ANIMAL BEHAVIOUR, 2007, 73, 55–63
doi:10.1016/j.anbehav.2006.06.005



# Defence behaviour against brood parasitism is deeply rooted in mainland and island scrub-jays

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*(Received 28 August 2005; initial acceptance 12 November 2005; final acceptance 28 June 2006; published online 13 November 2006; MS. number: A10233)*

When selection pressures for an adaptation relax, the trait may decline, or it may be maintained if there are no fitness costs. The interactions between avian brood parasites and their hosts are dynamic, with selection pressures changing as host or parasite ranges shift, or as parasites switch to new hosts once old hosts evolve defences. The extent to which hosts retain defences in the absence of parasites has important consequences to parasite–host coevolution. We tested whether island scrub-jays, *Aphelocoma insularis*, and western scrub-jays, *A. californica*, have maintained egg ejection behaviour in the absence of brood parasitism and provide an estimate of how long they have maintained ejection. Island scrub-jays and western scrub-jays ejected 100% of foreign eggs placed into their nests, and genetic analyses revealed no evidence of conspecific brood parasitism that could maintain ejection. Extreme variation in intraclutch egg appearance may result in hosts ejecting their own oddly coloured eggs, which would select against the maintenance of ejection. However, island, western and Florida scrub-jays, *A. coerulescens*, also an ejecter, showed less variation than the common grackle, *Quiscalus quiscula*, a species that has an extremely high level of intraclutch egg variation and may have lost its rejection defence, because it rejects its own oddly coloured eggs. Based on molecular clock analyses of mitochondrial DNA control region and ND2 sequences, island and western scrub-jays split approximately 140 000–151 000 years ago, western and Florida scrub-jays 1 000 000 years ago, and island and Florida scrub-jays 1 250 000 years ago. Ejection behaviour may have been maintained this long in the absence of parasitism, but it is possible that scrub-jays were parasitized as recently as the end of the Pleistocene 10 000 years ago, when cowbirds were more abundant. Nevertheless, these results indicate that (1) egg ejection is not a costly trait to maintain in scrub-jays, (2) brood parasites may not be able to alternate between well-defended hosts and hosts that have lost ejection defence following past episodes of parasitism and (3) brood parasites may have to deal with host communities that have well-developed defences by evolving specialized adaptations for a single host species or a small set of species.



*Keywords*: *Aphelocoma californica*; *Aphelocoma coerulescens*; *Aphelocoma insularis*; brood parasitism; egg ejection; Florida scrub-jay; host defence; island scrub-jay; molecular clock; western scrub-jay

Adaptations that have no current utility are relics of an organism's evolutionary past. These adaptations persist because the costs of maintaining them are minimal. Conditional behavioural traits that are expressed only in response to specific stimuli are most likely to be retained after selection has relaxed, because once the necessary stimuli have been removed, their lack of expression makes them neutral or nearly so. This has been demonstrated in prey species that show defences for thousands of years in the absence of particular predation pressures (Coss & Goldthwaite 1995; Byers 1997; Rydell et al. 2000). When such adaptations persist, they will be expressed when the selection pressures recur even though the pressures may appear to be novel ones from the perspective of human history.

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0003–3472/06/$30.00/0

Avian brood parasites lay their eggs in the nests of other bird species and rely on these hosts to raise their young. The most effective host adaptation against parasitism, other than avoiding parasitism altogether, is ejection of the parasite's eggs from the nest. As with antipredator behaviours, egg ejection behaviour is a conditional trait and may be retained for long periods in the absence of selection. The grey catbird, *Dumetella carolinensis*, retained egg ejection behaviour after it colonized Bermuda from North America, despite the absence of cowbirds on the island, and the loggerhead shrike, *Lanius ludovicianus*, has retained ejection from its ancestors in Eurasia that were parasitized by cuckoos, *Cuculus* spp. (Rothstein 2001). Likewise, great-tailed grackles, *Quiscalus mexicanus*, and boat-tailed grackles, *Q. major*, have retained ejection in the absence of cowbird parasitism, with the latter possibly having retained it for as long as 800 000 years (Peer & Sealy 2004a). However, there is evidence that at least one host may have lost egg ejection in the absence of parasitism. Common grackles, *Q. quiscula*, demonstrate extreme variation in the appearance of eggs within a clutch, which may have caused them to eject their own oddly coloured eggs, resulting in the loss of ejection (Peer & Bollinger 1997; Peer & Sealy 2004a).

Whether host defences such as egg ejection are maintained in the absence of parasitism is critical to long-term parasite–host coevolution. When a host evolves egg ejection behaviour, a parasite should shift to a new host that will accept its eggs. If egg ejection behaviour is lost in former hosts, the parasite can return to using these old hosts once new hosts evolve egg ejection. Hence, the interactions between parasites and hosts may continue through a cyclical process of parasitism and avoidance, or follow the coevolutionary cycles model of brood parasite–host coevolution (Rothstein 2001; see also Soler et al. 1998). In this manner, the parasite will be able to persist indefinitely because host adaptations are lost once selection has relaxed.

Alternatively, because brood parasitism is the only circumstance in which birds are regularly exposed to foreign eggs in their nests, egg ejection should rarely if ever be expressed in the absence of parasitism (Rothstein 1990). As a consequence, ejection may be retained for long periods after selection has been relaxed. In this case, brood parasites and their hosts will follow a single trajectory model of brood parasite–host coevolution because parasites will not return to using old hosts (Rothstein 2001). Once most hosts have become well defended, a parasite will be forced to specialize on just a few host species. For example, in order to circumvent egg ejection, a parasite will have to evolve a mimetic egg that will likely match only one or a few host species.

Here we test whether avifaunas become increasingly resistant to brood parasitism by examining egg ejection behaviour in the scrub-jays, *Aphelocoma* spp., of North America for which there is no evidence of brown-headed cowbird, *Molothrus ater*, parasitism (Ortega 1998). The island scrub-jay, *A. insularis*, is endemic to Santa Cruz Island off the coast of California where there are no breeding brown-headed cowbirds or other brood parasites. The western scrub-jay, *A. californica*, is sympatric with the cowbird in western North America, but there are no records of parasitism for this species (Ortega 1998). Both jay species are closely related to the Florida scrub-jay, *A. coerulescens*, and until recently all three were considered conspecific (Peterson 1992; AOU 1998; Saunders & Edwards 2000). The Florida scrub-jay ejects cowbird eggs despite the fact that it just recently became sympatric with brown-headed cowbirds and shiny cowbirds, *M. bonariensis*, in the late 1980s to early 1990s, and there are no records of parasitism (Cruz et al. 2000; Fleischer & Woolfenden 2004; B. D. Peer, unpublished data).

We tested whether the island and western scrub-jays demonstrate egg ejection in the absence of brood parasitism by experimentally parasitizing their nests. We also conducted genetic analyses to determine whether conspecific brood parasitism (CBP) maintains egg rejection in island and western scrub-jays. CBP is the only other known selection pressure for egg recognition and rejection in passerines. CBP tends to occur in colonial nesting species, waterfowl, precocial species, and species with specialized nesting sites that may be in short supply such as cavities (Rohwer & Freeman 1989; MacWhirter 1989). The two scrub-jay species do not demonstrate any of these traits. We quantified intraclutch egg colour variation in the three scrub-jay species and compared these data to those for the common grackle. Finally, we compared mtDNA sequence data for the three scrub-jay species to estimate divergence time, which provided an approximation of how long they have maintained ejection in the absence of brood parasitism.

## METHODS

### Experimental Parasitism

Island scrub-jays were experimentally tested for egg ejection in April of 2002 on Santa Cruz Island, California. Santa Cruz Island is approximately 40 km off the coast of California at its nearest location. Brown-headed cowbirds do not breed on the island. Scrub-jay nests were typically located in oaks, *Quercus* spp., in canyons or in the central valley of the island. Western scrub-jays were tested in Santa Barbara and San Luis Obispo counties, California, from 1973 to 1976.

Island scrub-jays were parasitized with artificial cowbird eggs made of plaster of Paris (see Rothstein 1975a). Only a single egg was added to each nest, and host eggs were removed from two nests. Western scrub-jays were parasitized with the same artificial cowbird eggs, jay-sized artificial cowbird eggs, and real loggerhead shrike and house sparrow, *Passer domesticus*, eggs. Single western scrub-jay eggs were removed in conjunction with parasitism, except in two instances: at one nest, no host eggs were removed, and at another the entire clutch of three scrub-jay eggs was replaced with three jay-sized artificial cowbird eggs. Eggs were added during the laying or incubation stages of the nesting cycle of both species, except in two cases where eggs were added to nests with recently hatched island scrub-jays. Despite the variation in the experimental parasitism procedure, there was no variation in the response of