Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world

M. de L. Brooke*, N. B. Davies and D. G. Noble

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

On Wicken Fen and nearby watercourses in eastern England, parasitism by cuckoos, *Cuculus canorus*, declined from 26% and 16% of reed warbler (*Acrocephalus scirpaceus*) nests in 1985 and 1986, respectively, to 2–6% of nests in 1995–97, owing to a decline in cuckoos. Experiments with model eggs showed that over this 12-year period there was a marked decline in host rejection of non-mimetic eggs, from rejection at 75% of reed warbler nests in 1985–86 to 25% of nests in 1997. Calculations suggest that this decline in host defences is too rapid to reflect only genetic change, and is more likely to be the outcome of adaptive phenotypic flexibility. Two other results show flexibility in host responses. First, there was a seasonal decline in rejection, which accompanied the seasonal decline in parasitism. Second, although rejection did not vary with proximity to a naturally parasitized nest within the 3.4 km² of Wicken Fen and its surrounds, there was no rejection at a small unparasitized population 11 km away. Flexible host defences will be advantageous when there are costs of rejection as well as short-term temporal changes and small-scale geographical variation in parasitism rate. Other recent studies reporting changes in host defences may also reflect phenotypic flexibility rather than evolutionary change.

Keywords: cuckoo; host defence; reed warbler; parasitism; phenotypic flexibility

1. INTRODUCTION

Avian brood parasites, including many cuckoos and cowbirds, rely entirely on host species to raise their offspring, and this interaction can give rise to coevolution of parasite adaptations and host counter-adaptations (Davies & Brooke 1989a,b; Rothstein 1990; Moksnes *et al.* 1991). Recent studies have shown that unparasitized populations of some host species exhibit lower defence levels (e.g. rejection of eggs unlike their own) than do parasitized populations (Cruz & Wiley 1989; Davies & Brooke 1989a; Soler & Møller 1990; Briskie *et al.* 1992; Lindholm & Thomas 1998). Furthermore, simultaneous changes in both parasitism and rejection have been documented within host populations. In Guadix, southern Spain, parasitism of magpies, *Pica pica*, by great-spotted cuckoos, *Clamator glandarius*, increased from ca. 40% of host nests in 1983 to ca. 60% in 1992, and experiments with non-mimetic model cuckoo eggs showed that magpie rejection increased significantly during this period from 61% to 89% (Soler 1990; Soler *et al.* 1994). In Japan, there has been a marked increase in parasitism of azure-winged magpies, *Cyanopica cyana*, by common cuckoos, *Cuculus canorus* (from 0 to 80% of host nests over the past 30 years in some host populations), also accompanied by a rapid increase in host rejection (Nakamura 1990; Takasu *et al.* 1993).

However, it is not clear that these differences or changes are examples of evolution in the sense of genetic

change. Although rapid changes in morphology and behaviour in bird populations can involve genetic change (Grant 1986; Berthold 1995), they can also reflect phenotypic flexibility, namely variable responses by individuals conditional on their environment. There is good evidence that hosts of brood parasites may vary their defences in relation to perceived parasitism pressure. For example, reed warblers, *Acrocephalus scirpaceus*, and meadow pipits, *Anthus pratensis*, are more likely to reject mimetic cuckoo eggs if they see a cuckoo at their nest (Davies & Brooke 1988; Moksnes & Røskaft 1989; Moksnes *et al.* 1993). Such flexibility is adaptive for hosts when they are faced with the possibility of making recognition errors when rejecting (Davies *et al.* 1996). It is possible, therefore, that variation between and within host populations reflects conditional responses by individuals to the presence of varying levels of parasitism rather than genetic differences in defence tactics (Zuniga & Redondo 1992; Lotem & Rothstein 1995; Lindholm & Thomas 1998).

Here we report a marked decline in egg rejection by a population of reed warbler hosts in response to a decrease in parasitism by cuckoos, comparing results we obtained in 1985–86 (Davies & Brooke 1988) with those a decade later, in 1995–97. The study therefore contrasts with the Spanish and Japanese studies mentioned above where an increase in parasitism was associated with an increase in rejection. We use data on the costs and benefits of egg rejection to calculate whether the rapid decrease in host rejection could represent genetic change alone, and conclude that it is more likely to involve host phenotypic flexibility. This view is supported by a

*Author for correspondence (mb10005@cus.cam.ac.uk).

seasonal decline in rejection and by small-scale geographical variation in rejection, both correlated with variation in parasitism rate.

2. METHODS

(a) *Study area*

The main study area in both 1985–86 and 1995–97 was Wicken Fen, Cambridgeshire, England, including Wicken Sedge Fen, St Edmund's Fen and Adventurers' Fen, south to Burwell Lode, an area of 3.4 km². In 1985–86, we also included Quy Fen, a small reedbed (0.1 km²) 7.5 km to the south of Wicken Fen. In 1997, we included Reach Lode, a reed-fringed dyke extending 3.4 km south-east of Wicken Fen. Reed warblers nested in the reeds along the dykes and in a large reed bed around Wicken Mere. Small differences in study sites between years had no effect on the results (see, for example, notes to table 1).

The earliest clutches were begun towards the end of May and laying continued until mid-July. There were *ca.* 500 pairs breeding on the whole study area and, although we did not attempt an accurate census, the numbers appeared to be about the same in the two study periods. Variation in number of nests found in different years is a reflection of field effort.

(b) *Field observations and experiments*

Most nests were found during the building or laying stages by 'cold searching' through the reeds, using a stick to part the vegetation. The nests were then visited daily or on alternate days to assess the progress of laying, and whether any cuckoo laid in the nest. About 10% of nests were found after laying was completed but before any eggs hatched. These nests were not used for model egg experiments (see below), but were used for assessing the overall level of parasitism.

Actual rates of parasitism will be underestimated if the hosts rejected cuckoo eggs before we had the chance to record them. However, the few cuckoo eggs that were actually rejected remained in the reed warbler nests for two or more days before rejection, so this effect will not be large (Davies & Brooke 1988). Furthermore, our results show that host rejection declines at lower levels of parasitism, so any underestimate of parasitism levels will be greater in years of higher parasitism rates. Therefore, if there is a bias, it will mean that the effects we report below will be stronger than our figures suggest.

To assess the reaction of reed warblers to cuckoo eggs, we inserted model cuckoo eggs into their nests. This part of the work was done in 1985–86 and in 1997. The eggs, of the same size and weight as real cuckoo eggs, were made of resin and painted with Rowney acrylic paints. Three types of model were used, to represent three different cuckoo genotypes:

1. Pied wagtail type: a pale greyish egg lightly freckled with brown spots.
2. Redstart type: an immaculate pale blue egg.
3. Reed warbler type: pale greenish eggs, more-or-less heavily speckled with green or brown spots.

The first two types were clearly different from the hosts' eggs ('non-mimetic'), whereas the third was mimetic. For further details of the models and egg types, see Davies & Brooke (1988). To avoid pseudoreplication, each reed warbler pair was tested only once with a particular type of model.

To mimic the laying habits of cuckoos, the model eggs were inserted during the afternoon into nests where laying was

Table 1. *Parasitism rates of reed warbler nests found at the egg stage on Wicken and Quy Fens, and on Burwell and Reach Lodes*

(Totals include all nests found and monitored during laying and after clutch completion. There is a highly significant difference in percentage of nests parasitized between the five study years ($\chi^2=80.3$, $p<0.001$). The 1985–86 figures differ slightly from those reported by Davies & Brooke (1988) because they then included only nests monitored during laying. In addition, their totals included nests from Little Wilbraham Fen where, in two years of fieldwork, no parasitized nests were recorded. The 1995–97 data include Wicken Mere, a large reedbed that was not monitored in 1985–86. Excluding the Mere data, the 1995–97 parasitism rates (sample size) were as follows: 1995, 1.7% (59); 1996, 1.4% (74); 1997, 6.6% (225). There remains a highly significant difference between the five study years ($\chi^2=47.1$, $p<0.001$).)

year	number of nests		percentage parasitized
	parasitized by cuckoo	not parasitized	
1985	34	98	25.7
1986	18	95	15.9
1995	6	162	3.6
1996	3	189	1.6
1997	21	348	5.7

underway, or on the day the final reed warbler egg had been laid. At the time of model insertion, a host egg was not removed as our earlier study showed that this did not influence the probability of rejection. The nests were then monitored by visits roughly every other day. The model egg was considered to have been rejected if it had disappeared from the nest by ejection, or if the nest had been deserted or built over, thereby burying the eggs in new nesting material. The model egg was considered to have been accepted if it was still present and being incubated six days after clutch completion, the same criterion as was used by Davies & Brooke (1988).

Because our previous study found that the presence of a stuffed cuckoo placed on a nest increased the probability that a mimetic model egg would be rejected, we repeated this protocol in 1997. We placed a stuffed cuckoo on the nest and allowed the reed warblers to observe it there for 5 min. The reed warblers responded by snapping their mandibles, giving 'churr' calls and occasionally attacking the stuffed cuckoo. We then removed the cuckoo and added a model egg to the nest.

The positions of all nests found were plotted on a 1:5000 Ordnance Survey map with an accuracy of ± 10 m. Distances from nests used in the model experiments to naturally parasitized nests were then measured from the map.

3. RESULTS

In the ten or so years since the 1985–86 fieldwork of Davies & Brooke (1988) there has been a marked decline in cuckoo parasitism of reed warblers in the vicinity of Wicken Fen (table 1). This accompanied a decline in cuckoos, from about 14 laying females in 1985 to about seven in 1997, as assessed by the distinctive eggs of individuals.

Over the same period there has been a significant decline in the rate at which reed warblers reject non-mimetic

Table 2. The rejection rate of model cuckoo eggs inserted into reed warbler nests on Wicken and Quy Fens, and along Burwell and Reach Lodes

(Numbers given are number of rejections/number of experiments (% rejection). There were no significant differences in the seasonally corrected rejection rates for the four treatments between 1985 and 1986.)

year	cuckoo model egg type			
	pied wagtail	redstart	reed warbler	reed warbler & stuffed cuckoo
1985–86	13/16 (81.3)	18/26 (69.2)	1/25 (4.0)	9/23 (39.1)
1997	18/69 (26.1)	14/57 (24.6)	6/39 (15.4)	5/30 (16.7)
χ^2_1	14.8	13.2	1.03	2.32
p	<0.001	<0.001	>0.30	>0.10

model eggs, namely the pied wagtail and redstart types (table 2). However, the reed warblers have not shown a change in their behaviour towards the mimetic model eggs. Rejection rates were low and remain low. When insertion of the mimetic model egg was accompanied by presentation of a stuffed cuckoo, the rejection rate was lower in 1997 than in 1985–86, but not significantly so. As a result of these changes in rejection behaviour, and especially the lower rejection rate of non-mimetic eggs, the differences between the four treatments, which were highly significant in 1985–86 ($\chi^2_3=32.0$, $p<0.001$), were no longer so in 1997 ($\chi^2_3=2.36$, $p>0.5$).

The decline in rejection rates has not been accompanied by a significant change in the manner in which model eggs are rejected. In 1985–86, 50 rejections were observed (data from Davies & Brooke (1988), including data additional to the 41 rejections of table 2). In 28 cases the model cuckoo egg was ejected, in 18 cases the clutch was deserted and in four the clutch was built-over. In 1997, there were 43 rejections, 18 by ejection, 24 by desertion and one involving building-over. The percentage of rejections by ejection has not significantly altered between the two study periods ($\chi^2_1=1.33$, $p>0.20$).

While the results discussed above reflect changes between years, there are also parallel changes within years. As the season progresses, so the parasitism rate and the rejection rate of non-mimetic eggs both fall (figure 1). A best-fit model using logistic regression was used to relate both of these rates to week of the breeding season. For parasitism rates, there was a significant difference between years ($\chi^2_1=26.8$, $p<0.001$) and between weeks ($\chi^2_1=6.1$, $p<0.013$). However, the interaction was not significant, indicating that the seasonal effect did not differ between years ($\chi^2_1=0.29$, n.s.). A comparable picture emerged from the analysis of rejection rates. There was a significant difference between years ($\chi^2_1=30.2$, $p<0.001$) and between weeks ($\chi^2_1=13.0$, $p<0.001$). However, the interaction was not significant, indicating that the seasonal effect did not differ between years ($\chi^2_1=0.46$, n.s.). There was no significant seasonal variation in the method of rejection.

Figure 1. (a) The proportion of reed warbler nests parasitized by cuckoos according to week of the breeding season. Week 1, first egg laid, 14–20 May, etc. Open circles, 1985–86; closed circles, 1997. Symbol size is proportional to $\log_{10}$ of sample size. The sample sizes (no. of clutches recorded) reading from left to right along the x-axis are for 1985–86: 18, 40, 41, 39, 39, 33, 27, 13, 3; and for 1997: 8, 34, 33, 49, 73, 52, 32, 31, 17, 4. (b) The proportion of non-mimetic model eggs rejected by reed warblers according to week of the breeding season. Remaining legend as (a). The sample sizes (no. of clutches in which we placed non-mimetic model eggs) reading from left to right along the x-axis are for 1985–86: 10, 12, 12, 9, 4, 1; and for 1997: 4, 6, 12, 11, 33, 25, 11, 14, 9, 1.

Because, at least in 1985–86, the sight of a stuffed cuckoo made rejection more likely, we asked whether local activity of cuckoos, as measured by the proximity of a naturally parasitized nest, influenced the likelihood that a non-mimetic model egg would be rejected. Three proximity measures were used.

- (1) The distance (m) between the focal nest and the nearest parasitized nest that season.
- (2) The distance (m) between the focal nest and the nearest nest parasitized earlier that season, i.e. earlier than six days after clutch completion at the focal nest, and therefore before the time limit for scoring responses to model eggs.

Figure 2. Histograms of the distance (1; see text) from nests where a non-mimetic cuckoo egg was either accepted or rejected by reed warblers to that season's nearest, naturally parasitized nest. Data are split between the two study periods, (a) 1985-86 and (b) 1997. Mean values for 1985-86 ($\pm$ s.e.; n) were 177.0 ± 57.2 m (10) and 124.0 ± 21.8 m (30) for nests where the model was accepted and rejected, respectively ($t=0.866$, 38 d.f., n.s.). Corresponding values in 1997 were 211.5 ± 23.3 m (94) and 196.3 ± 36.9 m (32; $t=0.348$, 124 d.f., n.s.).

- (3) The distance (m) between the focal nest and the nearest nest parasitized during the rejection period of the focal nest, the period from the laying of the first egg until six days after clutch completion.

Figure 2 shows that there was no significant difference in the value of distance (1) for nests where the non-mimetic model was accepted and where it was rejected. Similar, non-significant results (not presented) emerged when distance measures (2) and (3) were considered. Therefore the proximity of a naturally parasitized nest did not influence the likelihood of rejection.

4. DISCUSSION

(a) *Why the decline in rejection?*

Our principal finding is that, both within and between breeding seasons, rejection rate declines as parasitism rate

declines. A seasonal decline in host rejection has also been noted by Burgham & Picman (1989) and by Alvarez (1996). If the mechanism underlying the within-season change is the same as that underlying the between-season change, then the latter is unlikely to be due to genetic changes in the population. We now consider three hypotheses for the seasonal decline in rejection rate, which are not mutually exclusive.

One explanation is that the early breeders are mostly older birds which have already learnt the appearance of their own eggs, and therefore reject, whereas the later breeders include more first-time breeders which perceive the non-mimetic model as part of their own set of eggs, and therefore accept (Lotem *et al.* 1995). However, based on small samples, our earlier results (Davies & Brooke 1988) indicated that pairs with a known experienced breeder were not more or less likely to reject than pairs without such a bird. To test for a seasonal effect within experienced breeders, we also reanalysed some 1986 data. Of 12 pairs containing at least one known experienced breeder and tested with redstart models, four out of six rejected when tested before 18 June, and four out of six rejected when tested after 17 June. The absence of any seasonal decline in rejection in this small group of experienced breeders leaves open the possibility that the wider population decline in rejection is partly due to an increasing proportion of inexperienced birds nesting in the latter part of the season.

Another explanation arises from the fact that, late in the season, the chances of re-nesting are lower. Therefore, the balance of advantage may shift from rejection by desertion towards acceptance as there is always a possibility that an odd egg is, in fact, not a cuckoo's egg or, even if it is, that it will fail to hatch (Moksnes *et al.* 1993). Thus, the reed warbler which has not deserted will retain the possibility of rearing its own young (Petit 1991).

The third hypothesis is that the decline in rejection is an adaptive response to the seasonal decline in parasitism. Given rejection costs, a behavioural model suggests that acceptance becomes the best response at lower levels of parasitism (Davies *et al.* 1996). Of the three hypotheses discussed for the seasonal decline, this is the only one that can also apply to the observed decline in rejection between years.

According to our model, which takes account of the costs and benefits of rejection, it pays reed warblers to reject non-mimetic eggs above a parasitism rate of 14-32%, depending on the precise assumptions made about rejection costs in unparasitized nests, with the lower threshold being more realistic (Davies *et al.* 1996). Below this threshold, the warblers do best to accept. These predictions broadly agree with our observation of strong rejection (75%) in 1985-86 (16-26% parasitism) and weak rejection (25%) in 1995-97 (2-6% parasitism). They also accord, again broadly, with the seasonal declines in rejection (figure 1). In 1985-86, parasitism drops below the predicted threshold for rejection only around week 9 of the season, by which time the percentage rejection has declined to well below 50%. In 1997, parasitism levels are near the threshold only in the early part of the season and thereafter below it; rejection is near 50% only in the early part of the season but then rapidly declines.

Although our model broadly predicts the seasonal and between-year decline in rejection, it is not entirely satisfactory because it assumes that all rejections are by ejection, which enabled us to measure the costs and benefits only in terms of the current breeding effort. In fact, a large proportion of the rejections involved desertion, so the model needs to be refined to take account of current and future breeding attempts in a season.

(b) *How do reed warblers assess parasitism rate?*

If lower rejection rates are an adaptive response by individuals to a reduced rate of parasitism, the question of how the warblers assess the rate of parasitism arises. Davies & Brooke (1988) found that the presence of a stuffed cuckoo on a nest at the time a model was inserted increased the likelihood of rejection. However, the presence of a stuffed cuckoo did not assure rejection in 1985–86, and it had no detectable effect in 1997. Presumably other cues are also used.

A possibility is that the warblers assess the level of cuckoo activity in their own and neighbouring territories and adjust their response thresholds accordingly. We made no measurements of cuckoo activity *per se*. However, because the proximity of a parasitized nest did not predict the likelihood of rejection (figure 2), the warblers may be assessing cuckoo density over a somewhat wider area than the confines of Wicken Fen. This seems possible because the male cuckoo's call will carry 2 km in favourable conditions. It is therefore relevant that, in 1985–86, there was no parasitism in 29 reed warbler nests monitored on Little Wilbraham Fen, only 11 km from Wicken Fen. On Little Wilbraham Fen, none of five non-mimetic models were rejected as compared with 34 of 46 on Wicken Fen (Fisher exact test, $p=0.003$). Thus, although no behavioural difference was observed within our study site (maximum distance between the focal nest and the nearest nest parasitized during the rejection period of the focal nest was 1.4 km in 1985–86), a difference was observed over 11 km. Extending the picture further afield, Lindholm & Thomas (1998) compared the rejection rates of unparasitized reed warblers at Llangorse Lake, some 250 km west of Wicken Fen, with those of Wicken in 1985–86, and found the Llangorse rejection rates to be significantly lower.

(c) *Genetic change or phenotypic flexibility?*

Our discussion so far leads us to favour phenotypic flexibility as the explanation for the variation in rejection. To calculate whether the decline in rejection over the 12 years could, in principle, reflect rapid evolutionary change, we used the model of Takasu *et al.* (1993), which explores the population dynamics of a cuckoo–host association. It assumes that host response to parasitism is determined by two alleles, a rejector allele (R) and an acceptor allele (A) at a single autosomal locus. The original model assumes R is dominant, but we also present here the model's predictions, kindly calculated by F. Takasu (personal communication), if R is recessive. If R is dominant, genotypes RR and RA reject, while genotype AA accepts. If R is recessive, then RA becomes an acceptor. We assume that, in 1985, the system is in equilibrium. Acceptor pairs (both members of pair are

acceptors) and rejector pairs (at least one member is a rejector) coexist with frequencies of 0.25 and 0.75, respectively; hence the 75% rejection rate of unlike eggs (table 2). Thus, the frequency of rejector pairs corresponds to the proportion of nests at which rejection occurs. We then assume that the cuckoo disappears after 1985 (this assumption is of course more extreme than reality). The rate at which rejectors will disappear from the population then depends on the value of e (*sensu* Takasu *et al.* 1993), which is the ratio of the fitness of a rejector to that of an acceptor in the absence of parasitism and so measures the cost of rejection behaviour.

A high, but nevertheless plausible, rejection cost arises if rejector hosts adopt the behavioural rule of always ejecting the oddest egg in the nest (Davies *et al.* 1996). In this case, the assumed clutch of acceptors is four (the mean clutch size) and of rejectors three, and the value of e is $3/4$ (0.75). In this case, the rejection rate declines from the 1985 value of 75% to the 1997 value of 25% (table 2) in 19 years if R is dominant and in 25 years if R is recessive. (Following Green (1975) we assume 50% adult reed warbler mortality.)

However, the rejection cost is likely to be smaller because rejection errors in the presence of mimetic cuckoo eggs are made in only 30% of cases and reed warblers can only rarely be tricked into rejecting one of their own eggs in the absence of a cuckoo egg. Assuming recognition errors at only 30% of unparasitized nests, the fitness of rejectors is then $(0.7 \times 4) + (0.3 \times 3) = 3.7$, and the value of e is $3.7/4 = 0.925$ (Davies *et al.* 1996). The frequency of rejector pairs then decreases from 75% to 25% in 67 years if R is dominant and in 88 years if R is recessive. It is interesting that, at these intermediate rejection levels, the decline in rejection is little affected by whether R is dominant or recessive. That ceases to be true at the lowest rejection levels. Then, if R is dominant, it is always expressed and continues to decline. However, if R is recessive, most alleles occur as heterozygotes and are therefore very rarely expressed, with the result that further selection against R is slight (F. Takasu, personal communication).

These changes are rapid but, even under the extreme assumption of no cuckoo parasitism after 1985 and a high rejection cost, they are still not sufficient to explain the decline in rejection we observed over a decade. Our conclusion is that it is highly likely that phenotypic flexibility is involved in the behavioural change we have observed, both within and between seasons. Phenotypic flexibility in rejection rates is compatible with observations of the different behaviour in 1985–86 of the Wicken and Little Wilbraham reed warbler populations, which are unlikely to differ genetically as they occur only 11 km apart. It is also compatible with rejection differences on a larger geographical scale within Britain (Lindholm & Thomas 1998).

The magpies studied by Soler *et al.* (1994) increased rejection by 28% in nine years, an increase of around 3% per year. Similarly, recently parasitized populations of azure-winged magpies in Japan (Nakamura 1990; Takasu *et al.* 1993) increased rejection by between 2% and 3% per year. Our reed warbler population showed a 45–55% reduction in the rate of rejection of non-mimetic eggs in about 12 years (table 1), an annual decrease of some 4%, which is numerically similar to the rate increases reported

(Takasu *et al.* 1993; Soler *et al.* 1994). Phenotypic determination of rejection rates could allow those rates to increase or decrease at roughly similar rates, as observed. In contrast, it has been suggested, under a scenario of genetic determination, that the rate at which rejection behaviour declines may be slower than the spread of rejection behaviour (Davies & Brooke 1989b).

Phenotypic flexibility could well be adaptive for hosts of brood parasites. Cuckoo populations are often small on a local scale and prone to local extinction, so host populations are likely to experience wide variation in parasitism rates even over the lifetime of individual host birds (Lindholm 1998). We suggest that other studies that have reported host population differences (see § 1) may also, to some degree, reflect the outcome of conditional responses by individuals rather than microevolution.

These findings bear on two wider issues. First, for the purpose of theoretical discussions of how rapidly egg rejection behaviour might spread through a host population, it has been assumed that rejectors and acceptors are genetically different, and do not show context-dependent behavioural flexibility (Rothstein 1975; Kelly 1987; Davies & Brooke 1989b; Takasu *et al.* 1993). Although this assumption has the merit of simplicity, it may be wrong. Second, the findings raise a puzzle. Why do some species, not current cuckoo hosts (e.g. chaffinch, *Fringilla coelebs*, and reed bunting, *Emberiza schoeniclus*), show strong rejection of non-mimetic eggs? Davies & Brooke (1989b) suggested that the behaviour was a legacy of past encounters with cuckoos. But why then has rejection behaviour not declined as rapidly in these species as we have observed in the Wicken reed warbler population? Is it because the particularly high variability in the appearance of reed warbler eggs within a clutch increases the likelihood of recognition errors (Lotem *et al.* 1995)?

We thank the National Trust for allowing us to work at Wicken Fen, Chris Thorne and the Wicken Fen Group for research facilities, Elena Berg, Ian Hartley and Sue McRae for assistance in finding nests, Catherine Williams for analytical help, and Fugo Takasu for calculations based on his genetic model. The research was supported by the Natural Environment Research Council.

REFERENCES

- Alvarez, F. 1996 Model cuckoo *Cuculus canorus* eggs accepted by rufous bush chats *Cercotrichus galactotes* during the parasite's absence from the breeding area. *Ibis* **138**, 340–342.
- Berthold, P. 1995 Microevolution of migratory behaviour illustrated by the blackcap *Sylvia atricapilla*. *Bird Study* **42**, 89–100.
- Briskie, J. V., Sealy, S. G. & Hobson, K. A. 1992 Behavioral defences against avian brood parasitism in sympatric and allopatric host populations. *Evolution* **46**, 334–340.
- Burgham, M. C. J. & Picman, J. 1989 Effect of brown-headed cowbirds on the evolution of yellow warblers' anti-parasite strategies. *Anim. Behav.* **38**, 298–308.
- Cruz, A. & Wiley, J. W. 1989 The decline of an adaptation in the absence of presumed selection pressure. *Evolution* **43**, 55–62.
- Davies, N. B. & Brooke, M. de L. 1988 Cuckoos versus reed warblers: adaptations and counter-adaptations. *Anim. Behav.* **36**, 262–284.
- Davies, N. B. & Brooke, M. de L. 1989a An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *J. Anim. Ecol.* **58**, 207–224.
- Davies, N. B. & Brooke, M. de L. 1989b An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. *J. Anim. Ecol.* **58**, 225–236.
- Davies, N. B., Brooke, M. de L. & Kacelnik, A. 1996 Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc. R. Soc. Lond. B* **263**, 925–931.
- Grant, P. R. 1986 *Ecology and evolution of Darwin's finches*. Princeton University Press.
- Green, R. E. 1975 The survival of adult reed warblers. *Wicken Fen Group Rept* **7**, 16–21.
- Kelly, C. 1987 A model to explore the rate of spread of mimicry and rejection in hypothetical populations of cuckoos and their hosts. *J. Theor. Biol.* **125**, 283–299.
- Lindholm, A. K. 1998 Brood parasitism by the cuckoo on patchy reed warbler populations in Britain. *J. Anim. Ecol.* (In the press.)
- Lindholm, A. K. & Thomas, R. J. 1998 Differences between populations of reed warblers in defences against brood parasitism. *Behaviour*. (Submitted.)
- Lotem, A. & Rothstein, S. I. 1995 Cuckoo–host coevolution: from snapshots of an arms race to the documentation of microevolution. *Trends Ecol. Evol.* **10**, 436–437.
- Lotem, A., Nakamura, H. & Zahavi, A. 1995 Constraints on egg discrimination and cuckoo–host co-evolution. *Anim. Behav.* **49**, 1185–1209.
- Moksnes, A. & Røskaft, E. 1989 Adaptations of meadow pipits to parasitism by the common cuckoo. *Behav. Ecol. Sociobiol.* **24**, 25–30.
- Moksnes, A., Røskaft, E., Braa, A. T., Korsnes, L., Lampe, H. M. & Pedersen, H. Ch. 1991 Behavioral responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* **116**, 64–89.
- Moksnes, A., Røskaft, E. & Korsnes, L. 1993 Rejection of cuckoo (*Cuculus canorus*) eggs by meadow pipits (*Anthus pratensis*). *Behav. Ecol.* **4**, 120–127.
- Nakamura, H. 1990 Brood parasitism by the cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the azure-winged magpie *Cyanopica cyana*. *Jap. J. Ornithol.* **39**, 1–18.
- Petit, L. J. 1991 Adaptive tolerance of cowbird parasitism by prothonotary warblers: a consequence of nest-site limitation? *Anim. Behav.* **41**, 425–432.
- Rothstein, S. I. 1975 Evolutionary rates and host defences against brood parasitism. *Am. Nat.* **109**, 161–176.
- Rothstein, S. I. 1990 A model system for coevolution: avian brood parasitism. *A. Rev. Ecol. Syst.* **21**, 481–508.
- Soler, M. 1990 Relationship between the great spotted cuckoo *Clamator glandarius* and its corvid hosts in a recently colonised area. *Ornis Scand.* **21**, 212–223.
- Soler, M. & Møller, A. P. 1990 Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. *Nature* **343**, 748–750.
- Soler, M., Soler, J. J., Martinez, J. G. & Møller, A. P. 1994 Micro-evolutionary change in host response to a brood parasite. *Behav. Ecol. Sociobiol.* **35**, 295–301.
- Takasu, F., Kawasaki, K., Nakamura, H., Cohen, J. E. & Shigesada, N. 1993 Modelling the population dynamics of a cuckoo–host association and the coevolution of host defences. *Am. Nat.* **142**, 819–839.
- Zuniga, J. M. & Redondo, T. 1992 No evidence for variable duration of sympatry between the great spotted cuckoo and its magpie host. *Nature* **359**, 410–411.