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RESPONSES OF PARASITIZED AND UNPARASITIZED COMMON REDSTART (*PHOENICURUS PHOENICURUS*) POPULATIONS AGAINST ARTIFICIAL CUCKOO PARASITISM

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Abstract.—Brood parasitism selects for defensive mechanisms that enhance host fitness. Therefore, host populations under different parasitism pressures may express different levels of defense against brood parasites. We tested the rejection responses of currently parasitized and unparasitized Common Redstart (*Phoenicurus phoenicurus*) populations in Finland to artificial Common Cuckoo (*Cuculus canorus*) eggs. We predicted a higher level of defense in the parasitized population, but in fact the rejection rate was higher in the nonparasitized population. Nonmimetic artificial eggs were rejected more often than mimetic ones. Desertion probability was higher in the nonparasitized population and was independent of artificial egg type. Common Redstarts in the parasitized population rejected the artificial eggs mostly through ejection, whereas desertion was a more frequent rejection method in the nonparasitized population. Our results suggest that current selection pressures from brood parasites do not always explain the current levels of defense. *Received 5 March 2004, accepted 9 July 2005.*

Key words: among-population differences, brood parasitism, Common Cuckoo, Common Redstart, *Cuculus canorus*, egg recognition, egg rejection, nest desertion, *Phoenicurus phoenicurus*.

Respuestas de Poblaciones Parasitadas y No Parasitadas de *Phoenicurus phoenicurus* Contra el Parasitismo Artificial de *Cuculus canorus*

Resumen.—El parasitismo de nidada estimula la selección de mecanismos de defensa que aumentan la adecuación biológica del huésped. Por lo tanto, las poblaciones de huéspedes bajo diferentes presiones de parasitismo pueden expresar niveles diferentes de defensa contra el parasitismo de nidada. Evaluamos las respuesta de rechazo de poblaciones actualmente parasitadas y no parasitadas de *Phoenicurus phoenicurus* en Finlandia a la presencia de huevos artificiales de *Cuculus canorus*. Predijimos un nivel más alto de defensa en la población parasitada, pero en realidad la tasa de rechazo fue mayor en la población no parasitada. Los huevos artificiales no miméticos fueron rechazados más frecuentemente que los huevos miméticos. La probabilidad de deserción fue más alta en la población no parasitada y fue independiente del tipo de huevo artificial. Los individuos de *P. phoenicurus* de la población parasitada rechazaron los huevos artificiales generalmente arrojándolos del nido, mientras que la deserción fue un modo de rechazo más frecuente en la población no parasitada. Nuestros resultados sugieren que las presiones actuales de selección causadas por el parasitismo de nidada no siempre explican los niveles actuales de defensa.

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Interspecific brood parasitism by Common Cuckoos (*Cuculus canorus*; hereafter "cuckoos") drastically lowers host fitness, because the newly hatched cuckoo chicks evict host eggs or chicks from the nest (Payne 1977, 1997; May and Robinson 1985; Moksnes et al. 1990). Parasitism by cuckoos and nest predation are two important selective forces that affect the evolution of host nesting behavior. Parasitism results in host adaptations to reduce its harmful effects. Discrimination against alien eggs is the most widespread and effective antiparasite strategy for reducing the costs of avian brood parasitism (Rothstein 1990). This adaptation has favored, in turn, the evolution of egg mimicry by cuckoos as a counter-adaptation (Davies and Brooke 1988).

The occurrence of cuckoo parasitism is not always uniform across the geographic range of the host species (e.g. Lindholm 1999). Because the level of brood parasitism selects for defensive responses of the hosts (Davies and Brooke 1988, 1989a, b; Rothstein 1990), host populations under different parasitism pressures may reflect different levels of defense against the parasitic eggs. Current evidence supports this view; host populations living in sympatry with the brood parasite typically show higher levels of specific defenses against brood parasitism than allopatric populations (Davies and Brooke 1989a, Soler and Møller 1990, Briskie et al. 1992, Soler et al. 1999, Lindholm and Thomas 2000). Such population differences in behavior have been assumed to reflect genetic differences between populations and, thus, different stages in the coevolutionary "arms race" between the cuckoo and its host (Davies and Brooke 1989a, Soler and Møller 1990, Briskie et al. 1992). Hosts may retain their rejection behavior long after the parasitism pressure has abated (e.g. Rothstein 2001, Underwood et al. 2004).

Alternatively, behavioral changes in levels of defense among host populations could be attributable to phenotypic plasticity (Brooke et al. 1998, Lindholm 1999). Higher cuckoo densities at one site may stimulate hosts to inspect their eggs more often, thereby leading to higher rejection rates (Lindholm and Thomas 2000), which makes it difficult to know to what extent genetic changes are involved. Behavioral flexibility is supported by the fact that conditional factors (i.e. cuckoo presence at nests) significantly influence host rejection behavior (e.g. Davies and Brooke 1988, Moksnes et al. 1993).

We studied the rejection behavior against artificial cuckoo eggs in two Common Redstart (*Phoenicurus phoenicurus*; hereafter "redstart") populations to determine whether levels of antiparasite defenses vary according to the current parasitism pressure by cuckoos (see Lindholm and Thomas 2000). We used two study populations, one currently not parasitized and the other regularly parasitized by cuckoos. We predicted that the frequency of rejection against artificial cuckoo eggs would be higher in the frequently parasitized population.

Methods

Study species.—The redstart is a small (total length in a stretched posture 14 cm) migratory thrush (Turdidae). Redstarts arrive at their breeding sites, on average, 1–1.5 weeks earlier than cuckoos. The redstart is a secondary cavity-nester that also nests in nest boxes and rarely on the ground. The cuckoo is the only obligate interspecific brood parasite in Finland. Individual female cuckoos are host-specific and lay distinctive eggs, which match the eggs of their favorite hosts. The redstart is the cuckoo's main host in Finland (J. Rutila unpubl. data), and it is parasitized with the almost perfectly mimetic immaculate blue cuckoo egg morph, which occurs widely over the country (Wasenius 1936). The high level of mimicry between cuckoo and redstart eggs (Moksnes et al. 1995) and experimental evidence showing that redstarts have an intermediate rejection rate of nonmimetic cuckoo eggs (Rutila et al. 2002) suggest that the cuckoo and redstart have experienced a long coevolutionary interaction in Finland.

Average breeding density of the redstart on our Rovaniemi study area in northern Finland (66°29′N, 25°43′E) is 2.5 pairs per square kilometer, comparedwith 0.9 pairs per square kilometer in our Joensuu study area in southern Finland (62°37′N, 29°45′E). Although we did not assess cuckoo density directly, recent studies of the bird communities in these localities suggest a higher cuckoo abundance in Rovaniemi (0.4 pairs per square kilometer) than in Joensuu (0.3 pairs per square kilometer) (Väisänen et al. 1998).

Study design.—The study was conducted using nest boxes. Data from the currently unparasitized redstart population in Rovaniemi were collected during the breeding season of 2003.

Data from the parasitized redstart population in Joensuu were collected during the breeding seasons of 1999–2002. The Rovaniemi population was defined as unparasitized because no cuckoo parasitism was observed when nest boxes there were monitored during the years 1992–2003 (*n* = 137 checked redstart nests; J. Jokimäki et al. unpubl. data). By contrast, the average parasitism rate in the Joensuu area was 16.6% (*n* = 602 checked redstart nests between 1984 and 2002; J. Rutila et al. unpubl. data).

The distance between the two study areas is ~500 km. The areas are 50- to 80-year-old open Scots pine (*Pinus sylvestris*) forests with sparse shrub and field cover. Similar nest boxes designed especially for redstarts and cuckoos were used in both study areas. The boxes were about 12 × 12 × 20 cm (width, depth, and height, respectively), and cavity diameter was ~65 mm. All nest boxes were erected at ~1.5 m above ground (see details in Rutila et al. 2002).

We ”parasitized” redstart nests with similar artificial cuckoo eggs in both study areas. The eggs approximated real cuckoo eggs in both size (experimental eggs: 21.5 × 17.1 mm; real cuckoo eggs: 21.9 × 16.4 mm; Baker 1942) and weight (experimental eggs: 4.2 g; real cuckoo eggs: 3.6 g; Wyllie 1981). We made our artificial eggs of plaster of Paris and painted them with acrylic paints (Davies and Brooke 1989a, Soler and Møller 1990, Moksnes et al. 1993, Stokke et al. 1999). Hard artificial eggs may incur higher rejection costs for the host than real cuckoo eggs (Martin-Vivaldi et al. 2002). Because the redstart is a puncture ejector and the pecking marks can be seen in the plaster eggs, we were able to detect attempts to eject the model egg prior to desertion. According to our field observations, the redstarts never damaged their own eggs when they ejected the artificial cuckoo egg. Furthermore, nest desertion was rarely observed in the previous study using similar eggs (Rutila et al. 2002). Thus, use of artificial cuckoo eggs made of plaster is an appropriate method.

We assigned redstart nests randomly to one of the following three groups: (1) parasitized with mimetic eggs (artificial cuckoo eggs painted blue to resemble real redstart eggs); (2) parasitized with nonmimetic eggs (artificial cuckoo eggs painted with a grayish ground color and brown spots to resemble Brambling [*Fringilla montifringilla*] eggs, Brambling being another important host for the cuckoo in Finland; Wasenius 1936); and (3) control group of nests visited as frequently as the two experimentally parasitized groups but without egg manipulations. In both study areas, we placed the model eggs in redstarts' nests during their laying period in the afternoon at either the four- or the five-egg stage. The date of introduction of the model egg was about 2–3 days before the redstart started incubation. Experiments were conducted during the same laying cycle of the redstart in both study areas, and the model cuckoo eggs were similar in both areas. Each model egg was used only once during the study. We did not remove the host's own eggs from the box, because cuckoos usually do not remove any host eggs when they parasitize redstarts (Rutila et al. 2002). Our system corresponds well with the natural laying behavior of cuckoos. Each nest was checked six days after the beginning of the experiment, and the final results were coded as ”accepted” or ”rejected.” We selected this six-day response period because the redstart commonly waits until incubation before making a rejection decision (Rutila et al. 2002, J. Rutila unpubl. data). The result of the rejection of the model egg was further categorized as ”nest desertion” or ”egg ejection” by the host. If the model egg was ejected from the nest box or away from the nest cup, we categorized the response as ”ejection.” We classified abandoned nests as ”deserted.”

Statistical analyses.—We used generalized linear models (GENMOD procedure; SAS Institute 1996) to test the association between the occurrence of rejection at each nest and the experimental treatment (1 = parasitized with mimetic egg, 2 = parasitized with nonmimetic egg, 3 = nonparasitized) and locality (1 = Joensuu, 2 = Rovaniemi). The probability of rejection of each experimental egg was modeled as a binomial response variable (1 = rejection, 0 = acceptance) using a logistic link function. Similarly, we analyzed the association between method of rejection of the rejecting pairs, modeled as a binomial response variable (1 = ejection, 2 = desertion), and the experimental treatment and locality. Because no eggs were rejected in our control group of nests, experimental treatment has only two categories for this analysis. The starting models contained the main effects plus the only possible interaction. Model selection was done by removing, one by one, the effects that were furthest from statistical significance, starting with the highest-order interaction and ending with the main effects. All statistical tests were two-tailed and statistical significance was set at 0.05.

Results

Rejection probability was higher in the unparasitized redstart population than in the parasitized population ($\chi^2 = 4.16$, df = 1 and 104, $P = 0.04$; Tables 1 and 2). The rejection rate was 36.7% ($n = 30$) in the Rovaniemi area and 20.0% ($n = 80$) in the Joensuu area. In general, the nonmimetic artificial eggs were rejected more often than the mimetic ones ($\chi^2 = 21.40$, df = 2 and 106, $P < 0.0001$; Tables 1 and 2). The rejection rate of nonmimetic eggs was 41.2% ($n = 51$), that of the mimetic eggs was 15.8%, and the control pairs never rejected their own eggs ($n = 21$ nests). No effect of an interaction of locality and treatment on the rejection probability was observed.

Desertion probability was higher in the currently unparasitized population than in the parasitized population ($\chi^2 = 8.17$, df = 1 and 25, $P = 0.004$; Tables 1 and 2). In Rovaniemi, 72.7% ($n = 11$) of the redstarts deserted their nests, whereas 18.8% ($n = 16$) of redstarts deserted their nests in Joensuu. Desertion probability was not dependent on egg type ($\chi^2 = 0.66$, df = 1 and 24, $P = 0.42$), and no effect of an interaction between locality and treatment on desertion probability was observed ($\chi^2 = 0.55$, df = 1 and 23, $P = 0.46$; Table 2). Thus, regardless of mimicry or nonmimicry of host eggs, desertion was the most frequent method of rejection in the nonparasitized population in Rovaniemi.

Table 1. Reactions of redstarts to artificial parasitism with mimetic and nonmimetic eggs in the Rovaniemi and Joensuu study populations.

		Rejected		
	Accepted	Ejected	Deserted	Total
Rovaniemi (unparasitized)				
Mimetic eggs	5	1	3	9
Nonmimetic eggs	7	2	5	14
Control	7	0	0	7
Joensuu (parasitized)				
Mimetic eggs	27	1	1	29
Nonmimetic eggs	23	12	2	37
Control	14	0	0	14

Table 2. Factors influencing probability of egg rejection and nest desertion by redstarts. These are generalized models (SAS GENMOD procedure), with probability of rejecting or deserting a nest as dependent variables and locality (Joensuu vs. Rovaniemi) and experimental treatment (mimetic vs. nonmimetic artificial cuckoo egg) as independent fixed effects. Interaction among independent effects was taken into account in the analyses. Significant effects are in bold.

Independent effects	Rejection probability			Desertion probability		
	χ^2	df	P	χ^2	df	P
Locality*Treatment	2.68	2, 104	0.2600	0.55	1, 23	0.460
Locality	**4.16**	**1, 104**	**0.0400**	**8.17**	**1, 25**	**0.004**
Treatment	**21.40**	**2, 106**	**<0.0001**	0.66	1, 24	0.420

Discussion

We found an unexpectedly high rejection rate of artificial cuckoo eggs, regardless of their degree of mimicry, in the unparasitized population (Table 2). In addition, we found population differences in the method of rejection of cuckoo eggs: redstarts in the unparasitized population mainly deserted their nests when rejecting a cuckoo egg, whereas most redstarts in the parasitized population ejected it (Tables 1 and 2).

The rates of rejection by redstarts reported here contrast with a previous study of an unparasitized redstart population in northwestern Finland, where the cuckoo is practically absent (Järvinen 1984). Järvinen (1984) found no rejection of nonmimetic eggs during the laying stage of the host, and a rejection rate during incubation of 35% ($n = 31$). Järvinen (1984) had no data on mimetic eggs. However, it is impossible to compare our study and his reliably because Järvinen (1984) observed the host rejection behavior for only 24 h (and rejection often occurs after 24 h; J. Rutila unpubl. data), which may bias his results regarding acceptance during the redstart laying period. In addition, Järvinen (1984) parasitized redstarts' nests with real eggs of other passerine species, which differ greatly in size from cuckoo eggs. Finally, cuckoos rarely parasitize hosts during incubation, because eggs laid at that time have a lower chance of outcompeting the host's offspring (Davies 2000).

One possible explanation for the higher level of defense in our unparasitized study population is past parasitism by cuckoos, which may have selected for defensive mechanisms among redstarts in Rovaniemi. Later on, cuckoos may have shifted to another host with a lower level of defense, thereby increasing their reproductive success. Previous studies have revealed that redstarts may respond to cuckoo parasitism by ejecting the parasitic egg or by deserting its nest (Lagerström 1983, Rutila et al. 2002). Ejecting a cuckoo egg appears to be a low-cost method of rejection for redstarts, given that Rutila et al. (2002) reported no damage to redstart eggs when cuckoo eggs were ejected. However, nest desertion typically results in loss of time and energy, smaller clutch size, and lower fledgling survival during renesting (Rohwer and Spaw 1988, Davies and Brooke 1989b). Furthermore, in the northern latitudes (e.g. the Rovaniemi area), deserting a nest may be more costly because the shorter period available for breeding precludes renesting (Moksnes et al. 1993). The redstarts may have lost the more refined method of rejection (i.e. ejection) while retaining the tendency to desert the nest when a parasitic egg was detected. Although we found no parasitism by cuckoos in our redstart population in Rovaniemi, Wasenius (1936) reported the presence of the *Phoenicurus* egg morph in the north of Finland in the beginning of the 20th century, which suggests that redstarts there have been used as hosts in the past. We did not document any cost of ejecting cuckoo eggs (see also Rutila et al. 2002) that would make ejection the favored recognition trait to be retained by redstarts. However, ejection may be lost more easily than desertion because ejection requires two different traits (i.e. ability to recognize the cuckoo egg and ability to eject it). In addition, this hypothesis assumes that the study populations diverged genetically in the recent past and, thus, that they currently represent different stages in the coevolutionary arms race with the cuckoo (Davies and Brooke 1989b). If gene flow is high, similar rejection rates in both populations would be expected. Unfortunately, we do not have data on the genetic distance between the populations to assess this assumption.

Alternatively, differences between populations in the level of rejection may reflect conditional responses to cuckoo presence (Davies and Brooke 1988, Briskie et al. 1992, Moksnes et al. 1993, Alvarez 1996, Brooke et al. 1998, Lindholm and Thomas 2000). Conditional responses linked to cuckoo presence would support a prediction that the higher cuckoo abundance in Rovaniemi would stimulate the redstarts to inspect their eggs more often, thereby leading to higher rejection rates in this population. Our results provide support for this possibility, in that the rejection rate was higher in Rovaniemi. Although our study population at Rovaniemi was unparasitized, cuckoo abundance was higher in that area (Jokimäki and Huhta 1996, Väisänen et al. 1998). Hence, if the redstarts rely on cuckoo abundance as a cue to ascertain the risk of being parasitized, the presence of a denser cuckoo population at Rovaniemi may have induced a higher rejection rate. Nonetheless, conditional responses are an unlikely explanation for the pattern we found, because the evolution of recognition and rejection of cuckoo eggs by the redstarts is a prerequisite for the use of conditional stimulus leading to rejection.

In conclusion, we found no evidence that the currently unparasitized redstart population shows less defensive behavior against brood parasitism than the parasitized population. In addition, our results demonstrate that the method of rejection of host species may differ between populations. Whether these differences were caused by genetic variation or phenotypic plasticity is unknown. Our results suggest that current selection pressures by brood parasites do not always explain the current level of defenses, which perhaps could be better explained by the level of selection pressure exerted by brood parasites in the recent past.

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