Articles

Response of introduced European birds in New Zealand to experimental brood parasitism

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The loss of anti-parasite adaptations against the European cuckoo *Cuculus canorus* was studied in three European passerine species, song thrush *Turdus philomelos*, blackbird *T. merula*, and chaffinch *Fringilla coelebs*, introduced to New Zealand in the 19th century. Chaffinches in New Zealand ejected non-mimetic eggs at a rate similar to their source population in the United Kingdom, but both song thrushes and blackbirds in New Zealand rejected non-mimetic eggs at a higher rate than the United Kingdom. It is not clear if this difference reflects variation among hosts in their response to brood parasitism or if it is an artefact of subtle differences in the types of non-mimetic eggs tested. In contrast, all three introduced species showed little aggression to a taxidermic model of a European cuckoo presented at their nests. This differs from European populations of these species, where model cuckoos are typically attacked. Our results suggest that in the ~130 years since their release in New Zealand, introduced birds have lost recognition of the European cuckoo but not their ability to discriminate non-mimetic eggs. The differential loss of anti-parasite adaptations by introduced birds in New Zealand suggests that cyclical models of host/parasite co-evolution may need to take into account the differing rates at which different host adaptations are lost and gained.

The adaptations and counter-adaptations between brood parasites and their hosts is one of the best-studied examples of co-evolution among birds (Rothstein and Robinson 1998, Davies 2000). As brood parasitism reduces host fitness, anti-parasite adaptations such as rejection of parasitic eggs and nest defence against adult parasites are thought to have evolved to reduce the impact of parasitism. Anti-parasite behaviours may nonetheless carry a cost if a host mistakes its own egg for that of a parasite and ejects the wrong one, or if effort is wasted in defending nests against non-threatening targets (McLean 1987, Davies and Brooke 1988, Moksnes et al. 1990). As long as the probability of parasitism is high, these risks may be worth taking and anti-parasite adaptations should persist. However, in the absence of brood parasitism, recent work has suggested that host adaptations may decline if the costs of maintaining these defences are high (Davies and Brooke 1989a, Marchetti 1992).

Whether anti-parasite adaptations are costly has important consequences for understanding the co-evolutionary trajectories between hosts and parasites. For example, if brood parasites switch hosts to overcome anti-parasite defences, then host defences might be expected to disappear if the costs outweigh the benefits. This would then allow a parasite to re-exploit former hosts once their anti-parasite defences had been lost, and may ultimately lead to a series of co-evolutionary cycles as parasites switch back and forth between hosts to avoid their anti-parasite defences (Davies and Brooke 1989a, b, Rothstein 1990, Marchetti 1992). On the other hand, if the costs of anti-parasite adaptations are negligible, then previously exploited hosts are unlikely to lose their defences and parasites would overcome host defences only through continually exploiting new hosts or evolving more sophisticated counter adaptations to host defences (Rothstein 2001). This has been referred to as a single trajectory model of co-evolution between hosts and parasites (Rothstein 2001).

Studies of the apparent disappearance of anti-parasite adaptations in the absence of parasitism have

been equivocal (Rothstein 2001). For example, Davies and Brooke (1989a) tested the responses of meadow pipits *Anthus pratensis* and white wagtails *Motacilla alba* between Iceland, an island without any brood parasites, and England where both species are parasitized by the European cuckoo *Cuculus canorus*. Rates of rejection were significantly lower in Iceland than England, which Davies and Brooke (1989a) concluded was support for the hypothesis that anti-parasite adaptations are lost in the absence of parasitism. Similarly, rejection rates of European cuckoo eggs by the reed warbler *Acrocephalus scirpaceus* in England declined from 75% to 25% over a 12-year period in which the number of cuckoos fell dramatically (Brooke et al. 1998). Although the decline was attributed to behavioural flexibility rather than genetic change, the loss of this anti-parasite adaptation was taken of evidence of its high cost in the absence of brood parasitism (Brooke et al. 1998). In contrast, Rothstein (2001) found that both loggerhead shrikes *Lanius ludovicianus* in California, and grey catbirds *Dumetella carolinensis* in Bermuda nearly always rejected foreign eggs despite little contact with any brood parasite within historic times. He suggested these species retained egg discrimination abilities despite long periods of allopatry with brood parasites because of the low cost of their defences. In the case of the shrike, it is even possible that egg ejection behaviour was retained from ancestral congeners parasitized by cuckoos in Eurasia (Rothstein 2001).

The introduction of European birds to New Zealand provides an opportunity to investigate if adaptations against brood parasitism can be lost in the absence of its selective pressure. Beginning in the 1870's several species of European songbirds were established in New Zealand (Thomson 1922). Most had been subject to parasitism by cuckoos in Europe. However, these brood parasites were not introduced to New Zealand and although two species of native cuckoos are present in New Zealand, they parasitize introduced birds rarely (McLean 1988, Gill 1998). Thus, hosts that had been under selection from cuckoos in their native range were translocated to an environment with little risk of interspecific parasitism.

In this study we test the hypothesis that adaptations against brood parasitism decline when selection on hosts is removed. To determine if egg rejection behaviour has declined in the time since their introduction, artificial cuckoo eggs were experimentally added to the nests of three introduced species and their responses recorded. A taxidermic model of the European cuckoo was also presented to determine if hosts still recognise cuckoos and respond aggressively. These responses were then compared to data on the same species in Europe to estimate the relative loss of anti-parasite behaviour in European birds since their introduction to New Zealand. Although populations of European birds were

only founded in New Zealand about 130 years ago, at least 50 to 100 generations have passed since their introduction. If the costs of maintaining anti-parasite defences are high (as predicted from the co-evolutionary cycle hypothesis), then it might be expected that such behaviours have declined even in this short interval. In contrast, if the costs of anti-parasite defences are low (as predicted by the single trajectory hypothesis), then it might be expected that such behaviours remain unchanged in the absence of brood parasitism.

Material and methods

The response of introduced passerines to experimental cuckoo eggs was tested during 6 austral summers (October-December) from 1998–2003. The study area was located at Kowhai Bush, a 240 ha block of native forest located 10 km from Kaikoura, South Island, New Zealand. Three species of introduced birds were tested: song thrush *Turdus philomelos*, blackbird *T. merula*, and chaffinch *Fringilla coelebs*. The avifauna of this area has been the subject of numerous studies (Powlesland 1981, Gill 1982, 1983, Briskie 2003), and the site described by Gill (1980). All three introduced species are common.

We located nests by searching suitable habitat and following adult birds. Nests were flagged and visited at intervals of 3 to 5 days to monitor their progress. The response of birds to parasitism was tested by experimentally adding artificial eggs to their nests, as done by other workers (Rothstein 1975, Davies and Brooke 1989a, b). We tested host responses to three types of eggs: (1) long-tailed cuckoo *Eudynamys taitensis*, (2) shining cuckoo *Chrysococcyx lucidus*, and (3) European cuckoo. The eggs of both long-tailed and shining cuckoos are non-mimetic relative to the host eggs, while those of the European cuckoo were painted to mimic each respective host (Fig. 1). Eggs were made with model clay wrapped around a styrofoam ball and painted to mimic the eggs of each cuckoo. This allowed us to produce model eggs similar in size and mass to real eggs (real shining cuckoo eggs: 1.85 ± 0.06 (SD) g, n = 4 (Gill 1983), model eggs: 1.94 ± 0.10 (SD) g, n = 10; real long-tailed cuckoo eggs: 3.64 g (estimated from linear measures using Hoyt 1979), model eggs: 3.77 ± 0.12 (SD) g, n = 10; real European cuckoo eggs: 3.4 g, n = 31 (Wyllie 1981), model eggs: 4.80 ± 0.17 (SD) g, n = 10). It was not possible to use real cuckoo eggs and we could not test whether the response of birds to clay eggs differed from real eggs. However, previous studies have demonstrated that artificial eggs generally elicit similar responses to those of real eggs (Rothstein 1975, Davies and Brooke 1989a, b).

Artificial cuckoo eggs were added either during the laying (at least one host egg present) or early incubation
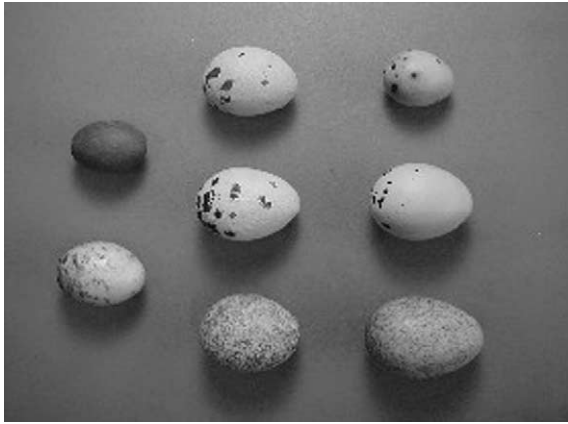
Fig. 1. Model cuckoo eggs and the real eggs of three host species introduced into New Zealand. Left column (from top to bottom): model shining cuckoo (olive-green; 18.5 × 12.5 mm), model long-tailed cuckoo (creamy-white with brownish blotches; 22.5 × 16.5 mm). Both species of cuckoo are native to New Zealand but neither mimics the eggs of the introduced hosts. Middle column: model European cuckoo eggs (all 24.0 × 19.0 mm) painted to mimic those of their corresponding host species in the right column. European cuckoo mimics (middle row) and their hosts (right row; from top to bottom): chaffinch (light brown with purple-brown spots; 20.0 × 14.0 mm), song thrush (light blue with dark brown spots; 27.0 × 20.5 mm), blackbird (light blue with fine reddish brown spots; 28.0 × 21.0 mm).

period of the host (days 1−5 of incubation). A single artificial cuckoo egg was added to each nest and no host eggs were removed. Both New Zealand and European cuckoos normally remove a host egg during parasitism, but Davies and Brooke (1988) have shown that removal does not affect the probability of host rejection in European hosts. Eggs were added between 07.00 and 13.00 NZST. Nests were then checked 24 h later to determine if hosts rejected the model egg. If the cuckoo egg was present after 24 h, we rechecked the nest 4 d later. If the egg was still being incubated after 5 d, we removed it and considered the cuckoo egg accepted (Rothstein 1975, Davies and Brooke 1989a, b). If the egg was present but cold, we classified nests as deserted. This was confirmed on subsequent visits to all these nests after the 5-day period. The cuckoo egg was considered ejected if it was missing from the nest but the nest was still active. We also tested the reactions of song thrush to conspecific brood parasitism by adding real song thrush eggs to their nests in the same manner as we tested responses to cuckoo eggs. Fresh song thrush eggs were used and were collected from nests not included in the study. We marked conspecific eggs with a small mark to differentiate them from host eggs. For all experiments, we tested each nest with only one type of egg, and to avoid testing the same birds twice, we did not parasitize nests within the same area as a nest tested

previously. As our procedures for parasitizing nests followed the protocol of Davies and Brooke (1989a) in the United Kingdom, we were able to compare our results in New Zealand with populations of the same species in their native range.

The response of introduced birds to a model European cuckoo was tested during two austral summers (October − December) from 2001−2002. The same three European species outlined in the above experiments were used to test the intensity of nest defence to a taxidermic model of the European cuckoo, Australian magpie *Gymnorhina tibicen* and a control. The control used was either a taxidermic mount of a blackbird or song thrush depending on the species being tested: if a song thrush nest was tested the blackbird model was used as a control and vice versa. For the chaffinch, the control was assigned randomly using either a blackbird or song thrush model. The magpie is not native to New Zealand and was used to test host responses to an introduced avian predator. All models were presented during the early incubation stage of the hosts (2 to 6 d after clutch completion), and to minimize responses to humans, a hide was set 5 to 10 m from the nest at least 2 h prior to any model presentation. The order of model presentation was assigned randomly. Each model was placed 0.5 m from the nest, with the model facing and level with the nest. At least 2 h separated the presentation of each model to give hosts time to recover and to avoid overlap in behavioural responses for each model. The behaviour of the host was recorded from the time a bird either approached the nest within 10 m or was heard alarm calling close to the model. Each trial ended after 2 minutes from the time the host first responded. Observations were recorded and later transcribed onto data sheets. For each presentation we recorded the number of alarm calls and the number of attacks on the model.

Results

All three species showed rejection of model eggs. The most common rejection behaviour noted was egg ejection (Table 1). Both song thrushes (Fisher exact test: P < 0.001), and blackbirds (Fisher exact test: P < 0.001) accepted the non-mimetic eggs of native cuckoos at a significantly lower rate than the mimetic eggs of European cuckoos (Table 1). Song thrushes also accepted conspecific eggs at a rate similar to mimetic European cuckoo model eggs (Fisher exact test: P = 0.26). As shining cuckoo eggs were smaller than each host's real eggs, it is possible the low rate of acceptance was due to the small size of this cuckoo's egg (Fig. 1). However, both song thrushes (Fisher exact test: P = 0.005) and blackbirds (Fisher exact test: P = 0.002)

Table 1. Responses of three species of European passerines in New Zealand to experimentally added model eggs of long-tailed and shining cuckoos (two native species with non-mimetic eggs) and to model eggs of European cuckoo that mimic each respective host. The response of song thrushes to conspecific eggs was tested by experimental addition of real eggs from other thrush nests.

Host species	Egg type	Number nests tested	Number accepted (%)	Number rejected (%)	
				By ejection	By desertion
Song thrush	Long-tailed cuckoo	27	6 (22)	20 (74)	1 (4)
	Shining cuckoo	29	2 (7)	25 (86)	2 (7)
	Mimetic European cuckoo	15	10 (67)	1 (7)	4 (27)
	Song thrush	14	8 (57)	5 (36)	1 (7)
Blackbird	Long-tailed cuckoo	18	3 (17)	14 (78)	1 (6)
	Shining cuckoo	13	2 (15)	11 (85)	0
	Mimetic European cuckoo	12	9 (75)	1 (8)	2 (17)
Chaffinch	Long-tailed cuckoo	8	5 (63)	1 (13)	2 (25)
	Shining cuckoo	9	2 (22)	7 (78)	0
	Mimetic European cuckoo	4	1 (25)	2 (50)	1 (25)

accepted long-tailed cuckoo eggs significantly less frequently than the European cuckoo eggs. As long-tailed cuckoo eggs were about the same size as European cuckoo eggs, but not mimetic (Fig. 1), the higher rate of rejection of long-tailed cuckoo eggs is likely due to differences in appearance rather than differences in size. Chaffinches did not differ in response to mimetic and non-mimetic eggs (Fisher exact test: $P = 0.38$) but our sample size was small. However, some egg ejection of all egg types was observed, including mimetic European cuckoo model eggs (Table 1).

Rejection rates of both song thrush and blackbird were significantly higher in their introduced New Zealand populations than in their native range in the United Kingdom (Table 2). Rejection of non-mimetic eggs was 27% higher by song thrush and 22% higher by blackbird in New Zealand than in the United Kingdom. In contrast, rejection rates for the chaffinch were similar in both countries. These differences are not the result of differing sample sizes, as similar numbers of nests were tested in both populations.

Few host eggs were lost during ejection at experimentally parasitized nests. Of 51 song thrush nests in which a parasitic egg was ejected, only 2 nests incurred a loss of host eggs during the 5-day period of testing: one host egg was lost at a thrush nest tested with a long-

Table 2. Rejection rates for all non-mimetic eggs by three species of European passerines introduced to New Zealand and for same species in their native range. Figures are number of nests in which foreign eggs were rejected relative to total number tested (%). Data for United Kingdom from Davies and Brooke (1989a).

Species	New Zealand	United Kingdom	P-value*
Song thrush	48/56 (86)	24/41 (59)	<0.005
Blackbird	26/31 (84)	21/34 (62)	0.032
Chaffinch	10/17 (59)	9/15 (60)	0.28

*Fisher exact test.

tailed cuckoo egg, and one host egg was lost at a thrush nest tested with a shining cuckoo egg. In both cases, host eggs disappeared on the same day as the parasitic egg. This rate of egg loss (3.9%) did not differ significantly from that observed in song thrush nests on the study site that were visited in the same manner but not parasitized (8.9% of 90 nests; Fisher exact test: $P = 0.16$). There was also no loss of host eggs in 26 (0%) blackbird nests in which parasitic eggs were ejected. This did not differ significantly from the 3.3% (1/30 nests) of nests with egg loss at blackbird nests that were visited but not parasitized (Fisher exact test: $P = 0.54$). Likewise, no host eggs were lost in 10 (0%) chaffinch nests with ejection of parasitic eggs compared to 3/19 (15.8%) chaffinch nests that were not parasitized (Fisher exact test: $P = 0.27$). Thus, the cost of ejecting parasitic eggs appears to be relatively small in all three species.

When presented with a model European cuckoo, none of the introduced species responded aggressively. While some alarm calling was noted when the European cuckoo model was presented, the response was similar to that given to the magpie and control models (Table 3). Physical attacks were uncommon and all were directed towards the magpie or control models. No physical contact with the European cuckoo model was made by any host. Røskaft et al. (2002) measured nest defence intensity of song thrushes, blackbirds and chaffinches in populations sympatric with the European cuckoo in Scandinavia and the Czech Republic. Although they used slightly different protocols, both blackbirds and chaffinches approached and attacked the model significantly more often in their European study populations than we observed in New Zealand (blackbird: 8/11 attacked model in Europe versus 0/7 in New Zealand; Fisher exact test: $P = 0.004$; chaffinch: 10/11 attacked model in Europe versus 0/3 in New Zealand; Fisher exact test: $P = 0.011$). There was no significant difference in the response of song thrushes to a

Table 3. Responses of three species of European passerines introduced to New Zealand to model of European cuckoo, Australian magpie and control. Figures are number of nests at which host either attacked model, or in parentheses, number of nests where alarm calls were given.

Host species	Number nests tested	Type of model		
		European cuckoo	Magpie	Control
Song thrush	10	0 (5)	0 (7)	1 (6)
Blackbird	7	0 (5)	0 (7)	1 (7)
Chaffinch	3	0 (2)	1 (3)	1 (3)

cuckoo model between Europe and New Zealand (2/14 attacked model in Europe versus 0/10 in New Zealand; Fisher exact test: P = 0.37) but aggression towards cuckoos was rare in both populations.

Discussion

We found that three species of European birds introduced into New Zealand over 130 years ago still retain high levels of egg recognition and egg rejection, despite the absence of any significant interspecific brood parasite. Indeed, song thrushes and blackbirds in New Zealand rejected non-mimetic eggs at a significantly higher rate than observed in the same species in their native range in Europe. On the other hand, no species appeared to retain any recognition of the European cuckoo when presented with a taxidermic model, unlike their counterparts sympatric with cuckoos in Europe. Our results therefore suggest that while some hosts may lose some anti-parasite defences in the absence of brood parasitism, other adaptations may not be lost or decline at a slower rate.

We found that recognition of the European cuckoo as a threat has apparently disappeared in our study species. In no case was the model attacked, which differs from the response of blackbirds and chaffinches in their native ranges, where models of cuckoos are attacked vigorously. The lack of an aggressive response towards the model European cuckoo in New Zealand was not due to the inability of introduced birds to recognize a potential threat, as we observed one case of a chaffinch attacking a native shining cuckoo that approached its nest (pers. obs.). Shining cuckoos have been observed robbing eggs from nests (unpubl. data), which suggests that recognition of adult cuckoos as a threat may be learnt from experience. In other words, introduced birds may fail to recognize a European cuckoo as they have not been exposed to it and have not learnt it as a threat. Thus, the loss of recognition of European cuckoos may not be a genetic change since blackbirds and chaffinches were introduced to New Zealand, but rather reflect a cultural loss of predator identification. Such a cultural loss might be quickly regained if these

species became sympatric with European cuckoos once again, and the speed at which this occurs may reduce the advantages to a brood parasite from switching between current hosts to previously parasitized hosts.

Unlike recognition of adult cuckoos, all three introduced species retained high levels of egg rejection. Indeed, rates of rejection in New Zealand for song thrushes and blackbirds appear to be higher than that in their native range. This difference is open to several interpretations and could even be a non-adaptive consequence of subtle differences in the types of non-mimetic eggs we used. For example, if the non-mimetic eggs used in our study were easier for hosts to detect than those used in studies in the native range of each species (Davies and Brooke 1988, 1989a, b), this could lead to a higher rate of rejection in New Zealand. In both our study and Davies and Brooke (1989a, b), non-mimetic eggs differed from host eggs in both spotting pattern and ground colour, but as we did not use the same eggs as Davies and Brooke (1989a, b), it is possible that some rejections could be a response to differences in eggs between the two studies. Further experiments in both native and introduced ranges using the same model eggs would be needed to determine if this is the explanation for the differences we found.

Alternatively, the higher rates of rejection by introduced hosts in New Zealand may be a real difference that has evolved since their introduction. For example, introduced species in New Zealand may reject non-mimetic eggs at a higher rate if they are heavily parasitized by native cuckoos, and if this has increased their egg recognition abilities. However, parasitism of introduced species by native cuckoos appears low. We examined nest record cards held by the Ornithological Society of New Zealand (OSNZ) and found that no introduced species act as a regular host. Only one instance of parasitism of the song thrush (0.08% of 1189 nests) was found (by a long-tailed cuckoo). No blackbirds (n = 1,254 nests) or chaffinches (n = 204 nests) were parasitized. Similarly, we did not observe any brood parasitism by native cuckoos on our study site at Kowhai Bush (n = 235 song thrush nests, n = 68 blackbird nests, n = 50 chaffinch nests). As all three hosts reject foreign eggs, it would be difficult to detect any such parasitism. Nonetheless, there is no

evidence for native cuckoos parasitizing introduced species that accept eggs. For example, no dunnocks *Prunella modularis* (n = 215 nests) have been recorded as hosting a native cuckoo despite being an acceptor and a common woodland bird in New Zealand (OSNZ nest records, and J. Briskie unpubl. data). Without more detailed observations, we cannot rule out some degree of parasitism on introduced species, although at present there is little evidence to indicate it is anything but rare.

Our interpretation of rejection behaviour among introduced species in New Zealand assumes that this behaviour evolved as a counter-adaptation to brood parasitism by European cuckoos. However, this may not be the case. In their native ranges, both blackbirds and song thrushes are currently used as hosts by the European cuckoo rarely, and it has been suggested they are unsuitable as hosts due to the large size of host eggs and inappropriate nestling diet (Moksnes et al. 1990). Instead, egg rejection in both species may have evolved as an adaptation to intraspecific brood parasitism and only fortuitously protects a potential host from interspecific brood parasites. Under this scenario, one would not expect a rejector species that became allopatric with an interspecific brood parasite to lose its rejection behaviour. Although no intraspecific brood parasitism has been detected using molecular paternity techniques in the chaffinch (Braa et al. 1992, Sheldon and Burke 1994, Stokke et al. 2004), Moskat et al. (2003) did find evidence for intraspecific parasitism in song thrushes. The low rate at which song thrushes in New Zealand rejected conspecific eggs suggests their discriminatory abilities are relatively poor; however, the non-mimetic eggs of interspecific brood parasites are easier to detect and might be rejected more often even if the selective advantage of egg discrimination was a by-product of intraspecific parasitism. At present we cannot rule out intraspecific brood parasitism as the reason for high rates of rejection in New Zealand, and it would be interesting to determine if both thrushes and blackbirds in New Zealand are subject to higher rates of intraspecific parasitism in their introduced ranges. Most introduced species in New Zealand occur at high densities (including the three species studied here), and it is possible that this has increased the rate of intraspecific parasitism, although there is no data at present to test this idea.

If egg rejection behaviour has been retained in introduced species in New Zealand in the absence of any obvious benefits, then the behaviour would have to be virtually cost-free to persist (Rothstein 2001). Rothstein (2001) suggests that even though small costs may be incurred by rejection of wrong eggs, these costs should be less than egg losses from predation or accidental breakage and therefore the adaptive value of this behaviour may be considered close to neutral. If the costs of egg rejection are low, such "behavioural relics" may even persist for 70 000 to 300 000 years (Rothstein 2001). We found that few host eggs disappeared in either our experimentally parasitized nests or control nests in New Zealand. This suggests that any costs of rejection are probably small, and it may simply be that 130 years is too short a period in which to detect a change in the rate of rejection. Why some species (e.g. reed warbler in England; Brooke et al. 1998) show a rapid decline in anti-parasite behaviours, while others do not (e.g. this study) is unclear. Apart from differences in the costs of rejection, it is possible that defences in some species have evolved as "hard-wired" and inflexible traits, while other species have evolved "plastic" responses that vary with the degree of risk. A hard-wired pathway may limit the ability of a host to modify its response to the probability of parasitism, but may nonetheless be advantageous in species with a low cost of egg rejection.

The study of introduced species provides an ideal way to study short-term evolutionary changes in the responses of hosts to the absence of brood parasites. The deliberate introduction of birds in many places around the world means that the date (and founder size) of such populations are known relatively accurately. For example, blackbirds and song thrushes were also introduced to Australia, a country lacking European cuckoos but also with a variety of native cuckoos. Have these populations also lost the recognition of European cuckoos? As the costs and benefits of host anti-parasite responses likely vary across species, inter-specific comparisons of the loss or retention of host responses would also be valuable in determining why some responses appear to decline and others do not. Such information will be important for understanding if the evolutionary interactions between hosts and parasites follows a single one-way trajectory, or if models of the cyclical loss and gain of adaptations and counter-adaptations between hosts and parasites are more likely.

approved by the Animal Ethics Committee of the University of Canterbury.

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