). Brood parasites in Europe and America, although scarcer, have been extensively studied and have provided the basis for the theoretical background in brood-parasitism

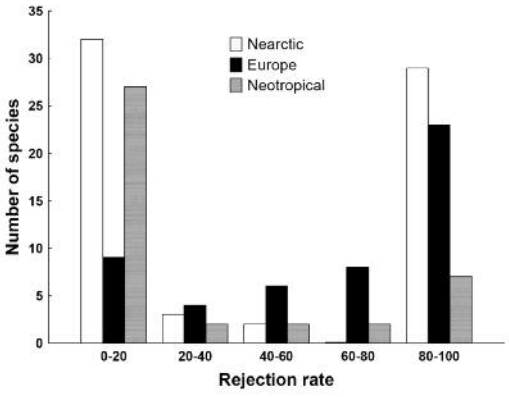


Fig. 1.—Number of potential host species presenting various rejection rates of experimentally introduced non-mimetic eggs in three different geographical regions.
[Número de especies hospedadoras potenciales que presentan diferentes tasas de expulsión de huevos no miméticos en tres áreas geográficas diferentes.]

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studies. These well-known species include the common cuckoo *Cuculus canorus* and great spotted cuckoo *Clamator glandarius* in Europe, and the brown-headed cowbird *Molothrus ater* and shiny cowbird *M. bonariensis* in America.

There are major differences between these four brood parasite species with respect to their parasitic strategies and the responses of their hosts. For instance, both European cuckoos are specialist brood parasites (the common cuckoo at the individual female level (Gibbs *et al*., 2000)), parasitising only one or just a few host species, while brown-headed as well as shiny cowbirds are generalists. Nevertheless, being a generalist is not characteristic of all parasitic cowbirds; one species in South America, the screaming cowbird *M. rufoaxillaris*, is an extreme specialist, using one species as the host almost exclusively (Fraga, 1998). On the other hand, there is another difference with respect to the evolution of the coloration of parasitic eggs and the egg-rejection strategies used by their hosts: host rejection of non-mimetic eggs has selected for the evolution of host-egg mimicry by the common cuckoo (Davies and Brooke, 1988) resulting in sympatric host-specific races –or gentes– that lay eggs matching those of each particular host species (Brooke and Davies, 1988; Moksnes and Røskaft, 1995; Gibbs *et al*., 1996; Stoddard and Stevens, 2010). It has frequently been emphasised that cowbirds have not evolved egg mimicry (Rothstein, 1990; Gibbs *et al*., 1997; Davies, 2000; Stokke *et al*., 2002) but egg mimicry has not evolved in the great spotted cuckoo either (Soler *et al*., 2003). Thus, absence of egg mimicry is not a special characteristic of parasitic cowbirds.

Egg rejection rates by European and American hosts

Brood parasitism in general, and rejection rates in particular, have been reviewed recently (Davies, 2011; Kilner and Langmore, 2011; Feeney *et al*., 2014; Soler, 2014; Medina and Langmore, 2015) but differences in rejection rates between Europe and America have not been discussed since Rothstein 1990, 1992). The most important and clear difference between brood parasite-host interactions in Europe and America is the rejection rates. Rothstein (1990, 1992) emphasised that there were sharp differences in rejection rates between host species from Europe and America. In particular, most potential cowbird hosts in America show either close to 100% or 0% rejection of experimental non-mimetic eggs and most common cuckoo hosts in Europe show intermediate rejection rates. Since Rothstein's review, many new potential host species have been tested in egg-recognition experiments and we now have information on nearly three times as many hosts as in Rothstein's study (see table S1 in Supplementary Electronic Material). As evident in fig. 1, which presents the number of potential host species relative to rejection rates in three different geographical areas, the scenario described by Rothstein remains valid: intermediate rejection rates (i.e. between 20%-80%) are almost absent in Nearctic and Neotropical hosts (7.6% and 15%, respectively) while they are more frequent in Europe (i.e. common cuckoo hosts; 36%; $\chi^2 = 14.5$, $P = 0.001$ and $\chi^2 = 5.01$, $P = 0.02$, respectively; fig. 1). Two apparent differences can be mentioned: firstly, the number of Neotropical hosts showing a rejection rate close to 0% has increased to some extent (from 13 out of 22 species (59.1%) in Rothstein's study to 27 out of 40 species (67.5%) now; fig. 1); and, secondly, the number of common cuckoo hosts showing a rejection rate close to 100% has also increased (from 6 out of 18 species (33.3%) in Rothstein's study to 23 out of 50 species (46%) now; fig. 1). However, differences are not statistically significant in either case ($\chi^2 = 0.44$, $P = 0.51$ and $\chi^2 = 0.87$, $P = 0.35$, respectively).

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The more complete information available presented in fig. 1 suggests three main conclusions: an initial one that was suggested by Rothstein (1990) and two others derived from the new data set, which were not indicated by Rothstein's data:

Firstly, a rejection rate of close to 0% is much more frequent in Nearctic and Neotropical hosts (48.5% and 67.5%, respectively) than in European common cuckoo hosts (18.0% $\chi^2 = 11.57$, $P = 0.007$ and $\chi^2 = 22.69$, $P < 0.0001$, respectively; fig. 1). The main explanation for this difference is that cuckoos are an ancient lineage that evolved 65-144 million years ago (Davies, 2000), whereas cowbirds appeared only 2.8-3.8 million years ago (Rothstein *et al*., 2002).

Secondly, in European common cuckoo hosts, a rejection rate of close to 100% is more frequent than previously assumed by Rothstein (1990) (see above; fig. 1). Many recent studies have reported further cases of potential cuckoo host species that are not currently parasitised but exhibit very high rejection rates of non-mimetic eggs (Braa *et al*., 1992; Honza *et al*., 2004; Procházka and Honza, 2003; Stokke *et al*., 2004; Rutila *et al*., 2006; Vikan *et al*., 2009; Martín-Vivaldi *et al*., 2012) suggesting that they underwent high parasitism pressure in the past and that rejection behaviour is a cost-free defence in these species (reviewed in Soler, 2014).

Thirdly, a rejection rate close to 100% is very similar in Nearctic (43.9%) and in European (46%) hosts, and higher than that reported in Neotropical ones (17.5%) ($\chi^2 = 7.76$, $P = 0.005$ and $\chi^2 = 8.12$, $P = 0.004$, respectively; fig. 1). This last point has never previously been noted or discussed.

Host size and the evolution of egg-rejection behaviour

Three major potential long-term evolutionary outcomes of brood parasite-host coevolution can be distinguished (Soler, 2014): lack of rejection (when the rejection rate is 10% or less), successful resistance (when egg rejection is 90% or more) and coevolutionary cycles, which always occur in species showing an intermediate rejection rate (10%-90%; Soler, 2014). The results of simple exploratory comparisons (χ^2), considering the 159 species included in table S1 (Supplementary Electronic Material), show that host size has an important effect on the evolutionary outcomes reached with respect to egg-rejection rates (fig. 2; see also table S1 in Supplementary Electronic Material). More importantly, firstly, lack of rejection is more frequent in small Nearctic and Neotropical host species than in small European hosts ($\chi^2 = 5.28$, $P = 0.02$ and $\chi^2 = 8.67$, $P = 0.03$, respectively; fig. 2A). Secondly, intermediate rejection rates are more abundant among small European host species compared to small Nearctic and Neotropical hosts ($\chi^2 = 11.54$, $P = 0.0007$ and $\chi^2 = 24.53$, $P < 0.0001$, respectively; fig. 2B). Thirdly, successful resistance is considerably more frequent (a) in small European host species compared to small Nearctic and Neotropical hosts ($\chi^2 = 27.02$, $P < 0.0001$ in both cases; fig. 2C); (b) in medium-sized Nearctic host species compared to medium-sized European or Neotropical hosts ($\chi^2 = 30.22$, $P < 0.0001$ and $\chi^2 = 26.47$, $P < 0.0001$, respectively; fig. 2C); and (c) in large Nearctic host species compared to large European or Neotropical hosts ($\chi^2 = 15.48$, $P = 0.0001$ in both cases; fig. 2C). Interestingly, an evolutionary outcome of successful resistance is rare among Neotropical hosts regardless of their size (fig. 2C). The first two results have been discussed elsewhere (Rothstein, 1990, 1992; Davies, 2000) but the third point has never before been mentioned, despite spectacular differences: of hosts presenting successful resistance, 17 out of 19 (89.5%) small hosts are from Europe while 16 out of 17 (94.1%) medium-sized and 11 out of 13 (84.6%) large hosts are from North America (fig. 2C). Undoubtedly, the 17 European hosts have

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evolved successful resistance as a response to parasitism by the common cuckoo, given that all of them are considered to be (or have been in the past) hosts of that species (Davies, 2000; see table S1 in Supplementary Electronic Material). Which brood-parasite is responsible for the evolution of successful resistance in the medium-sized and large hosts of North America? With respect to medium-sized hosts, egg rejection pre-

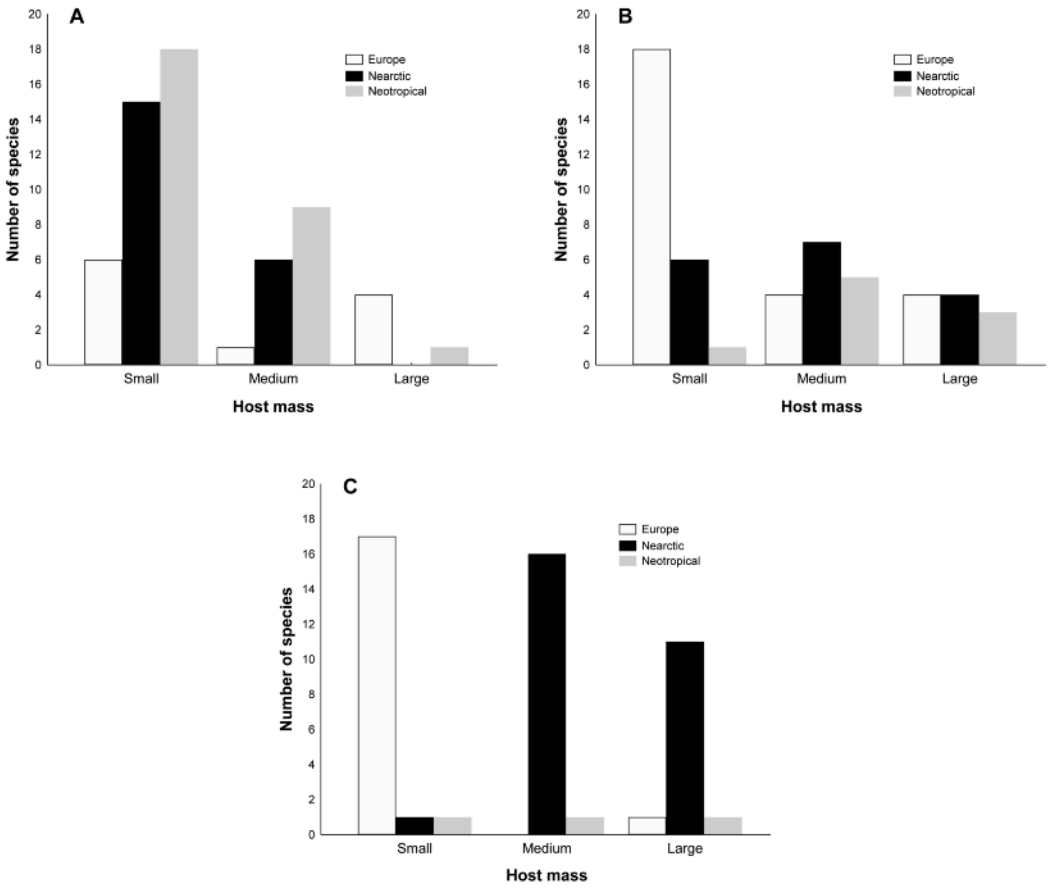


FIG. 2.—Number of potential host species presenting each coevolutionary outcome according to host body mass and continent. In terms of mass, hosts were considered to be small, medium and large when weighing < 30 g, 30-75 g and > 75 g, respectively. For the coevolutionary outcomes, lack of rejection (fig. 2A) was considered to apply when the rejection rate was 10% or less, successful resistance (fig. 2C) when egg rejection was 90% or more, and intermediate rejection rate (fig. 2B) when in between. *[Número de especies hospedadoras potenciales que presentan cada uno de los resultados coevolutivos según peso y continente. En términos de peso, las especies hospedadoras fueron consideradas como pequeñas, intermedias y grandes cuando pesaban < 30, entre 30 y 75, y > 75 g, respectivamente. Para los resultados coevolutivos, se consideró ausencia de expulsión (fig. 2A) cuando la tasa de expulsión era 10% o menos, resistencia exitosa (fig. 2C) cuando la tasa de expulsión era 90% o más, y tasa de expulsión intermedia (fig. 2B) cuando dicha tasa de expulsión estaba entre 10% y 90%.]*

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sumably evolved as a response to parasitism by bronzed cowbirds *Molothrus aenus*, which usually parasitise hosts that are as large or larger than themselves (Carter, 1986), or by brown-headed cowbirds, which in the past could have preferentially parasitised large hosts (Peer and Sealy, 2004a) because these are able to provide more food and rear a larger number of parasitic nestlings (Rothstein, 1975a; Peer and Sealy, 2004a). Later, when most medium-sized hosts evolved egg-rejection ability, brown-headed cowbirds would have been forced to switch to smaller hosts (Rothstein, 1975a; Mason, 1980; Peer and Sealy, 2004a). In fact, currently, only two of the 16 medium-sized hosts are considered common hosts of the brown-headed cowbird, seven are only rarely parasitised, and seven have never been found to be parasitised (i.e. are considered non-host species; see table S1 in Supplementary Electronic Material). However, the case of large hosts is different and deserves more detailed analysis.

Egg rejection by large-sized host species in North America vs. Europe

Several of the large hosts in North America are sympatric with larger cowbird species in Mexico and Central America (the bronzed cowbird and giant cowbird *Molothrus oryzivora*). Thus, rejection ability in some large hosts could have been selected under pressure from these cowbirds, especially in the case of grackles *Quiscalus* spp. as suggested by Peer and Sealy (2004a). However, this possibility is less likely in the case of corvids because giant cowbirds usually parasitise only large colonial icterids (Ortega, 1998).

Most potential large hosts in North America (11 out of 15, 73.3%; see table S1 in Supplementary Electronic Material) not only exhibit successful resistance but in addition their high rejection ability has been maintained for a long period of time in the absence of conspecific brood parasitism (Bolen *et al*., 2000; Underwood *et al*., 2004), even after speciation processes (Bolen *et al*., 2000; Rothstein, 2001; Peer and Sealy, 2004b), signifying that they suffered from very costly brood parasitism and also that they won the arms race against their brood parasites (Rothstein, 2001; Soler, 2014).

It has been suggested that egg rejection in potential large hosts in North America has also been mediated by parasitism by cowbirds during the Pleistocene, about 10,000 years ago, when cowbirds were presumably more abundant (Peer *et al*., 2011a; Peer *et al*., 2011b). This possibility seems unlikely because most of these host species (see table S1 in Supplementary Electronic Material, and table 1) are too large to be considered appropriate cowbird hosts, given that when cowbirds parasitize large hosts, cowbird nestlings are not able to overcome the size advantage of host nestlings (Dearborn and Lichtenstein, 2002; Rivers *et al*., 2010) and most of these species are much larger than any current cowbird hosts. Thus, brown-headed cowbirds cannot have been responsible for provoking the strong selection pressures needed to favour the evolution and fixation of successful resistance in these large hosts.

The egg-rejection ability of current Nearctic species could also have evolved in an ancestral species that was parasitised by the common cuckoo in the Palaearctic (Bolen *et al*., 2000; Rothstein, 2001; Underwood *et al*., 2004). This second possibility could be correct in the case of some medium-sized species such as the loggerhead shrike *Lanius ludovicianus* and the American robin *Turdus migratorius*, which belong to Old World genera in which all species are rejectors (Lovászi and Moskát, 2004; Grim *et al*., 2011; Martín-Vivaldi *et al*., 2012).

Until now, the same explanation has been provided for most of the eight North

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TABLE 1

Relevant information on mass, host status, and rejection rate of non-mimetic eggs in all corvid species in which egg-recognition experiments have been performed on any continent.

[Información relevante sobre peso, estatus y tasa de expulsión de huevos no miméticos en todas las especies de córvidos en las que se han hecho experimentos de reconocimiento de huevos en cualquiera de los continentes.]

Scientific name	Mass (g)	Actual or potential parasite species	Host status	Rejection rate (%)	Continent/ Biome	References
Aphelocoma californica	85.0	?	Non-host	100.0	Nearctic	Peer *et al*. (2007)
Aphelocoma coerulescens	77.1	?	Non-host	100.0	Nearctic	Peer *et al*. (2007)
Aphelocoma insularis	108.5	?	Non-host	100.0	Nearctic	Peer *et al*. (2007)
Corvus brachyrhynchos	412	?	Non-host	21.0	Nearctic	Underwood *et al*. (2004)
Corvus corax	1292.5	*Clamator glandarius*	Non-host	0.0	Europe	Soler (1990)
Corvus corone	499	*Clamator glandarius*	Common	0.0	Europe	M. Soler *et al*. (2002)
Corvus macrorhynchos	725	—	Non-host	21.0	Asia	Begum *et al*. (2012)
Corvus monedula	200.5	*Clamator glandarius*	Rare	0.0	Europe	Soler (1990)
Corvus splendens	308	*Eudynamys scolopaceus*	Common	9.1	Asia	Begum *et al*. (2012)
Cyanocitta cristata	85	?	Rare	100.0	Nearctic	Peer and Rothstein (2010)
Cyanopica cooki	70.5	*Cuculus canorus* *Clamator glandarius*	Non-host	73.7	Europe	Avilés (2004)
Cyanopica cyanus	99	*Cuculus canorus*	Common	34.7	Asia	Nakamura *et al*. (1998)
Perisoreus canadiensis	67.5	?	Non-host	0.0	Nearctic	Sealy *et al*. (2009)
Pica hudsonia	172.5	?	Non-host	100.0	Nearctic	Underwood *et al*. (2004)
Pica nutalli	142	?	Non-host	100.0	Nearctic	Bolen *et al*. (2000)
Pica pica	200.5	*Clamator glandarius*	Common	76.5	Europe	J.J. Soler *et al*. (1999a)
Pyrrhocorax pyrrhocorax	291	*Clamator glandarius*	Rare	0.0	Europe	Soler (1990)

American corvid species listed in table 1: rejection ability could have evolved as a response to common cuckoo parasitism in a common ancestor of the three species of scrub-jays *Aphelocoma* spp. and the blue jay *Cyanocitta cristata* (Peer *et al*., 2007) and in a common ancestor of the two magpies *Pica* spp. (Rothstein, 2001; Bolen *et al*., 2000; Underwood *et al*., 2004). However, this seems very unlikely in the first four species because rejection is not fixed in the corvid family, i.e. only some species are able to eject experimental non-mimetic eggs (Soler, 1990). Moreover, the common cuckoo does not parasitise corvids, other than the azure-winged magpie *Cyanopica cyanus* in Asia (Nakamura, 1990; Nakamura *et al*., 1998; but not the Iberian magpie *C. cooki* in Europe). The great spotted cuckoo does so but it only regularly parasitises magpies and carrion crows *Corvus corone* and only magpies show rejection capacity (Soler, 1990; see table 1).

This possibility of rejection ability evolving as a response to cuckoo parasitism in a common ancestor is also very unlikely in the two North American magpie species, because rejection rates of non-mimetic eggs reported in both of them (100%; Bolen *et al*., 2000; Underwood *et al*., 2004) are higher than those reported in the Eurasian magpie not only in allopatric populations but even in populations that are sympatric with great spotted cuckoos, in which the rejection rate is significantly higher than in allopatric populations (Soler *et al*., 1999). In some allopatric European Eurasian magpie populations rejection rates have been reported to reach about 50% (52.9-57.9% in four of them; Soler *et al*. 1999) and even much lower; for example 25% in Eljovo, Bulgaria (Soler *et al*., 1999); and 0% in Uppsala, Sweden (Soler and Møller, 1990). Furthermore, in Seoul, South Korea, the rejection rate by magpies is also 0% (Sang-im Lee; personal communication). Even more, considering mimetic eggs, the rejection rate by North American black-billed magpies *Pica hudsonia* (50%) was much higher than those reported for magpies in European allopatric (with the great spotted cuckoo) populations (7.1%-26.3% ejection; Soler *et al*., 1999), and even higher than those reported for magpies in the majority of European sympatric populations: only in two of them was the ejection rate of mimetic eggs higher than 50%, while in six of them it was lower (18.8%-43.8%; Soler *et al*., 1999).

It has also been suggested by some authors as an unlikely possibility that egg recognition in North America corvids evolved as a response against an extinct brood parasite, either a cowbird (Peer and Rothstein, 2010) or a cuckoo (Rothstein, 2001; Peer *et al*., 2011b). Here I suggest that this is the most probable hypothesis for two main reasons:

Firstly, although recognition and rejection capacity could be maintained in absence of recognition and rejection costs (Davies *et al*., 1996; Rothstein, 2001; Peer *et al*., 2011a), what cannot be accepted is an increase and establishment of that capacity in North America magpie populations in the absence of selection pressures exerted by inter- or intraspecific brood parasitism.

Secondly, the American crow *Corvus brachyrhynchos* also presents a considerable rejection rate (21% of non-mimetic eggs and 8% of mimetic eggs Underwood *et al*., 2004; table 1) whereas in the other continents no species of the genus *Corvus* has been found to discriminate against non-mimetic eggs (Yom-Tov, 1976; Soler, 1990), even where it is the favourite host of a brood parasite, as in the case of the house crow *Corvus splendens* in India (Dewar, 1907; in Davies, 2000). Begum *et al*. (2012) reported a low ejection rate among house crows in Delhi (India; 1 out of 22), but this result is strange considering that Dewar (in Davies, 2000) found that house crows accepted chicken eggs and even golf balls experimentally introduced in their nests. Perhaps the experimental egg

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that was considered ejected disappeared for some other reason. Another strange result in Begum *et al*., (2012) concerns large-billed crows *Corvus macrorhynchos* since they found that seven out of 16 non-mimetic eggs were deserted (none was ejected); as the authors themselves stated, it is very difficult to understand why birds that are perfectly able to grasp-eject, desert nests instead of just ejecting the model egg. Clearly, a control group in which nests were not experimentally parasitised would be needed (Soler *et al*., 2011) to assess the significance of this result, given that nest desertion may occur in response to predation risk and other factors unrelated to brood parasitism, including disturbance by the researcher (Székely *et al*., 1996; Hosoi and Rothstein, 2000; Servedio and Hauber, 2006).

Thus, I suggest that the higher discrimination capacity shown by large potential North America host species, especially corvids, despite absence of selective pressures by brood parasites in recent history, strongly implies that rejection in these species evolved in response to selection pressures provoked by at least one extinct brood parasite in the New World, either an extinct large cowbird species or an extinct cuckoo species. The possibility of a large cowbird would be supported by the fact that high parasitism rates exert strong selection for host defences and parasitism rates on most cowbird hosts are usually much higher than those on cuckoo hosts. Thus, the high occurrence of large species with fixed rejection could have been provoked by an abundant and large-sized extinct cowbird species. However, considering the high discrimination capacity retained by large potential host species in North America, the extinct brood parasite more likely was a Cuculidae species, because although virulence varies enormously, and many small host species of cowbirds are unable to raise any of their own chicks (Rothstein, 1975b), cowbirds are in general less virulent brood parasites than cuckoos, as shown by the low rejection rate (if any) evolved in contemporary cowbird hosts, regardless of the duration of sympatry (Davies, 2000). Numerous fossils of cowbirds (Lowther, 1993) and cuckoos (Davies, 2000) have been found. Thus, future research looking for fossils of brood parasites could solve the question of which of the two alternative hypotheses on the existence of an extinct brood parasite (cowbird or cuckoo) is correct. If it was a cuckoo species, it was probably larger than the great spotted cuckoo because parasitism by the great spotted cuckoo of its large carrion crow host (a similar size to *C. brachyrhynchos*) is not costly enough to favour the evolution of egg rejection in this host species: the cuckoo nestlings are unable to outcompete their larger host nestmates; Soler *et al*., 2002).

Conventional brood-parasitism theory frequently assumes that when a host overcomes its brood parasite, the parasite will be forced to switch to another host species with less-evolved defences (Davies and Brooke, 1989; i.e. the evolutionary alternation model; Nuismer and Thompson, 2006), while the possibility that the brood parasite could go extinct is hardly ever considered (Rothstein, 2001; Peer *et al*., 2011a, 2011b). This is probably the consequence of the traditional focus on the study of a pair of traits (i.e. defence-counterdefence). However, in consideration of the currently widely accepted idea that hosts have evolved several different lines of defence that can operate at different stages of the breeding cycle, and that brood parasites need to evolve counter-adaptations against all of these (Davies, 2011; Soler, 2014), the possibility of parasite extinction should to be considered a more probable event (Soler *et al*., 2014). For instance, individual-based simulations by Gilman *et al*. (2012) have suggested that when coevolution involves multiple traits, victims have an evolutionary

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advantage in any victim-exploiter system. This means that hosts need to overcome their brood parasite with only one effective defence in order to escape from brood parasitism, whereas brood parasites must overcome all effective host defences (Gilman *et al*., 2012).

Conclusion

Here I have argued that the high rejection capacity shown by large-sized potential hosts, especially corvids, from North America, in comparison to other European and Asian corvid species, evolved as a response to a highly virulent extinct brood parasite, either an extinct large cowbird or, more likely, an extinct cuckoo species, which lost the arms race against their large hosts. Recent studies in the field of brood parasitism have provided information on rejection rates in many potential host species that has allowed the identification of the crucial effect of host size on the evolution of egg-rejection behaviour, discussed in this paper. The challenge for experimental researchers in the near future will be to provide information about egg-recognition behaviour in more species, and more populations of the same species, in order to fully understand the coevolutionary relationships between brood parasites and their hosts with respect to egg-rejection defence.

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Bibliography

Begum, S., Moksnes, A., Røskaft, E. and Stokke, B. G. 2012. Responses of potential hosts of Asian cuckoos to experimental parasitism. *Ibis*, 154: 363-371.

Bolen, G. M., Rothstein, S. I. and Trost, C. H. 2000. Egg recognition in yellow- billed and black-billed magpies in the absence of interspecific parasitism: implications for parasite-host coevolution. *Condor*, 102: 432-438.

Braa, A. T., Moksnes, A. and Røskaft, E. 1992. Adaptations of bramblings and chaffinches towards parasitism by the common cuckoo. *Animal Behaviour*, 43: 67-78.

Brooke, M. de L. and Davies, N. B. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, 335: 630-632.

Brooke, M. de L., Davies, N. B. and Noble, D. G. 1998. Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. *Proceedings of the Royal Society of London B*, 265: 1277-1282.

Carter, M. D. 1986. The parasitic behaviour of the bronzed cowbird in south Texas. *Condor*, 88: 11-25.

Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats*. T. and A. D. Poyser. London.

Davies, N. B. 2011. Cuckoo adaptations: trickery and tuning. *Journal of Zoology*, 284: 1-14.

Davies, N. B. and Brooke, M. de L. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour*, 36: 262-284.

Davies, N. B. and Brooke, M. de L. 1989. An experimental study of co-evolution between the cuckoo *Cuculus canorus* and its hosts. II. Host egg markings, chick discrimination and general discussion. *Journal of Animal Ecology*, 58: 225-236.

Davies, N. B., Brooke, M. de L. and Kacelnik, A. 1996. Recognition errors and probability of

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parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proceedings of the Royal Society of London B*, 263: 925-931.

DAWKINS, R. and KREBS, J. R. 1979. Arms races between and within species. *Proceedings of the Royal Society of London B*, 205: 489-511.

DEARBORN, D. C. and LICHTENSTEIN, G. 2002. Begging behaviour and host exploitation in parasitic cowbirds. In, J. Wright and M. L. Leonard (Eds.), *The evolution of begging: competition, cooperation and communication*, pp. 361-388. Kluwer Academic Publishers.

DEL HOYO, J., ELLIOT, A. and CHRISTIE, D. A. (Eds.) 2003-2011. *Handbook of the Birds of the World*. Vol: 8-16. Lynx Edicions. Barcelona.

DUNNING, J. B. 1993. CRC *Handbook of avian body masses*. CRC Press. Boca Raton.

FEENEY, W. E., WELBERGEN, J. A. and LANGMORE, N. E. 2014. Advances in the study of coevolution between avian brood parasites and their hosts. *Annual Review of Ecology, Evolution, and Systematics*, 45: 227-246.

FRAGA, R. M. 1998. Interactions of the parasitic screaming and shiny cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the bay-winged cowbird (*M. badius*). In, S. I. Rothstein and S. K. Robinson (Eds.): *Parasitic Birds and Their Hosts: Studies in Coevolution*, pp. 173-193. Oxford University Press. Oxford.

FRIEDMANN, H., KIFF, L. F. and ROTHSTEIN, S. I. 1977. A further contribution to knowledge of the host relations of the parasitic cowbirds. *Smithsonian Contributions to Zoology*, 235: 1-75.

GIBBS, H. L., BROOKE, M. D. and DAVIES, N. B. 1996. Analysis of genetic differentiation of host races of the common cuckoo *Cuculus canorus* using mitochondrial and microsatellite DNA variation. *Proceedings of the Royal Society of London B*, 263: 89-96.

GIBBS, H. L., MILLER, P., ALDERSON, G. and SEALY, S. G. 1997. Genetic analysis of brown-headed cowbirds *Molothrus ater* raised by different hosts: Data from mtDNA and microsatellite DNA markers. *Molecular Ecology*, 6: 189-193.

GIBBS, H. L., SORENSON, M. D., MARCHETTI, K., BROOKE, M. D., DAVIES, N. B. and NAKAMURA, H. 2000. Genetic evidence for female host-specific races of the common cuckoo. *Nature*, 407: 183-186.

GILMAN, R. T., NUISMER, S. L. and JHWUENG, D.-C. 2012. Coevolution in multidimensional trait space favours escape from parasites and pathogens. *Nature*, 483: 328-330.

GRIM, T., SAMAŠ, P., MOSKÁT, C., KLEVEN, O., HONZA, M., MOKSNES, A., RØSKAFT, E. and STOKKE, B. G. 2011. Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? *Journal of Animal Ecology*, 80: 508-518.

HONZA, M., PROCHAZKA, P., STOKKE, B. G., MOKSNES, A., RØSKAFT, E., CAPEK, M. and MRLIK, V. 2004. Are blackcaps current winners in the evolutionary struggle against the common cuckoo? *Journal of Ethology*, 22: 175-180.

HOOVER, J. P. 2003. Multiple effects of brood parasitism reduce the reproductive success of prothonotary warblers *Protonotaria citrea*. *Animal Behaviour*, 65: 923-934.

HOSOI, S. A. and ROTHSTEIN, S. I. 2000. Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Animal Behaviour*, 59: 823-840.

JOHNSGARD, P. A. 1997. *The avian brood parasites: deception at the nest*. Oxford University Press. Oxford.

KILNER, R. M. and LANGMORE, N. E. 2011. Cuckoos *versus* hosts in insects and birds: adaptations, counter-adaptations and outcomes. *Biological Review*, 86: 836-852.

LOVÁSZI, P. and MOSKÁT, C. 2004. Break-down of arms race between the redbacked shrike (*Lanius collurio*) and common cuckoo (*Cuculus canorus*). *Behaviour*, 141: 245-262.

LOWTHER, P. E. 1993. Brown-headed cowbird (*Molothrus ater*). In, A. Poole and F. Gill (Eds.): *The Birds of North America*, 47. Academy of Natural Sciences. Philadelphia.

MARCHETTI, K. 1992. Costs to host defense and the persistence of parasitic cuckoos. *Proceedings of the Royal Society of London B*, 248: 41-45.

MARTÍN-VIVALDI, M., SOLER, J. J., MØLLER, A. P., PÉREZ-CONTRERAS, T. and SOLER, M. 2012. Importance of nest site and habitat in egg recognition ability of potential hosts of the European cuckoo *Cuculus canorus*. *Ibis*, 155: 140-155.

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MASON, P. 1980. *Ecological and evolutionary aspects of host selection in cowbirds*. Ph. D. diss., Univ. of Texas.

MEDINA, I. and LANGMORE, N. E. 2015. The costs of avian brood parasitism explain variation in egg rejection behaviour in hosts. *Biology Letters*, 11: 20150296. http://dx.doi.org/10.1098/rsbl.2015.0296

MOKSNES, A. and RØSKAFT, E. 1995. Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *Journal of Zoology*, 236: 625-648.

NAKAMURA, H. 1990. Brood parasitism by the cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the azure-winged magpie *Cyanopica cyanea*. *Japanese Journal of Ornithology*, 39: 1-18.

NAKAMURA, H., KUBOTA, S. and SUZUKI, R. 1998. Coevolution between the common cuckoo and its major hosts in Japan. In, S. I. Rothstein and S. K. Robinson (Eds.): *Parasitic Birds and Their Hosts: Studies in Coevolution*, pp. 94-112. Oxford University Press. Oxford.

NUISMER, S. L. and THOMPSON, J. N. 2006. Coevolutionary alternation in antagonistic interactions. *Evolution*, 60: 2207-2217.

ORTEGA, C. P. 1998. *Cowbirds and Other Brood Parasites*. University of Arizona Press. Tuscon.

PEER, B. D. and ROTHSTEIN, S. I. 2010. Phenotypic plasticity in common grackles in response to repeated brood parasitism. *Auk*, 127: 293-299.

PEER, B. D. and SEALY, S. G. 2004a. Fate of grackle (*Quiscalus* spp.) defenses in the absence of brood parasitism: implications for long-term parasite-host coevolution. *Auk*, 121: 1172-1186.

PEER, B. D. and SEALY, S. G. 2004b. Correlates of egg rejection in hosts of the brown-headed cowbird. *Condor*, 106: 580-599.

PEER, B. D., KUEHN, M. J., ROTHSTEIN, S. I. and FLEISCHER, R. C. 2011a. Persistence of host defence behaviour in the absence of avian brood parasitism. *Biology Letters*, 7: 670-673.

PEER, B. D., MCINTOSH, C. E., KUEHN, M. J., ROTHSTEIN, S. I. and FLEISCHER, R. C. 2011b. Complex biogeographic history of *Lanius* shrikes and its implications for the evolution of defences against avian brood parasitism. *Condor*, 113: 385-394.

PEER, B. D., ROTHSTEIN, S. I., DELANEY, K. S. and FLEISCHER, R. C. 2007. Defence behavior against brood parasitism is deeply rooted in mainland and island scrub-jays. *Animal Behaviour*, 73: 55-63.

PROCHÁZKA, P. and HONZA, M. 2003. Do common whitethroats (*Sylvia communis*) discriminate against alien eggs? *Journal für Ornithologie*, 144: 354-363.

RIVERS, J. W., LOUGHIN, T. M. and ROTHSTEIN, S. I. 2010. Brown-headed cowbird nestlings influence nestmate begging, but not parental feeding, in hosts of three distinct sizes. *Animal Behaviour*, 79: 107-116.

ROHWER, S. and SPAW, C. D. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evolutionary Ecology*, 2: 27-36.

ROLDÁN, M. and SOLER, M. 2011. Parental care parasitism: How unrelated offspring attain acceptance by foster parents? *Behavioral Ecology*, 22: 679-691.

RØSKAFT, E., ROHWER, S. and SPAW, C. D. 1993. Costs of puncture ejection compared with costs of rearing cowbird chicks for northern orioles. *Ornis Scandinavica*, 24: 28-32.

ROTHSTEIN, S. I. 1975a. An experimental and teleonomic investigation of avian brood parasitism. *Condor*, 77: 250-271.

ROTHSTEIN, S. I. 1975b. Evolutionary rates and host defenses against avian brood parasitism. *American Naturalist*, 109: 161-176.

ROTHSTEIN, S. I. 1990. A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics*, 21: 481-508.

ROTHSTEIN, S. I. 1992. Brood parasitism, the importance of experiments and host defences of avifaunas on different continents. *Proceedings of the Pan-African Ornithological Congress*, 7: 521-535.

ROTHSTEIN, S. I. 2001. Relic behaviours, coevolution and the retention versus loss of host defences after episodes of avian brood parasitism. *Animal Behaviour*, 61: 95-107.

ROTHSTEIN, S. I., PATTEN, M. A. and FLEISCHER, R. C. 2002. Phylogeny, specialization, and brood parasite-host coevolution: some possible pitfalls of parsimony. *Behavioral Ecology*, 13: 1-10.

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RUTILA, J., JOKIMAKI, J., AVILÉS, J. M. and KAISANLAHTI-JOKIMAKI, M. L. 2006. Responses of parasitized and unparasitized common redstart (*Phoenicurus phoenicurus*) populations against artificial cuckoo parasitism. *Auk*, 123: 259-265.

SERVEDIO, M. R. and HAUBER, M. E. 2006. To eject or to abandon? Life history traits of hosts and parasites interact to influence the fitness payoffs of alternative anti-parasite strategies. *Journal of Evolutionary Biology*, 19: 1585-1594.

SOLER, J. J., AVILÉS, J. M., SOLER, M. and MØLLER, A. P. 2003. Evolution of host egg mimicry in a brood parasite, the great spotted cuckoo. *Biological Journal of the Linnean Society*, 79: 551-563.

SOLER, J. J., MARTÍNEZ, J. G., SOLER, M. and MØLLER, A. P. 1999. Genetic and geographic variation in rejection behavior of cuckoo eggs by European magpie populations: an experimental test of rejecter-gene flow. *Evolution*, 53: 947-956.

SOLER, M. 1990. Relationship between the great spotted cuckoo *Clamator glandarius* and its corvid hosts in a recently colonized area. *Ornis Scandinavica*, 21: 212-223.

SOLER, M. 2014. Long-term coevolution between avian brood parasites and their hosts. *Biological Reviews*, 89: 688-704.

SOLER, M. and MØLLER, A. P. 1990. Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. *Nature*, 343: 748-750.

SOLER, M., RUIZ-CASTELLANO, C., FERNÁNDEZ-PINOS, M. C., RÖSLER, A., ONTANILLA, J. and PÉREZ-CONTRERAS, T. 2011. House sparrows selectively eject parasitic conspecific eggs and incur very low rejection costs. *Behavioral Ecology and Sociobiology*, 65: 1997-2005.

SOLER, M., SOLER, J. J., PÉREZ-CONTRERAS, T. and MARTÍNEZ, J. G. 2002. Differential reproductive success of great spotted cuckoos *Clamator glandarius* parasitising magpies *Pica pica* and carrion crows *Corvus corone*: the importance of parasitism costs and host defences. *Avian Science*, 2: 25-32.

SORENSON, M. D. and PAYNE, R. B. 2002. Molecular genetic perspectives on avian brood parasitism. *Integrative and Comparative Biology*, 42: 388-400.

STODDARD, M. C. and STEVENS, M. 2010. Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society of London B*, 277: 1387-1393.

STOKKE, B. G., MOKSNES, A. and RØSKAFT, E. 2002. Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds. *Evolution*, 56: 199-205.

STOKKE, B. G., RUDOLFSEN, G., MOKSNES, A. and RØSKAFT, E. 2004. Rejection of conspecific eggs in chaffinches: The effect of age and clutch characteristics. *Ethology*, 110: 459-470.

SZÉKELY, T., WEBB, J. N., HOUSTON, A. I. and MCNAMARA, J. M. 1996. An evolutionary approach to offspring desertion in birds. *Current Ornithology*, 13: 271-330.

UNDERWOOD, T. J., SEALY, S. G. and MCLAREN, C. M. 2004. Experiments on egg discrimination in two North American corvids: further evidence for retention of egg ejection. *Canadian Journal of Zoology*, 82: 1399-1407.

VIKAN, J. R., STOKKE, B. G., FOSSØY, F., JACKSON, C., HUHTA, E., RUTILA, J., MOKSNES, A. and RØSKAFT, E. 2009. Fixed rejection responses to single and multiple experimental parasitism in two *Fringilla* hosts of the common cuckoo. *Ethology*, 115: 840-850.

YOM-TOV, Y. 1976. Recognition of eggs and young by the carrion crow (*Corvus corone*). *Behaviour*, 59: 247-251.

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Table S1: Relevant information on mass, status, rejection rate and coevolutionary outcomes in each potential host species from Europe and America.

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