Females are responsible for ejection of cuckoo eggs in the rufous bush robin

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ABSTRACT

Rufous bush robin, *Cercotrichas galactotes*, nests were experimentally parasitized in order to test which sex is responsible for egg ejection. We tested nests belonging to the same individuals (male, female or pair) in 2 consecutive years. Whether the eggs were rejected did not depend on environmental variables such as laying date and clutch size, and did not change between tests, when the two consecutive nests tested belonged to the same pair members, supporting the idea that some individuals reject odd eggs, while others accept them. The expected frequencies for rejection and acceptance, if females were the sex responsible for ejection behaviour, did not differ from the observed frequencies when the same female owned both the nests tested. However, the expected frequencies calculated for males as if they were the sex responsible differed from those observed, when the same male owned both the nests tested. A lower percentage of females than males changed ejection behaviour. These results show that female rufous bush robins are responsible for egg ejection.

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Brood parasitism is a breeding strategy in which the parasites receive parental care from unrelated individuals, the hosts (Rothstein 1990). Avian brood parasites usually reduce the host's reproductive output drastically and thus select for the development of host defences, such as recognition and rejection of parasite eggs (Rothstein 1990). These host defences select for counteradaptations in the parasite, such as egg mimicry and rapid laying behaviour (Brooke & Davies 1988; Rothstein 1990). This process is thought to be a clear example of a coevolutionary arms race (Brooke & Davies 1988; Davies & Brooke 1988, 1989a,b; Moksnes et al. 1990, 1993; Rothstein 1990; Soler & Møller 1990; Briskie et al. 1992; but see Brooker & Brooker 1996).

Comparative analyses have shown that intraclutch variation in colour and markings of host eggs is related to the response to parasitic eggs, with a small degree of variation among host eggs in a clutch increasing the probability of recognition and hence rejection of cuckoo eggs (Øien et al. 1995; Soler & Møller 1996). However, Brooker & Brooker (1996) concluded that rejection behaviour of hosts depends on ecological or life history variables, such as clutch size and duration of the breeding season. This result provides evidence for the evolutionary equilibrium hypothesis, which posits that acceptance of a

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parasitic egg, even after recognition, could be an adaptive decision, resulting from a balance between rejection costs and benefits (e.g. Zahavi 1979; Rohwer & Spaw 1988; Lotem et al. 1992; but see Røskaft et al. 1993).

Models explaining coevolution between brood parasites and their hosts are mostly based on the arms race hypothesis (e.g. Kelly 1987; Takasu et al. 1993; but see Brooker et al. 1990). The question about which sex is responsible for egg recognition and rejection is relevant in this context, because if both sexes are responsible, the rejector trait will spread faster among the population than if only one sex is responsible (Rothstein 1975; Sealy & Neudorf 1995). If the female is responsible for egg recognition, selection coefficients must be halved when used to calculate rates of gene substitution because rejector alleles in males will have the same fitness as acceptor alleles (Rothstein 1975). Several authors have assumed that only host females eject parasitic eggs (e.g. Rothstein 1975; Davies & Brooke 1988; Lotem et al. 1992). Currently, there are only a few observational data on which sex rejects eggs. For example, observations of northern orioles, *Icterus galbula*, showed that females carried out all the ejections (Rothstein 1977; Rohwer et al. 1989). The same pattern was also observed for eastern kingbirds, *Tyrannus tyrannus* (Bazin 1991), and video-recorded chaffinches, *Fringilla coelebs*, and blackcaps, *Sylvia atricapilla* (Moksnes et al. 1994). It is not surprising that females are responsible for recognition of foreign

eggs, because they lay and incubate the clutch, spending more time than males in the nest, thereby facilitating the recognition of their own eggs. Sealy & Neudorf (1995), however, recorded two male northern orioles ejecting experimentally introduced parasitic eggs, and Pinxten et al. (1991) recorded male European starlings, *Sturnus vulgaris*, removing conspecific parasitic eggs.

In the present study, we approached this topic experimentally in a colour-ringed population of rufous bush robins, *Cercotrichas galactotes*, parasitized by common cuckoos, *Cuculus canorus*. In this host species, only the female incubates (Cramp 1988). We experimentally parasitized nests belonging to the same individuals (male, female or pair) in 2 consecutive years. We first analysed whether rejection behaviour was determined environmentally (depending on factors such as laying date or clutch size), rather than genetically (varying between individuals). Other environmental factors such as time of day or presence of cuckoos in the breeding area did not vary because all experimental eggs were introduced in the afternoon and when common cuckoos were present in the breeding area. We also took age or experience of birds into account, correcting for the probability of learning to recognize eggs. Furthermore, we tested if observed frequencies for maintenance and change of responses over the two tests differed from expected frequencies, calculated for each sex being responsible for egg recognition. We tested the following hypotheses.

(1) If females are responsible for responses to parasitic eggs, we predicted that when the same female owned the two nests tested in consecutive years and her mate changed, the observed frequencies for maintenance and change of responses between years would not differ from expected frequencies calculated if females were the sex responsible. We also predicted that when the same male owned the two nests tested and his mate changed, the observed frequencies of rejection and acceptance during the second year would differ from expected frequencies, calculated if males were the sex responsible.

(2) If males are responsible for behavioural responses against parasitic eggs the opposite predictions apply.

Of course, there is the alternative hypothesis that both sexes could be responsible for egg ejection, but our data do not allow us to make predictions from this hypothesis because expected frequencies calculated for both sexes as responsible for egg ejection will not differ from the observed frequencies as a consequence of the sex responsible of egg ejection being included in these frequencies.

METHODS

We carried out the study during 1994–1996 in Los Palacios, 20 km southeast of Sevilla, Spain (37°9′N, 2°14′W), at 12 m above sea level, in a vineyard area with scattered fruit trees and small patches used for vegetable production. This region has a Mediterranean climate with rainy autumns and springs, and dry and hot summers (above 40°C at noon).

Male and female rufous bush robins have been captured since 1993 at this site, with net traps and mist nets, and given numbered aluminium rings (ICONA) and colour plastic rings, to allow individual identification.

In our tests, we used nonmimetic and mimetic model eggs in 1994 and only mimetic model eggs in 1995 and 1996. We made the model eggs by filling two rubber moulds of common cuckoo eggs with plaster of Paris. Once dry, we painted the mimetic model eggs with a yellowish background and brown spots so that they resembled two types of real cuckoo eggs recorded in rufous bush robin nests in our study area (one with many small, light-brown spots all over the egg, with a few large, dark-brown spots, and the other with only a few dark spots concentrated around the wider end; for a picture of a real cuckoo egg of the latter type, see Alvarez 1994). Models also resembled these two kinds of cuckoo eggs in size, shape and colour pattern. Nonmimetic model eggs were similar to natural cuckoo eggs in size and shape, but painted red. Finally, we covered the models with a thin layer of lacquer to simulate the sheen of real eggs. Each model was used only once.

We experimentally parasitized rufous bush robin nests by randomly introducing one type of model egg into each nest (but without removing one of the host eggs) in the afternoon during the egg-laying period of the host or during the first 3 days of incubation. Experimental nests were examined twice a week, and we considered models accepted if they remained in the nest being incubated 7 days after introduction. Model eggs were considered rejected if they were ejected.

To test the possible relationship between environmental factors and behavioural responses, we used laying date and clutch size of first clutches as indicators of duration of breeding season and/or territory quality (because Brooker & Brooker (1996) proposed that species with long breeding seasons and small clutches should be acceptors, whereas rejectors should be those with large clutches and short breeding seasons), and the birds' responses to experimental model eggs in first clutches as the dependent variable in a logistic regression analysis. We included in this analysis all individuals tested in 1994 and those of 1995 that were not tested in 1994, in order to avoid pseudoreplication. Percentage of variance explained was calculated by the least squares method, and probabilities by the maximum likelihood method.

To test if maintenance or change of the behavioural responses depended on the sex of the hosts, we tested nests of the same individuals in several years. In six cases the pair remained mated between years, but in the other cases only the male or the female remained between tests (eight and seven cases, respectively; Fig. 1). We analysed whether the response to cuckoo eggs changed between 2 consecutive years in relation to the sex of the owner of the two nests tested. Although we tested some individuals in more than 2 years, we only used data of the first two tests for nests of each individual in order to avoid pseudoreplication. We tested nests of 11 males and 12 females during 1994–1995 and nests of three males and one female during 1995–1996, performing a total of 27 experiments, each consisting of two tests in 2 consecutive years.
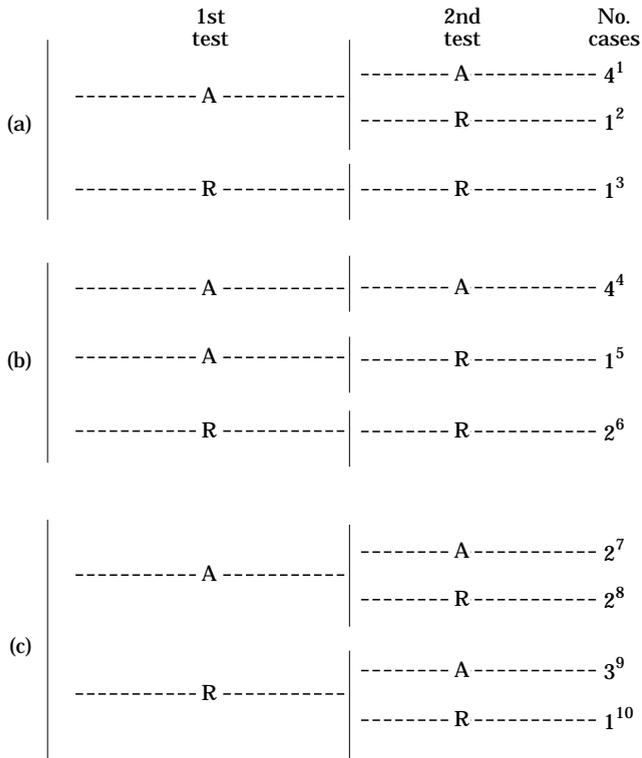
Figure 1. Responses (accept, A or reject, R) of rufous bush robins to model cuckoo eggs according to the pair member that owned the two nests tested in 2 consecutive years. (a) Male and female remained the same during the two tests, (b) only the female owned both nests tested, (c) only the male owned both nests tested. Superscripts indicate different types of response recorded.

We included in the analyses the tests performed with mimetic and nonmimetic model eggs, because rufous bush robins did not respond differently to these types of model (mimetics: 33 accepted, $N=53$; nonmimetics: 8 accepted, $N=14$; Fisher's exact test: $P>0.7$). However, different types of model (one type of nonmimetic and two types of mimetic model) were used to test several individuals in successive years (10 out of 14 males and 10 out of 13 females). Although this can increase the probability of a change in response, we did not find any differences in probability of change between males tested twice with the same type of model and those tested with two types of model (two different models: four individuals changed, $N=10$; same model: three individuals changed, $N=4$; Fisher's exact test: $P>0.3$). However, females changed their response more frequently when tested twice with the same type of model than when tested with two types of model (two different models: no individual changed, $N=10$; same model: two individuals changed, $N=3$; Fisher's exact test: $P=0.015$). Thus, the use of different types of model between tests did not increase the probability of changing the response, and for females the opposite trend was recorded.

To test which sex is responsible for the response to odd eggs, we compared observed and expected frequencies. Two expected frequencies were calculated according to the sex hypothesized to be responsible for the response (Table 1). We first calculated the annual percentage of acceptor and rejector response in our population during 1994–1996 ($\bar{X}\pm$SD; acceptor response: $61.87\pm6.45\%$, $N=3$ years; rejector response: $38.10\pm6.35\%$, $N=3$ years). When individuals of the sex considered to be responsible for egg recognition remained the same in different years, we would expect the same response in the second test, but when the individuals of the sex considered responsible differed between tests, we calculated expected frequencies based on the probability of mating with an acceptor (62%) or a rejector (38%) individual. For example, there were nests of five females that we tested in 2 consecutive years and that accepted the model in the first test (Table 1, first and second rows). If females are considered the sex responsible, the expected frequencies for the second test would be five acceptors and no rejectors (Table 1, third column), but if males are considered the sex responsible, the expected frequencies would be 3.1 acceptors (62%, $N=5$) and 1.9 rejectors (38%, $N=5$; Table 1, second column).

These expected frequencies may not be correct if individuals learn to recognize their eggs. Expected frequencies must be corrected for the probability of learning when

Table 1. Observed (O) and expected (E) frequencies for the four types of response of rufous bush robin to model eggs when considering the results of tests made in 2 consecutive years

| Response | | Sex that remained the same between tests | | | | | | | | | | |
| | | Female | | | Male | | | | Male and female | | |
1st	2nd	O	E_M	E_F	EL_F	O	E_M	EL_M	E_F	O	E_M	E_F
A	A	4	3.10	5	4	1	3	2.4	1.86	4	5	5
A	R	1	1.90	0	1	2	0	0.6	1.14	1	0	0
R	A	0	1.24	0	0	3	0	0	2.48	1	0	0
R	R	2	0.76	2	2	1	4	4	1.52	0	1	1
Changed		1	3.14	0	1	5	0	0.6	3.62	2	0	0
Maintenance		6	3.86	7	6	2	7	6.4	3.38	4	6	6

These frequencies are presented according to the sex of individuals that remained the same between tests. A=Acceptor response; R=Rejector response. E=expected frequency if males (E_M) or females (E_F) are the rejector sex. Expected frequencies considering probability of learning are presented as EL_M and EL_F. Rows labelled Changed and Maintenance indicate the sum of the rows with a different or the same response between the two tests, respectively.

individuals of the sex considered to be responsible for the response were the same in subsequent years. However, when the sex considered responsible for egg recognition does not coincide with the individual remaining between tests, expected frequencies are the same, because they depend only on the probability of mating with a rejector or acceptor individual. We considered that the probability of learning is 0.20, because this was the proportion of the five acceptors in the first test that rejected in the second one (Fig. 1a), when pair members remained mated between tests. Thus, when the individual remaining was of the sex considered responsible, the expected frequency for the acceptor response in the second test was 0.80 of the sample size that accepted the model in the first test, and 0.20 of this sample size was considered the expected frequency for the rejector response in the second test.

As frequencies were low, we compared observed and expected frequencies using two-tailed Fisher's exact tests (Siegel & Castellan 1988). In two cases, expected frequencies were approximated to units in order to perform a Fisher's exact test, and these frequencies were close to the observed frequencies, making the test more conservative. We made post hoc comparisons using one-tailed Fisher's exact tests in order to check whether expected frequencies calculated for females differed from observed frequencies when the same male was the owner of the two nests tested. Moreover, we used the Statistica for Windows program (Statsoft 1993) to compute the significance level for the difference between two percentages by the one-tailed probability calculator.

RESULTS AND DISCUSSION

None of the environmental factors explained a significant proportion of the variation in egg rejection behaviour (laying date=6%; clutch size=1%) of the population (maximum likelihood; laying date: $\chi^1_2=1.75$, NS; clutch size: $\chi^2_2=0.5$, NS; both variables: $\chi^2_2=2.3$, NS). Therefore, it appears that variation in environmental conditions is not an important determinant of variation in the response of rufous bush robins to experimental parasitism.

Figure 1 shows the responses to experimental parasitism based on pair members that remained the same in two consecutive tests between years. When pair members remained mated between tests (Fig. 1a), we expected responses to be the same in both years. When comparing observed and expected frequencies for change and maintenance of the response in these cases (Table 1), we found no significant difference (Fisher's exact test: $P=0.5$). Thus, this result supports the idea that responses depend on individuals and not on environmental conditions.

In one case, however (response 2 in Fig. 1a), the model was accepted in the first test and rejected in the second. This may be explained by a learning process, which may occur in some host species not only during the first breeding attempt but also during the life span. Such a learning process has been used to explain the rapid increase in rejection rate in a host population of the great spotted cuckoo, *Clamator glandarius* (Soler et al. 1994) and in another common cuckoo host, the azure-winged magpie, *Cyanopica cyanea* (Nakamura 1990). Accordingly,

we might expect that individuals can change their response from acceptance to rejection as a result of learning.

Inconsistency between tests could reflect simple errors even after learning. This may account for changes in response from rejection to acceptance (response 3 in Fig. 1a). In this case, experimental conditions did not differ between tests but the model type did, although it does not increase the probability of changing the response (see Methods). This could be the consequence of a simple error where the host failed to recognize a cuckoo egg when it was actually parasitized. This type of error has not been described to date, probably because it is a difficult error to detect. Individuals need to be ringed and several experiments made with the same individuals, recording them first as rejectors and later as acceptors. Thus, a change from acceptance in the first test by an individual or pair to rejection in the second may be due to learning (before the second test) or to a recognition error in the first test. However, although this situation may confound the results, the finding of significant differences between observed and expected frequencies calculated for males and females (including the probability of learning) will be stronger because, owing to these types of errors, the tests are more conservative.

Testing the Hypotheses

When the same female owned the two nests tested and was considered the sex responsible for egg recognition, observed and expected frequencies for change and maintenance of the response did not differ significantly (Table 1; Fisher's exact test: $P=1.0$). However, when the same male owned the nests and was considered the sex responsible for egg recognition, observed and expected frequencies calculated for change and maintenance of the response were significantly different (Table 1; Fisher's exact test: $P=0.01$). These results support the hypothesis that the female is the sex responsible for rejection of cuckoo eggs, and refute the hypothesis that the male is.

Several factors, however, may influence the results observed in two consecutive tests.

(1) As we saw above, errors of egg recognition, which result in a rejector failing to recognize when it is parasitized, may increase expected frequencies for the acceptor responses. Unfortunately, we have only one result for a rejection response in which both pair members remained between tests (Fig. 1a), making it impossible to estimate the probability of this type of error.

(2) Parasitized hosts may erroneously eject one of their own eggs instead of the cuckoo egg (Molnar 1944; Davies & Brooke 1988; Lotem et al. 1995). This type of error may also affect observed frequencies, because an individual ejecting one of its own eggs may be considered to be accepting, although it is a rejector. We recorded this type of error in one case (second test, in one of two cases for response number 7 in Fig. 1c). This nest contained four eggs when we introduced the model egg, but on the following visit to the nest, it contained the model egg and only three robin eggs. We excluded this case from the analyses and Table 1, because it is not justifiable either to

correct for this type of error by considering it as acceptance in the first test and rejection in the second, or to include this case without correction.

(3) In some cases, learning may take place. This process could affect expected frequencies because some individuals that accepted in the first test might reject in the second. Table 1 shows expected frequencies after correcting for learning (see Methods). According to the first hypothesis, when the same female owned the two nests tested and was considered the sex responsible for egg recognition, observed and expected frequencies did not differ (Fisher's exact test: $P=1.0$). However, when the male was the owner and considered responsible for egg recognition, observed and expected frequencies differed marginally (Fisher's exact test: $P=0.054$). Thus, after correcting for the probability of learning, the results still supported the first hypothesis and rejected the second.

We have tried to explain every case where the response towards the model eggs changed between two subsequent tests. However, another possibility is that individuals that are able to recognize the foreign egg sometimes decide not to reject it.

When females are considered to be the sex responsible for egg recognition, expected frequencies for females should not differ from observed frequencies when the same male owned the two nests tested. In agreement with the hypothesis that females are responsible for rejection behaviour, the result of this comparison was not significant (one-tailed Fisher's exact test: $P=0.5$). Another piece of evidence supporting the first hypothesis comes from a comparison of the probabilities of a change in response with respect to sex. The percentage of females that changed their response (23%, $N=13$) was marginally lower than that of males (54%, $N=13$; difference between two percentages: $P=0.059$). These results allow us to conclude that females are responsible for egg recognition in the rufous bush robin.

Acknowledgments

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