Rapid increase of host defence against brood parasites in a recently parasitized area: the case of village weavers in Hispaniola

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Passerine hosts of brood parasitic birds usually vary in their ability to discriminate and reject alien eggs. Two main hypotheses have been suggested to explain the persistence of acceptor individuals in species that are exploited by brood parasites. The evolutionary lag hypothesis postulates that some hosts have not yet evolved the ability to discriminate against alien eggs. Once the ability to recognize the parasitic egg has appeared by mutation, it spreads because of the selective advantage of rejection. Parasites are then selected to produce more mimetic eggs, in order to escape host discrimination, which eventually ends up in an arms race between the parasite and the host. The evolutionary equilibrium hypothesis is based on the assumption that rejection behaviour is costly in the absence of parasitism, because of recognition errors. Acceptor hosts can persist when parasitism rate fluctuates or is consistently low. Indirect evidence for costs of rejection in the absence of parasitism has been provided by Cruz & Wiley, who reported low rejection rate for a population of village weavers (*Ploceus cucullatus*) introduced from Africa to Hispaniola (West Indies) more than a century ago. In Africa the species is parasitized by *Chrysococcyx* cuckoos and shows high levels of egg discrimination. Since no brood parasite was present in Hispaniola, Cruz & Wiley suggested that rejection was selected against in the absence of parasitism due to recognition costs. Introduction of village weavers in Hispaniola, therefore, provided a unique opportunity to test the decline of an adaptation. During the past century the shiny cowbird (*Molothrus bonariensis*) has expanded its range, invading most of the West Indies from South America. It was first observed in Hispaniola in 1972, and it started to exploit village weavers as a host. Given that shiny cowbirds substantially reduce the reproductive success of weavers, we should expect higher rejection rates nowadays compared to those reported by Cruz & Wiley 16 years ago. In agreement with this prediction, we found a high rejection rate of cowbird model eggs (89.3%, 95% CI = 81.1–97.5%), moderate levels of rejection of non-mimetic weaver model eggs (67.5%, 95% CI = 52.5–82.5%) and rather low levels of rejection of mimetic weaver model eggs (25%, 95% CI = 4–46%). The rejection rate of artificial cowbird eggs has therefore increased from 13.8% (95% CI = 5–22.6%) to 89.3% in 16 years. To check whether this rapid increase in host resistance is compatible with a genetic microevolutionary change, we built a population dynamics model where, as an upper bound, resistance is inherited by the progeny with a probability of one. This simple model shows that observed changes of rejection rate are compatible with a genetic microevolutionary shift only under the most favourable scenario for rejecters to spread. Relaxing one or several of these assumptions (e.g. high parasitism rate, absence of rejection costs) considerably lengthens the period needed for rejecters to spread. We suggest that both genetic and learning processes might be involved in the observed changes.

Keywords: egg recognition; evolutionary change; *Molothrus bonariensis*; *Ploceus cucullatus*; rejection behaviour

1. INTRODUCTION

Avian brood parasites lay their eggs in the nests of another species, which incubates and rears their offspring (Rothstein 1990). By reducing the reproductive success of their foster parents, avian brood parasites exert strong selection pressures on their hosts. As a consequence, many hosts have evolved defence mechanisms, such as recognition and rejection of parasitic eggs and nest-guarding behaviour. Despite the benefits of egg rejection, not all hosts reject parasitic eggs (Davies & Brooke 1988; Moksnes & Røskft 1989; Soler & Møller 1990). There

are two general explanations for the lack of rejection behaviour in hosts. The evolutionary lag hypothesis (Dawkins & Krebs 1979; Davies & Brooke 1988; Rothstein 1990) poses that hosts have not yet evolved the ability to discriminate against alien eggs, and stand one step behind the parasite in an arms race toward increased egg mimicry and increased egg discrimination. The evolutionary equilibrium hypothesis (Marchetti 1992; Lotem *et al.* 1992) predicts that polymorphism in rejection behaviour can be maintained if rejecter hosts suffer costs of rejection. Discriminating hosts may make mistakes and instead of rejecting the parasitic egg, reject their own

eggs. Under strong selection pressures imposed by the parasites (i.e. high probability for a host being parasitized) it pays to be a rejecter, because the benefits of resistance outweigh eventual recognition errors. However, when the parasitism rate is low or parasites are absent, the costs of resistance outweigh the benefits and hosts should become acceptors (Davies *et al.* 1996). Examples of recognition costs have been provided for a few host species of the European cuckoo (*Cuculus canorus*) (Marchetti 1992; Lotem *et al.* 1992; Davies *et al.* 1996).

Because rejection is costly in the absence of parasitism, the evolutionary equilibrium hypothesis predicts temporal changes in rejection behaviour as a function of parasitism rate. A way to explore the dynamics of rejection behaviour as a function of changes in parasitism rate is to study host species that have been transplanted into novel environments and have evolved for considerable amounts of time in such parasite-free conditions. The village weaver (*Ploceus cucullatus*) in Hispaniola (West Indies) is one such species.

The village weaver is a small passerine widely distributed across East, West and South Africa. Village weavers are parasitized by cuckoo species belonging to the genus *Chrysococcyx*, especially the diderick cuckoo (*Chrysococcyx caprius*) (Collias & Collias 1970; Victoria 1972). As for the European cuckoo, nestlings of *Chrysococcyx* cuckoos evict host eggs and nestlings (Reed 1968). Therefore, reproductive success of parasitized nests is often zero. Given the cost induced by diderick cuckoos, one should expect that village weavers have evolved defences against brood parasitism. In agreement with this hypothesis, Victoria (1972) showed that village weavers reject eggs introduced into their nests if they are sufficiently different in colour from their own eggs, and assumed that such behaviour is an adaptive response to *Chrysococcyx* parasitism (Victoria 1972).

The village weaver was introduced into Hispaniola from Africa as early as the 18th century (De Saint Mery (1797) in Cruz & Wiley 1989). Since then the species has spread and is now common throughout the island. No brood parasite was present on Hispaniola until 1972 (Post & Wiley 1977), and introduced village weavers have therefore evolved in the absence of parasitism for decades. According to the evolutionary equilibrium hypothesis of resistance to brood parasites, village weavers should have lost their ability to recognize and eject alien eggs, under the assumption of recognition errors. Experiments conducted in 1982 on village weavers in Hispaniola have shown low discrimination against non-mimetic eggs (rejection rate 14.5%, 95% CI = 4.5–24.5%), and this has been considered as a decline of an adaptation (rejection behaviour) in the absence of parasitism (Cruz & Wiley 1989). Interestingly, an avian brood parasite, the shiny cowbird (*Molothrus bonariensis*) has recently expanded its range and colonized most of the West Indies from the South American continent (Bond 1973). The shiny cowbird was first observed in Hispaniola in 1972 (Post & Wiley 1977). It rapidly spread and began to exploit the village weaver as a host. Parasitism rate of village weavers has increased from 1.3% (12 out of 936 nests) in 1974–1977 to 15.7% (21 out of 134 nests) in 1982 (Cruz & Wiley 1989). Although cowbird nestlings do not evict host nestlings, they usually outcompete them. Thus parasitized

nests are less productive than unparasitized ones (i.e. more than 50% reduction in number of fledged young; Cruz & Wiley 1989). Given the detrimental impact of shiny cowbirds on reproductive success of village weavers, selection should favour individuals able to recognize their own eggs and reject dissimilar ones. Village weavers in Hispaniola, therefore, provide a good opportunity to investigate the evolution of host defence in response to recent exposure to brood parasitism.

Here we report the results of a field study carried out in 1998 on rejection behaviour of village weavers in the Dominican Republic.

2. MATERIALS AND METHODS

Experiments were carried out during summer 1998 in the Dominican Republic on natural breeding birds. The colonies were located primarily in the proximity of Bayahibe (three colonies), Nagua (three colonies) and Rio San Juan (two colonies). The distances between these three localities range from 50 km to 160 km.

The village weaver is a colonially nesting species endemic to sub-Saharan Africa. It is abundant in cultivated areas (rice, maize, sugar fields) and considered an agricultural pest. In the Dominican Republic, active colonies can be found throughout the year (Arendt & Vargas Mora 1984). Most colonies were found in trees near rice or sugar fields. Like village weavers, cowbirds prefer disturbed habitats, usually in association with agriculture and livestock.

Because species that reject parasitic eggs are generally not detectable from observations in the field, we used model eggs to artificially parasitize weaver nests. Artificial eggs were made of plaster of Paris, coated with acrylic paint and glazed. In Hispaniola, eggs of village weavers range in colour from light blue–green to dark blue–green, with or without spots (Cruz & Wiley 1989). Therefore, we used these two background colours. Half of the eggs in each colour group were spotted, the other half left plain. Artificial cowbird eggs were white with brown spots, like natural cowbird eggs. Size and mass of artificial eggs closely matched those of real eggs.

Artificial eggs were placed in weaver nests during the egg-laying or incubation period. All eggs were placed in nests in the morning to simulate the timing of natural parasitism by the cowbird. We assume that rejection rate is independent of the laying period, as shown by Davies & Brooke (1989) with hosts of the European cuckoo. In most nests we placed two artificial eggs, a white egg to mimic cowbird parasitism and a blue or green egg to mimic intraspecific parasitism (weaver egg). In some nests, we introduced a mimetic weaver egg (closely matching colour and spottedness of eggs present in the nest), and in other nests we introduced a non-mimetic weaver egg (dissimilar from the eggs present in the nest, but corresponding to a phenotype existing in the population). When adding an artificial egg we did not remove a host egg. Previous work on seven host species of the European cuckoo has shown that rejection rates are similar whether or not one host egg is removed (Davies & Brooke 1989). After nests were parasitized, we monitored them 24 h later to determine host response (Cruz & Wiley 1989). Victoria (1972) has shown that in most instances, village weavers reject the foreign egg within 24 h. Eggs were considered rejected if they were no longer present in the nest or still in the nest but pecked. Desertion (i.e. nest abandonment) was also considered as a rejection, because Cruz & Wiley (1989) showed,

Figure 1. Rejection rates of mimetic weaver eggs, non-mimetic weaver eggs and cowbird eggs for village weavers in Hispaniola. Open and filled circles represent data gathered in 1982 (Cruz & Wiley 1989) and 1998, respectively. Bars are 95% confidence intervals.

using control nests, that experimental manipulation never triggered nest desertion.

3. RESULTS

Overall, we observed 83 weaver clutches, none of which were parasitized by the shiny cowbird. Of these, we experimentally parasitized 58 nests in eight colonies. In 54 of the manipulated nests we introduced two artificial eggs, in four only one artificial egg (two nests with a cowbird egg, one nest with a non-mimetic egg and one nest with a mimetic egg).

The rejection rate increased significantly with the degree of dissimilarity between the model egg and the eggs present in the nest ($\chi^2_2 = 29.25$, $p < 0.0001$, figure 1). Rejected models were often found on the ground underneath, generally pecked open. Cowbird eggs were particularly damaged.

The rejection rate was higher for non-mimetic than for mimetic weaver eggs (67.5%, 27 out of 40 versus 25%, 4 out of 16; $\chi^2_1 = 8.35$, $p = 0.004$). This result is consistent with those reported by Victoria (1972) on an African population of village weavers kept in aviaries, where the rejection rate was significantly higher for non-mimetic eggs as compared to mimetic ones ($\chi^2_1 = 78.68$, $p < 0.001$). A log-linear model, comparing our results to those of Victoria (1972) showed that rejection rates of mimetic and non-mimetic eggs were not different in the two populations (egg type: $\chi^2_1 = 59.36$, $p < 0.0001$; population: $\chi^2_1 = 2.21$, $p = 0.14$; egg type $\times$ population: $\chi^2_1 = 1.65$, $p = 0.20$; figure 2).

We found much higher rejection rates of alien eggs than those reported by Cruz & Wiley (1989) 16 years ago (log-linear model: egg type, $\chi^2_2 = 14.10$, $p = 0.0009$; year: $\chi^2_1 = 49.15$, $p < 0.0001$; egg type $\times$ year: $\chi^2_2 = 11.28$, $p = 0.004$; figure 1). They found that rejection rates were low and similar independently of the degree of difference between the introduced eggs and host eggs (as in this study they used three egg types: mimetic, non-mimetic,

Figure 2. Rejection rates of mimetic and non-mimetic eggs for village weavers. Open and filled dots represent data for an African population (Victoria 1972) and Hispaniolan birds in 1998, respectively. Bars are 95% confidence intervals.

cowbird ($\chi^2_2 = 0.33$, $p = 0.85$)). The significant interaction between egg type and year shows that the difference between the two studies is due to rejection of non-mimetic and cowbird model eggs (figure 1). A local test confirmed that the rejection rate of mimetic eggs did not differ between 1982 and 1998 (11.7%, seven out of 60 versus 25%, four out of 16; Fisher's exact probability test, $p = 0.229$).

As already mentioned, in most nests we introduced two model eggs, a cowbird egg and either a mimetic or a non-mimetic weaver egg. Using two model eggs could have biased rejection rates. To check this issue, we investigated whether the probability to eject the cowbird model was affected by the presence of a mimetic or a non-mimetic weaver egg. The rejection rate of cowbird model eggs was not significantly different when comparing nests containing a mimetic weaver egg or a non-mimetic one (86.7% (13 out of 15); cowbird eggs were rejected when introduced with a mimetic egg, 89.7% (35 out of 39) were rejected when introduced with a non-mimetic egg; Fisher's exact test, $p = 1.0$). We went a step further in comparing the rejection rate of non-mimetic eggs with the rejection rate of cowbird eggs introduced with mimetic eggs. This comparison thus involves different nests. The rejection rate of cowbird eggs introduced with mimetic eggs (86.7%, 13 out of 15 nests) was not significantly different from that of non-mimetic eggs (67.5%, 27 out of 40 nests, Fisher's exact test, $p = 0.192$). Similarly, we compared rejection rate of non-mimetic eggs with rejection rate of cowbird eggs introduced with mimetic eggs, comparison which again involves different nests. We found that cowbird eggs were significantly more rejected than mimetic eggs (rejection rate of cowbird eggs: 89.7% (35 out of 39); rejection rate of mimetic eggs: 25% (4 out of 16); Fisher's exact test, $p < 0.0001$).

Comparing data reported by Cruz & Wiley (1989) with data reported by Victoria (1972) shows that the rejection rate of mimetic eggs does not differ significantly

between the two populations ($\chi^2_1=0.1$, $p=0.75$), whereas the rejection rate of non-mimetic eggs does ($\chi^2_1=43.97$, $p < 0.001$).

Among the 83 clutches observed, we found little evidence for intraspecific parasitism. In only one case did we find two eggs with different sizes and colour patterns, which could suggest laying by two different females. Very low levels of intraspecific parasitism in village weavers have also been reported by Victoria (1972) and Cruz & Wiley (1989).

4. DISCUSSION

We found high rejection of non-mimetic eggs in village weavers. Comparison of our results with those reported by Cruz & Wiley (1989) suggests a very rapid increase in cowbird egg rejection from 13.8% (95% CI=5–21.8%) to 89.3% (95% CI=81.1–97.5%) in 16 years.

Rapid phenotypic changes raise the question of the mechanism underlying these modifications. Behavioural traits can be particularly flexible, and rapid changes in behaviour might reflect a plastic response to changing environmental conditions rather than a genetic microevolutionary shift. On the other hand, examples of rapid microevolutionary change of life-history traits have been reported (e.g. Reznick *et al.* 1990).

Although most coevolutionary models of brood parasitism assume a genetic basis of host resistance (i.e. Takasu *et al.* 1993), virtually no estimate of genetic variation of rejection behaviour exists. On the other hand, there is accumulating evidence for conditional resistance to brood parasites. Hosts might perceive risk of parasitism (e.g. density of adult parasites) and plastically adjust their behavioural response in order to minimize the cost of rejection errors (i.e. Davies *et al.* 1996). Rapid changes in rejection rates might thus be due to flexible behavioural adjustments to variable levels of parasitism.

A pure genetic microevolutionary change is based on the differential selection imposed by brood parasites on resistant and susceptible hosts, and on the heritability of resistance; the higher the selection differential and the heritability, the faster the microevolutionary change. Avian brood parasites are supposed to exert strong selection pressures on their host (although the cost of parasitism depends on the parasite and the host species), which should favour the evolution of defence mechanisms such as parasite egg recognition and rejection (Rothstein 1990). The shiny cowbird was first observed in Hispaniola in 1972 (Post & Wiley 1977). Since then the shiny cowbird has started to parasitize the village weaver. Cruz & Wiley (1989) reported an increasing parasitism rate from the period 1974–1977 (1.3%, 12 out of 936 nests) to 1982 (15.7%, 21 out of 134 nests) (an increase in the rate of 2.9% per year). They also showed that cowbird parasitism exerted a detrimental effect on the reproductive success of weavers, since the average number of fledglings produced in parasitized nests is reduced by more than 50%, compared to non-parasitized nests. Is this selection pressure sufficiently high to result in such a dramatic increase in resistance in 16 years?

To address this question we built a simple deterministic population dynamics model where the probability of acceptor and rejecter hosts transmitting their strategy to

the offspring is one. The number of acceptor ($N_a(t)$) and rejecter ($N_r(t)$) females in the population can be described by the following equations:

$$N_a(t+1) = s(t) \times N_a(t) + s(t) \times 0.5 \times N_a(t) \times (p \times n_{ap} + (1-p) \times n_{np}), \quad (1)$$

and

$$N_r(t+1) = s(t) \times N_r(t) + s(t) \times 0.5 \times N_r(t) \times (p \times n_{rp} + (1-p) \times (1-c) \times n_{np}), \quad (2)$$

where $s(t)$ is the survival rate (for simplicity, assumed to be the same for all age classes), p is the parasitism rate, n_{np} is the average number of young fledged per unparasitized nest, n_{ap} is the average number of young fledged per parasitized nest of acceptor hosts, n_{rp} is the average number of young fledged per parasitized nest of rejecter hosts (rejecters also pay a cost of parasitism because female cowbirds, on average, remove one host egg when laying), c is the rejection cost in the absence of parasitism. Survival was considered to be density dependent [$s(t) = 0.6/(1 + 0.008 \times (N_a(t) + N_r(t)))$]. We assumed the sex ratio to be 1:1. The initial conditions were fixed as $N_a(0)/N_r(0) = 9/1$, $p = 0.15$, $n_{np} = 1.8$, $n_{ap} = 0.7$, $n_{rp} = 1.4$, according to values reported by Cruz & Wiley (1989).

Numerical simulations showed that about 45 years are needed for the rejection rate to increase from 10% to 80% when parasitism (p) increases at a rate of 2.5% per year until a threshold of 50% nests parasitized is reached, and when there are no rejection costs ($c = 0$). Considering the higher threshold of parasitism (i.e. 80%) gives similar results (about 40 years to go from a 10% to an 80% rejection). Obviously, introducing a rejection cost slows down the spread of rejecters. For a rejection cost of 0.05 (i.e. 5% fecundity reduction), more than 50 years are needed for the rejection rate to increase from 10% to 80%. Changes in the rejection rate similar to those observed in Hispaniola are only found when parasitism rate is fixed at a high level (i.e. 80%) from the beginning.

These results suggest that selection pressures imposed by cowbirds on weavers can be sufficiently strong to produce rapid genetic changes in rejection frequencies only under the most favourable scenario for rejecters, that is heritability of rejection behaviour equal to one, high parasitism rate and absence of rejection costs. Relaxing one or several of these assumptions considerably lengthens the period needed to reach 80% rejection. On the other hand, we considered only one clutch per year, which is certainly an underestimation. However, even with several clutches per year, it seems unlikely that the observed changes are the results of a pure genetic microevolutionary shift. We suggest that both genetic and learning processes might be involved in the observed changes.

Other genetic models of the evolution of rejection behaviour have found similar results, although most of these models are based on the assumption that rejection is under the control of one locus, with two alleles. Rothstein (1975) calculated that parasitized populations would require from 20 to 100 years to change from 80% acceptance to 80% rejection of cowbirds' eggs, and Takasu *et al.*

(1993) also calculated that under certain circumstances a rejecter allele can spread rapidly in a host population.

Rapid evolutionary changes of rejection behaviour have been observed in two other brood parasite–host systems, in areas of presumed recent sympatry (Nakamura 1990; Soler *et al.* 1994). In Japan, the azure-winged magpie (*Cyanopica cyana*) has been exposed to cuckoo (*Cuculus canorus*) parasitism for about the past 20 years and its rejection rate has attained 41.7% during this period. Another Japanese population, at Nagano, has been parasitized for about 15 years and showed a rejection rate of 34.7% (Nakamura 1990). These results support the idea that frequency of egg rejection increases with the duration of exposure to parasitism, and that evolution of defence could be very rapid. Whether these results reflect microevolutionary changes is open to debate. Recently, Brooke *et al.* (1998) have provided convincing evidence that a rapid decline of rejection rate in reed warblers (*Acrocephalus scirpaceus*) is probably due to flexible behavioural adjustment to variable cuckoo parasitism rate. Experiments with model eggs showed a marked decline in host rejection of non-mimetic eggs, from 75% in 1985–1986 to 25% in 1997. Cuckoo parasitism similarly decreased from 25.7% in 1985 to 5.7% in 1997. Furthermore, Brooke *et al.* (1998) found a seasonal decline in rejection, which accompanied the seasonal decline in parasitism. This last result suggests that the decline in rejection is likely to be the outcome of adaptive phenotypic flexibility. To our knowledge, weavers in Hispaniola represent the only species where both a decline and a rapid increase in rejection have been documented as a consequence of absence and subsequent colonization of a brood parasite.

We did not find any nests containing cowbird eggs or nestlings. This could be the result of two different phenomena: (i) given the high rejection rate of cowbird model eggs, the probability of finding a parasitized nest of an acceptor individual should be very low. Parasitism might go unnoticed if rejection occurs within 24 h, as suggested by Victoria (1972); (ii) low parasitism rate could be an adaptive response of cowbirds to host rejection. As rejection becomes widespread within a host, selection on cowbirds might decrease parasitism of the resistant host. A plausible scenario would be that a high weaver rejection rate drives cowbirds to exploit other hosts. At least four other species are cowbird hosts in Hispaniola, as mentioned by Cruz & Wiley (1989).

Egg discrimination is not the only defence that hosts have against brood parasites. Aggression against brood parasites might prevent parasitism by limiting laying opportunities. Nest defence might be particularly efficient in colonial species, where several individuals can co-operate to prevent brood parasites from entering the colony. Support for this hypothesis comes from studies on red bishops (*Euplectes oryx*), a close relative of village weavers that are also parasitized by diderick cuckoos in Africa. Red bishops attack and harass diderick cuckoos that sit exposed or approach a colony (Friedmann 1948). This nest defence might be the mechanism explaining the negative correlation between colony size and parasitism rate observed in this species (Lawes & Kirkman 1996). Nest defence specifically directed towards brood parasites requires hosts being able to discriminate between para-

sitic and non-parasitic species. Village weavers offer a good opportunity to test the specificity of nest defences, because weavers of Hispaniola have been in contact with two brood parasites during their recent history: the current parasite (shiny cowbird) and the ancient parasite (diderick cuckoo). Preliminary observations on weaver reactions towards four models (a female shiny cowbird; a diderick cuckoo; a violet cuckoo (*Chrysococcyx xanthorhynchus*), an Asian parasite that has never been in contact with village weavers; and cotton wool tied to model the shape of a bird) placed close to active nests showed similar levels of aggression towards the four decoys (M. Robert and G. Sorci, personal observations). These observations suggest that nest defence is not particularly aimed at preventing brood parasitism, and that village weavers do not discriminate against brood parasites with which they have different duration of sympatry. However, more observations are needed to ascertain the robustness of these results.

Learning processes are important determinants of animal behaviour. The evolution and expression of egg discrimination and parasite recognition may represent a good example of interaction between genetic determinism and behavioural flexibility. Further work should focus on the relative importance of these two forces on the evolution of resistance to brood parasites.

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