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Does the cuckoo benefit from laying unusually strong eggs?

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Brood-parasitic birds such as cuckoos and cowbirds lay eggs with unusual by strong shells. Three main hypotheses have been proposed to explain the adaptive significance of this trait. The present study focused on the puncture resistance hypothesis and tested its critical prediction that increased eggshell strength enhances the probability that the parasitic egg is accepted by the host. To address the problem, we experimentally parasitized marsh warbler, *Acrocephalus palustris,* nests with three types of real eggs having similar size but differing in eggshell strength and/or mimicry: (1) great reed warbler, *Acrocephalus arundinaceus,* eggs painted to be nonmimetic; (2) common cuckoo, *Cuculus canorus,* eggs painted in the same way; and (3) unmanipulated cuckoo eggs. When we controlled for mimicry, ejection of strong-shelled (cuckoo) eggs was considerably more costly than ejection of weak-shelled (great reed warbler) eggs. However, nonmimetic cuckoo eggs were not more likely to be accepted than nonmimetic great reed warbler eggs, suggesting no effect of eggshell strength alone on rejection decisions. Mimetic cuckoo eggs were accepted more often than the eggs painted to be nonmimetic suggesting that mimicry primarily determines the probability of rejection. Thus, we found no support for the puncture resistance hypothesis in marsh warblers, which is a host with well-developed defence mechanisms against cuckoo parasitism.

Keywords: *Acrocephalus palustris*; brood parasitism; cuckoo; *Cuculus canorus*; eggshell strength; marsh warbler; mimicry; puncture resistance

Some bird species have evolved eggs with unusually strong shells in response to specific selection pressures (e.g. Mallory & Weatherhead 1990; Picman & Honza 2002; Boersma et al. 2004). Among such species are the brood-parasitic cuckoos and cowbirds (Spaw & Rohwer 1987; Picman 1989; Brooker & Brooker 1991; Picman & Pribil 1997). Three hypotheses have been proposed to explain the adaptive significance of strong eggs in brood parasites (Lack 1968; Spaw & Rohwer 1987; Brooker & Brooker 1991). One of them, called the puncture resistance hypothesis, considers strong shells of brood-parasitic eggs to be an adaptation that increases the costs of ejection in their hosts, thereby making acceptance more likely (Swynnerton 1918; Spaw & Rohwer 1987; Rohwer & Spaw 1988; Rohwer et al. 1989; Røskaft et al. 1990). Many small hosts of brood parasites cannot grasp the relatively large parasitic egg in their mandibles to eject it from the nest because of limitations in their bill size (Moksnes et al. 1991). Rather, they have to make a puncture hole in the shell in order to be able to grasp and eject the parasitic egg. Puncturing an unusually strong egg, however, may be either impossible or costly as the host may damage its own eggs (e.g. Davies & Brooke 1988; Rohwer et al. 1989; Antonov et al. 2006a). Because of such costs, small-billed hosts may do better to accept the parasitic egg under some circumstances (Spaw & Rohwer 1987; Røskaft et al. 1990; Røskaft & Moksnes 1998; Avíles et al. 2005; Servedio & Hauber 2006). Acceptance could be better than rejection for some hosts of cowbirds that are reared alongside host chicks if the costs of parasitism are not higher than the costs of renesting after desertion or of removing the parasitic egg (but see Lorenzana & Sealy 2001). Eggshell strength alone could have been sufficient to constrain the evolution of puncture ejection in brown-headed cowbird, *Molothrus ater,* hosts as this parasite has not evolved egg mimicry (Spaw & Rohwer 1987). This has been thought to be unlikely for the common cuckoo, *Cuculus canorus* (hereafter cuckoo), and other parasitic cuckoos whose chicks evict host eggs or young from the nest, as it should always pay their hosts

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to reject (Rothstein 1990). Thus, it is considered that such brood parasites can increase the probability of acceptance only by evolving mimetic eggs that may go undetected by the host (Rothstein & Robinson 1998; Kilner 2006; Krüger 2007). In line with this expectation, the eggs of evicting brood parasites often mimic host eggs very well and in some cases mimicry has evolved to perfection (Baker 1942; Moksnes & Røskaft 1995; Moksnes et al. 1995; Higuchi 1998; Moskát & Honza 2002). Nevertheless, evictor cuckoos in general, and the cuckoo in particular, still lay eggs of unusually high structural strength (Picman & Pribil 1997) which do render rejection costly, at least in small-billed hosts (Antonov et al. 2006a).

Given the high temporal and spatial variation in parasitism rate and host rejection rates among several host–parasite systems (Brooke et al. 1998; Lindholm 1999; Soler et al. 1999a; Stokke et al. 2007a; 2008) and the variation in costs associated with recognition and rejection within and among hosts, selection should favour flexible responses to an odd egg in the nest (Lotem et al. 1995; Alvarez 1996; Davies et al. 1996; Lindholm 2000; Lindholm & Thomas 2000). There is evidence for such conditional responses and the importance of motivation to reject eggs in cuckoo hosts (Moksnes et al. 1993a; Davies & Brooke 1988; Lindholm 2000; Soler et al. 2000; Hauber et al. 2006). The motivation of the host to reject may depend on a number of factors, for example, perceived risk of parasitism, nesting stage, number of host eggs present, costs of recognition and rejection, prospects of successful renesting, and perhaps age and/or experience (Røskaft & Moksnes 1998; Rodríguez-Gironés & Lotem 1999; Moskát 2005; Stokke et al. 2005; Moskát & Hauber 2007). There is at least one study showing that recognition of a foreign egg (pecking) may not necessarily lead to rejection (Lindholm 2000). Thus, strong eggshells of cuckoo eggs may increase the probability that they survive host pecking attempts when ejection is difficult (and costly), and the host motivation to reject is low. A continuum of egg mimicry is likely to be linked with a corresponding continuum of host motivational states to reject the foreign egg. The strong eggshell may thus interact with the effect of mimicry in determining rejection decisions in cases where mimicry is close to the host recognition threshold (Stokke et al. 2005, 2007b; Hauber et al. 2006). In this way, some mimetic cuckoo eggs may be pecked, but not rejected because of the relatively low level of certainty of the host about their parasitic origin, resulting in low motivation to reject. Thus, flexibility in host responses and the role of motivation suggest a possible pathway where the strong eggshell may also be important in evicting cuckoos.

In this study we aimed to evaluate the puncture resistance hypothesis for the maintenance of unusually strong eggs in the cuckoo. As a model host species we used the marsh warbler, *Acrocephalus palustris*, a major cuckoo host in Europe which rejects cuckoo eggs by puncture ejection (Gärtner 1982; Schulze-Hagen 1992; Moksnes & Røskaft 1995; Antonov et al. 2006b). In a previous study (Antonov et al. 2006a), we found support for the two main predictions of the puncture resistance hypothesis as set out by Spaw & Rohwer (1987). First, we showed that ejection of real cuckoo eggs is costly for marsh warblers. Second, ejection costs are significantly higher when the egg being ejected has a stronger shell (cuckoo egg) than a control egg of a similar size but much less resistant to puncture (great reed warbler, *Acrocephalus arundinaceus,* egg). However, the critical prediction of the puncture resistance hypothesis is that a stronger eggshell must increase the probability that the parasitic egg is accepted by the host. This prediction has not been tested so far, and is the main focus of this study. To address the problem, we experimentally parasitized marsh warbler nests with three types of foreign egg differing in shell strength and mimicry: (1) great reed warbler eggs painted to be nonmimetic, (2) cuckoo eggs painted in the same way; and (3) real cuckoo eggs, which were not manipulated (mimetic).

The goals of this study were two-fold. First, we estimated the influence of eggshell strength and mimicry as predictors for ejection costs. By comparing the frequency and magnitude of ejection costs among the three treatments, we predicted that (1) ejection of nonmimetic cuckoo eggs is more costly than ejection of non mimetic great reed warbler eggs because of the eggshell strength effect alone, and (2) ejection of mimetic cuckoo eggs is more costly than ejection of nonmimetic cuckoo eggs as mimicry may pose recognition problems in addition to the effect of eggshell strength. Second, we evaluated the significance of eggshell strength as a possible constraint on rejection. In connection with this, we videorecorded host responses to the experimental eggs and related the presence of pecking (egg discrimination) to the probability of rejection. If cuckoo eggshell strength is an important constraint on rejection we predicted that (3) both nonmimetic egg types would be pecked but cuckoo eggs would be accepted significantly more often. Finally, if mimicry (motivation) can increase the probability of acceptance of the strong-shelled egg, we predicted that (4) discriminated (pecked) mimetic cuckoo eggs would be accepted significantly more often than discriminated nonmimetic ones.

METHODS

Study Area and Species

The fieldwork was carried out between 15 May and 20 June 2005 and 2006 in northwestern Bulgaria. The study area was situated between the villages of Zlatia (43°46′N, 23°30′E), Ignatovo (43°46′N, 23°28′E) and Dolni Tsibar (43°48′N, 23°31′E). Here, marsh warblers breed at high densities (5–8 pairs/ha) in various types of rank herbaceous vegetation. It is one of four main cuckoo host species in this area and as many as 28% of the nests are parasitized on average (Antonov et al. 2006b).

Experimental Procedure and Field Protocol

Only host nests found during the nest-building or early laying stage and that were not parasitized by cuckoos were used in the experiments. Each nest was experimentally parasitized at the end of laying, after four or five eggs had been laid. Marsh warblers normally lay clutches of four or