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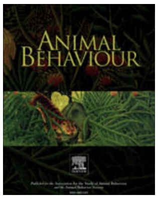

Increased host tolerance of multiple cuckoo eggs leads to higher fledging success of the brood parasite

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In birds, multiple parasitism is the laying of two or more eggs by one or more parasitic females in a single host nest. Several cognitive mechanisms may explain how multiple parasitism could affect parasite egg discrimination by hosts. Rejection based on discordance predicts that multiple parasitism provides a perceptually more error-prone way for hosts to reject parasitism because more foreign eggs decrease the chance that any one egg is perceived as most dissimilar and recognized as foreign, unless parasite eggs are all similarly highly nonmimetic. In contrast, rejection based on clutch uniformity predicts that in multiple parasitism egg rejection is more error-proof if mimicry by parasite eggs is variable, because increased variation in egg appearance makes for easier egg rejection for hosts. Finally, true egg recognition, that is, rejection based on memory of the host's own eggs, predicts no differences in rejection rates from nests with single or multiple parasitism. We studied common cuckoos, *Cuculus canorus*, parasitizing a population of great reed warblers, *Acrocephalus arundinaceus*, in Hungary where multiple parasitism was frequent. Hosts rejected parasite eggs less often in nests with multiple parasitism than in nests with single parasitism. These observations were confirmed by experimental parasitism and support the rejection based on discordance hypothesis. As hosts were more likely to tolerate cuckoo eggs in nests with multiple parasitism, we found that multiple parasitism more than doubled cuckoos' reproductive output per host nest compared to single parasitism.

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Avian obligate brood parasites lay their eggs in nests of host species, and leave parental care of their offspring to the unrelated foster parents (Davies 2000). Caring for a parasite offspring is a costly task for a host (Hauber 2006). For example, in evictor species the young brood parasite attempts to displace all nest content (Wyllie 1981; Honza et al. 2007a), including eggs and nestmates. Consequently, the brood parasite typically grows up alone, eliminating all host reproduction (Kilner 2005; Krüger 2007). Hosts can reduce the negative consequences of brood parasitism through antiparasite defence, involving aggression against the adult parasite (Davies & Brooke 1988; Røskaft et al. 2002a; Davies et al. 2003; Moskát 2005; Dyrcz & Halupka 2006; Honza et al. 2006), egg discrimination (e.g. Davies & Brooke 1989; Moksnes et al. 1991) and/or chick discrimination (Payne et al. 2001; Langmore et al. 2003; Schuetz 2005; Grim 2006; Anderson & Hauber 2007). Consequently, the evolution of both brood parasitism and host responses reflects naturally and sexually selected morphological and life history trade-offs within and across parasite taxa and refined perceptual and cognitive mechanisms of host species' defences (Krüger & Davies 2002; Garamszegi & Avilés

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2005; Hauber & Kilner 2007; Krüger et al. 2007; Parejo & Avilés 2007).

Consequences of Multiple Parasitism

When the relative population density of brood parasites is high compared to that of hosts, some host nests may contain more than one parasite egg, so that they are multiply parasitized (Wyllie 1981; Moskát et al. 2006). Irrespective of whether multiple parasitism (or superparasitism) is due to the laying of eggs by the same or different females (McLaren et al. 2003; Ellison et al. 2006), it is typically thought to be costly to brood parasites because parasitic chicks compete more vigorously than do host chicks (Hauber 2003), leading to the reduction of per capita egg-to-fledging success of the parasite (Trine 2000; Hoover 2003). Multiple parasitism is especially costly for evictor brood parasites whose chicks displace all eggs and nestmates following hatching (Honza et al. 2007a) and it has been hypothesized to be implicated in the evolution of both egg removal by laying parasites and the similarity between host and specialist parasite eggs (Davies & Brooke 1988; Brooker et al. 1990).

Multiple parasitism is common in some hosts of the brown-headed cowbird, *Molothrus ater* (Trine 2000; Hoover 2003; McLaren et al. 2003), the shiny cowbird, *Molothrus bonariensis* (Lea & Kattan 1998; Tuero et al. 2007), the bronzed cowbird, *Molothrus aeneus* (Ellison et al. 2006), and also in the great spotted cuckoo, *Clamator glandarius* (Martínez et al. 1998; Soler & Soler 1999). However, it is a relatively rare phenomenon in hosts of the common cuckoo, *Cuculus canorus* (hereafter ‘cuckoo’), an evictor brood parasite, which are typically parasitized at a rate below 20% (e.g. Schulze-Hagen 1992; Davies 2000; Rutila et al. 2002; Avilés et al. 2005; Antonov et al. 2006, 2007; Stokke et al. 2007a). Thus, most cuckoo chicks that hatch successfully (Øien et al. 1998) do not need to compete with or evict other parasite eggs and chicks from parasitized broods. In contrast, an unusually high level (ca. 64%) of cuckoo parasitism occurs in the great reed warbler, *Acrocephalus arundinaceus*, in the Hungarian Great Plain (Moskát & Honza 2002), where a high rate of multiple parasitism has also been reported: 35% of the parasitized clutches ($N = 123$) were multiply parasitized by two to four cuckoo eggs, and so 58% of all cuckoo eggs ($N = 187$) were found in nests with multiple cuckoo eggs (Moskát & Honza 2002). Egg collections in Hungarian museums (C. Moskát, unpublished data) and other reports on historical data suggest that such a high level of parasitism has existed for at least the last 80–100 years (e.g. Baker 1942; Molnár 1944; Moskát & Honza 2002).

Behavioural Responses of Hosts

Multiple parasitism may also have critical implications for the host’s reproductive success and behavioural responses to parasitism. At the fitness level, more parasite eggs mean greater chances of elimination or reduction of the host’s own brood and caring for more genetically unrelated young, thus reducing the foster parents’ current (Trine 2000; Hauber 2002; Hoover 2003) and future reproductive outputs (Payne & Payne 1998; Hauber 2002; Hauber & Montenegro 2002).

The evidence suggests a negligible effect of multiple parasitism on recognition by hosts of nonevictor parasites. Indeed, experiments with *Molothrus* cowbird hosts have shown that single parasite eggs are as likely to be accepted or rejected as multiple foreign eggs (e.g. Rothstein 1975a; Davies 2000). Similar results were reported for magpie, *Pica pica*, hosts of great spotted cuckoos in Spain (Soler & Møller 1990). In contrast, although studies of multiple parasitism on hosts of evictor parasites are sparse (e.g. Brooker et al. 1990), these suggest that multiple parasitism may affect host recognition. For instance, Honza & Moskát (2005) experimentally parasitized great reed warbler clutches in Hungary by two different, but both nonmimetic, model common cuckoo eggs, and found increased host rejection of the nonmimetic eggs relative to experimental single parasitism with a nonmimetic egg. However, in natural cases of cuckoo parasitism in the Hungarian great reed warbler population, the cuckoo eggs generally show a good visual match as judged by human eyes (Baker 1942; Southern 1954; Moskát & Honza 2002; Lovászi & Moskát 2004; Fig. 1) and spectrophotometry (Cherry et al. 2007a). If mimicry is so good, hosts may treat foreign eggs as their own (Hauber et al. 2006; Moskát & Hauber 2007). Therefore, the research by Honza & Moskát (2005) cannot be regarded as a typical case of parasitism in that naturally parasitized great reed warbler population. In addition, the use of two nonmimetic eggs in that earlier experiment did not allow a test for contrasting predictions of alternative cognitive explanations for egg rejection. Here, we designed a new treatment to simulate parasitism more realistically to add experimental data to observations of natural parasitism and to address alternative cognitive scenarios involved in the hosts’ responses to multiple parasitism.

Alternative Cognitive Mechanisms of Host Responses

The rejection by discordance hypothesis (Rothstein 1975b, 1982; Marchetti 2000; Servedio & Lande 2003) assumes that egg appearance is perceived relative to the appearance of other eggs in the clutch so as to generate a distribution of pairwise dissimilarities. In this cognitive scenario, therefore, it is parasitism per se, rather than the identity of individual parasite eggs that is perceived by the host (Hauber et al. 2004; Hoover et al. 2006). Accordingly, this cognitive scenario predicts that multiple parasite eggs of different levels of mimicry will lead to lower rejection rates than single parasite eggs because more foreign eggs would reduce the chance that any single egg is considered the most dissimilar. In contrast, when two parasite eggs are highly dissimilar in multiple parasitism, each foreign egg is expected to be recognized, so this method would result in increased rejection rates.

Alternatively, the hypothesis that rejection is based on limited intraclutch variation (Davies & Brooke 1989; Stokke et al. 1999; Moskát et al. 2008a; Schulze-Hagen et al. 2009) predicts that through evolutionary time, host species or populations of a host species that are more frequently parasitized by cuckoos would evolve eggs more homogeneous in appearance within a nest than populations with lower rates of parasitism (Øien et al. 1995; Soler & Møller 1996; Moskát et al. 2002; Avilés & Møller 2003). From a cognitive perspective, individual hosts would use clutch uniformity of their perceived own eggs to identify parasitism (Stokke et al. 1999; Moskát et al. 2008a). Thus, provided that foreign eggs are nonmimetic (i.e. they cannot be considered among the host’s own set of eggs), multiple parasitism in a host clutch will lead to increased recognition of the parasite eggs. If a nest contains two or more parasite eggs that differ in the extent of their mimicry relative to the host’s eggs, this should also increase the perceived variation of the entire clutch within the nest and lead to increased rejection of parasitism.

Finally, the true egg recognition (recognition from memory) hypothesis predicts that birds compare the characteristics of eggs in a clutch to a memory template of their own or otherwise acceptable egg phenotype, which could be inherited and/or learned (Rothstein 1974; Moksnes 1992; Hauber & Sherman 2001; Hauber et al. 2006; Moskát & Hauber 2007). If the match of a parasite egg to the internal template is close, hosts would accept this egg as their own (Reeve 1989; Davies et al. 1996; Hauber et al. 2006; Moskát & Hauber 2007; Stokke et al. 2007b). Thus, this scenario predicts the same frequency of rejection for foreign eggs for single and multiple

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