# Relationship between the Common Cuckoo *Cuculus canorus* and its host, the Redstart *Phoenicurus phoenicurus*

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In 1981—83 the reaction to foreign eggs of a regular Cuckoo host, the Redstart, was examined in experiments conducted in NW Finnish Lapland, at the northern edge of the distribution areas of the two species. Altogether 81 foreign eggs were introduced into the nests of 35 different females. These eggs were accepted in the egg-laying phase, but in the incubation phase about 1/3 of the females were "ejectors". None of the introductions of foreign eggs resulted in desertion of the nest. Despite the rarity of the Redstart and the recent decline in its numbers in NW Finnish Lapland, the rejection frequency was relatively high. It is suggested that "population flux" may partly explain the dimorphic behaviour of Redstart females. Native Redstarts of the far north may have been mainly "acceptors", because northern Lapland lies outside the main distribution area of Redstart-Cuckoos, whereas immigrants from southern areas were probably mainly "ejectors". The arrival of Cuckoos coincided with the start of egg-laying by the Redstart, and the period suitable for parasitism by the Cuckoo in NW Finnish Lapland was about 1—25 June.

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## Introduction

In the first decades of the present century the very variable eggs of the Common Cuckoo *Cuculus canorus* were highly prized among oologists. The by-product of the extensive egg-collecting was an increase in our knowledge of the habits of this mysterious bird (e.g. Chance 1922, Baker 1942). Recently, several authors have paid much attention to the Cuckoo (v. Haartman 1976, 1981, Löhrl 1979, Wyllie 1981, Gärtner 1982). Wyllie's (1981) monograph, in particular, has cast new light on many obscure concepts and summed up our present knowledge of its life history.

v. Haartman's (1981) fascinating paper on the co-evolution of the Cuckoo and its most common host in Finland, the Redstart *Phoenicurus phoenicurus,* made me decide to perform experiments on the rejection of foreign eggs by the Redstart. v. Haartman (1981) made experiments with a total of nine pairs in SW Finland during seven years. In restricted material there is the possibility that some of the Redstart pairs are studied in several years (cf. Ruiter 1941). Thus, for instance, an abnormally sensitive or insensitive female may bias the results.

My first task was to obtain sufficient data for a single breeding season, to overcome the possible bias of a small annual number of experiments. My primary aim was to test the hypothesis put forward by v. Haartman (1981) that the Redstart female is dimorphic, the populations containing both "acceptors" and "rejectors". My comparatively extensive data, collected during three summers at the northern edge of the distribution areas of the two species, led me to some new interpretations of the relationship between the Cuckoo and the Redstart. At present no published studies exist on rejection of Cuckoo eggs by the Redstart in natural conditions, i.e. we do not know how the Redstart behaves when it is heavily parasitized by real Cuckoos. Therefore, some of the results and interpretations are presented very tentatively.

## Study area, material and methods

My study area was a mountain birch wood in the Kilpisjärvi area in NW Finnish Lapland (about 69°03'N, 20°50'E; for details, see A. Järvinen 1983). In northern Finland the density of the Redstart is higher than in southern Finland (Merikallio 1958), but in northernmost Lapland, where my data were collected, its density is rather low: in box-free mountain birch woods about 0.7 pairs/km$^2$, and in mountain birch woods with nest-boxes about 1.5 pairs/km$^2$ (A. Järvinen 1983).

The Cuckoo is also less numerous in northern Lapland than further south (Merikallio 1958), and seems long to have been scarce in NW Finnish Lapland (Munsterhjelm 1911, Suomalainen 1912, Montell 1917). According to the local people (U. Viik, pers. comm.), the frequency of singing Cuckoos has also declined at Kilpisjärvi during the last few decades. In mountain birch woods in northern Finnish Lapland the present Cuckoo density seems to average about 0.1—0.2 pairs/km$^2$ (O. Järvinen & Väisänen 1976, A. Järvinen & Pietiäinen 1982). Despite their relatively low numbers, both species are natural inhabitants of my study area (e.g. Munsterhjelm 1911, A. Järvinen & Pietiäinen 1982, A. Järvinen 1983).

In any one area there may be 2—3 Cuckoo 'gentes' specialized on different host species (Wyllie 1981). In NW Finnish Lapland the Cuckoo usually parasitizes Brambling *Fringilla montifringilla* nests, but Redstart nests are also used (Montell 1917, Wasenius 1936). Cuckoos victimizing Redstarts usually lay blue eggs that mimic the host eggs very closely (Wasenius 1936).

All the Redstart nests considered in this study were in nest-boxes. In 1981—83 I introduced altogether 81 foreign eggs into 35 different Redstart nests (Table 1). The eggs used in the experiment were those of the Brambling, Meadow Pipit *Anthus pratensis* and Redpoll *Carduelis flammea*. These differ in coloration from the Redstart eggs, and are also somewhat smaller. The experiments covered the whole egg-laying and incubation period of the Redstart (see Results).

In most of the nests different kinds of eggs were tried in the two phases of the breeding cycle. The foreign egg was introduced into the Redstart nest around noon (the Cuckoo usually lays in the afternoon or evening rather than in the morning as do its hosts; Wyllie 1981). If the foreign egg was still in the nest 24 hours later, I considered it "accepted" and removed it (in a few tests a longer time interval did not result in a higher ejection rate; cf. v. Haartman 1981).

The data concerning the egg-laying period of the Redstart at Kilpisjärvi were derived from A. Järvinen (1983). The dates of the first singing Cuckoos are obtained from my own observations and notes deposited at Kilpisjärvi Biological Station of the University of Helsinki.

## Results

The reactions of the Redstart females did not differ with the species of the foreign egg. For instance, if a female ejected a Meadow Pipit egg, it also ejected a Brambling egg and vice versa. During the egg-laying phase all the 32 females accepted a foreign egg, no matter whether it was introduced at the beginning or end of this phase (Fig. 1). In contrast, during the incubation phase 11 of the 31 females (35 %) were "ejectors". The reactions of the females to foreign eggs did not seem to differ between different parts of the incubation phase: as soon as incubation had started some of the females became "ejectors" (Fig. 1).

Early in the incubation phase (the first five days), a slightly smaller proportion (33 %) of the eggs was ejected than later in the phase (41 %), but this difference was not significant (Fig. 1; Fisher exact probability test). During the incubation phase there were more "acceptors" in 1981 than in 1982 (Fig. 1; Fisher exact probability test, $P<0.05$), but otherwise the years were similar. No nests were deserted due to introduction of foreign eggs.

The first Redstarts start to lay at Kilpisjärvi at the end of May or the beginning of June (Fig. 2). The arrival of Cuckoos (singing males) seems to coincide with the start of egg-laying of the Redstart (Fig. 2). Thus, the period suitable for parasitism by the Cuckoo is about 1–25 June (the Redstart has an average clutch of six eggs at Kilpisjärvi).

Table 1. The number of Redstart nests and foreign eggs in this study. In the first experiments during the egg-laying and incubation periods each egg was introduced into a different nest. In the repeat experiments a second foreign egg was introduced one or more days after the first egg.

| Year | No. of nests | Laying period | | | Incubation period | | |
|---|---|---|---|---|---|---|---|
| | | First exp. | Repeat exp. | Total | First exp. | Repeat exp. | Total |
| 1981 | 13 | 11 | 1 | 12 | 11 | 3 | 14 |
| 1982 | 13 | 12 | 0 | 12 | 11 | 11 | 22 |
| 1983 | 9 | 9 | 1 | 10 | 9 | 2 | 11 |
| Total | 35 | 32 | 2 | 34 | 31 | 16 | 47 |

## Discussion

A major prerequisite for successful parasitism by the Cuckoo at high latitudes is that it breeds at

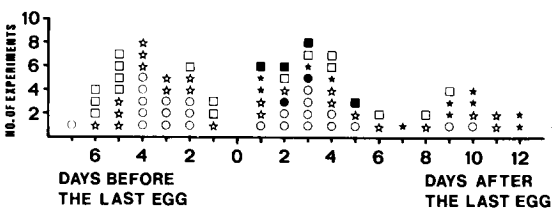


Fig. 1. The reaction of Redstart females to foreign eggs in different phases of the egg-laying and incubation periods at Kilpisjärvi. Dots = 1981, stars = 1982 and squares = 1983. Open symbols = accepted eggs, closed symbols = ejected eggs.

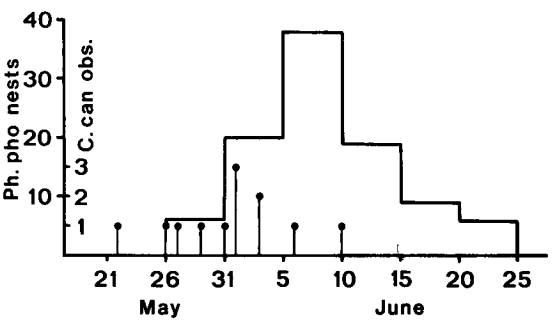


Fig. 2. The numbers of the first eggs laid by the Redstart in five-day periods at Kilpisjärvi in 1966—80 (left scale, histogram), and the observations of the first singing Cuckoo males in the same area in 1968—83 (right scale).

the same time as the host. The Cuckoo seems to arrive at Kilpisjärvi around the start of the egg-laying of the Redstart (Fig. 2). The use of the dates of the first singing Cuckoo males as an indicator of spring arrival may involve several sources of error, but according to Wyllie (1981), "it is reasonable to assume that Cuckoos sing within a day or two of arrival at their breeding sites." In England the males seem to arrive a few days before the females (Wyllie 1981), but it is uncertain whether such a difference exists in the north.

At Kilpisjärvi the first male Cuckoos arrived in late May — early June, before the last snow had melted and about two weeks before the mountain birches came into leaf. In Central Europe the Cuckoo starts laying about three weeks after its arrival, thus missing the early nests of its hosts (Wyllie 1981). In the north the laying schedules of both the Cuckoo and its hosts are probably so compressed that it must lay soon after its arrival. If Cuckoos waited as long in Northern as in Central Europe, there would be no nests to parasitize (cf. Fig. 2). According to data presented by v. Haartman & Söderholm-Tana (1983), in Finland the egg-laying of the Cuckoo seems to follow soon after its arrival.

Although the Cuckoo arrives later in the north, its main laying season seems to be roughly the same (June) in the south (cf. Wyllie 1981) and the north (present study). This means that phenologically the Cuckoo is breeding earlier in the north. Fig. 2 suggests that (1) the breeding season of the Cuckoo approximately coincides with that of the Redstart, and that (2) in the north the period suitable for parasitism is short (at most about 4—5 weeks) compared to that in Central Europe (Wyllie 1981). Therefore, in the north an individual Cuckoo female may not be able to lay as many eggs as in the south (in Central Europe Cuckoo females lay 10—15 eggs at two-day intervals; Wyllie 1981).

The average arrival date of the Cuckoo in Helsinki (60°N), southern Finland, is 5 May (N=13; v. Haartman et al. 1967—72). The corresponding dates for Rovaniemi (66°30′; Komonen 1962), Muonio (68°N; Montell 1917), Kilpisjärvi (69°N; present study) and Skibotn (Norway 69°30′N; Haftorn 1971) are, respectively, 22 May (N=15), 1 June (N=14), 1 June (N=12) and 27 May (N=8). Cuckoo migration appears to advance more rapidly from southern Lapland to northern Lapland than from southern Finland to southern Lapland (cf. also v. Haartman & Söderholm-Tana 1983).

There are several ways in which a host can fight against a nest parasite. The host may abandon the nest, it may build the nest over the foreign egg, or it can throw it out (e.g. Wyllie 1981). The results in the present study suggest that the Redstart uses the last method. The fact that not a single Redstart nest was deserted due to introduction of foreign eggs accords with the view that species frequently parasitized by Cuckoos do not desert their nest as easily as unusual hosts (Table 16 in Wyllie 1981).

The study of Rensch (1924) suggests that regular Cuckoo hosts learn to recognize their own eggs as soon as they are laid. In view of this, it is strange that the Redstart did not react in any way to foreign eggs during the egg-laying phase, thus behaving like the Pied Flycatcher *Ficedula hypoleuca* female, which is practically never victimized by the Cuckoo (v. Haartman 1952). Similarly, Gärtner (1982) observed that near Hamburg 13 % of 38 non-mimicking eggs of the Cuckoo laid in nests of the Marsh Warbler *Acrocephalus palustris* were accepted and 79 % were ejected, and that most of the ejections occurred in the beginning of the incubation period (8 % of the nests were deserted). One possibility is that the Redstart recognizes her eggs, but does not throw out odd eggs. From the host's point of view it apparently makes little difference in which phase ejection occurs, provided it happens before the parasite's egg hatches.

The Cuckoo usually lays its eggs during the egg-laying phase of the host (Wyllie 1981). v. Haartman (1981) concluded that the ejection of foreign eggs, though rare, is evidently not restricted to a particular phase of the Redstart's breeding period. At Kilpisjärvi removal seems to be restricted to the incubation phase. In this phase removal seems to take place relatively often, and its frequency does not seem to rise appreciably towards the end of the incubation phase.

In a study performed by v. Haartman (1981) in SW Finland 1 or 2 of 8 or 9 Redstart females ejected a foreign egg (there was one unclear case in the egg-laying phase). v. Haartman (1981) suggested that the Redstart is dimorphic regarding this behavioural trait. He proposed two alternative explanations of this dimorphism. One alternative ("dimorphism as a steady state") is that the almost perfect mimicry by the Cuckoo has removed the selection pressure on the host to reject odd eggs. The other alternative ("transitory dimorphism") is based on the recent decline of the Redstart population in Finland, which may have made parasitism by the Cuckoo impossible, and allowed the Redstart to abandon its antiparasite behaviour.

The rate of rejection was almost the same in Latvia, the Soviet Union (40 %; Vilks 1972), as at Kilpisjärvi, about 1300 km further north (35 %; present study). According to the theoretical considerations of v. Haartman (1981), in the sparse (about 1 Redstart pair/km$^2$; A. Järvinen 1983) and dwindling Redstart population (A. Järvinen 1981) of the Kilpisjärvi area, the rejection rate should be low. This is clearly not the case

and the present results disagree with both the "transitory dimorphism" hypothesis and the "dimorphism as a steady state" hypothesis. Thus the rarity and recent decline in numbers of the Redstart do not seem to have lowered rejection frequency. Lagerström's (1983) extensive data (187 Cuckoo eggs in 430 Redstart nests) support this view. Lagerström (1983) reported a high (60 %) rejection rate of Cuckoo eggs by the Redstart in southern Finland (61°30'N) in 1975—83. He suggested that the ability of the Redstart to recognize foreign eggs is of comparatively recent origin, and this development may have contributed to the decline in Cuckoo numbers in Finland.

According to v. Haartman (1981), northern Lapland lies outside the main distribution area of Redstart-Cuckoos. Thus in northern Lapland there should be less selection pressure for the Redstart to have evolved discrimination against foreign eggs than further south. Despite this fact, about 1/3 of the females ejected foreign eggs from their nests right at the beginning of the incubation period.

Why, then, did some Redstart females eject a foreign egg at Kilpisjärvi while others did not? One possible explanation is that the Kilpisjärvi population is not completely isolated from southern populations. There may be a certain influx of Redstarts (probably mainly first-breeders) from the central distribution area of the Redstart-Cuckoos, which would cause a relatively high discrimination rate.

In NW Finnish Lapland the above hypothesis would explain the dimorphic behaviour of the females: the "native" Redstarts (perhaps about 2/3 of all Redstarts breeding in the area) would be mainly "acceptors", whereas the "tourists" from southern areas would be mainly "ejectors". Similarly, this would explain the possible annual differences in the ejection rate; they would simply reflect the fluctuating annual immigration pressure caused, for instance, by varying weather conditions in spring, or varying breeding success in different parts of the range of the species.

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## Selostus: **Leppälinnun ja käen välisistä suhteista**

Leppälinnun suhtautumista vieraisiin muniin sekä leppälinnun ja käen pesimä- ja saapumisaikoja tutkittiin Kilpisjärvellä, missä molemmat lajit esiintyvät levinneisyysalueensa pohjoisrajalla. Pesinnän eri vaiheissa leppälinnun pöntöissä sijainneisiin pesiin asetettiin järripeipon, niittykirvisen tai urpiaisen munia vuorokauden ajaksi. Kokeita tehtiin 1981—83 yhteensä 81, 35:llä eri naaraalla (taul. 1).

Muninta-aikana naaraat hyväksyivät vieraan munan, mutta haudontavaiheessa n. 1/3 niistä poisti vieraan munan (kuva 1). Kirjoituksessa verrataan saatuja tuloksia v. Haartmanin (1981) aikaisemmin esittämiin tuloksiin ja pohditaan syitä leppälintunaaraiden kahdenlaiseen käyttäytymiseen. Erääksi mahdollisuudeksi esitetään dimorfismin johtuvan alueelle etelämpää, leppälintukäen päälevinneisyysalueelta saapuvista yksilöistä, joille olisi kehittynyt taipumus poistaa käen muna pesästä. Kokeet leppälinnun reaktiosta pesään asetettuihin vieraisiin muniin eivät välttämättä anna totuudenmukaista kuvaa leppälinnun ja käen suhteista, minkä vuoksi tarvittaisiin tietoja käen 'oikeasti' loisimien leppälintujen suhtautumisesta pesäloisen muniin.

Käki saapui Kilpisjärvelle touko-kesäkuun vaihteessa (kuva 2), kasvillisuuden kehitykseen nähden varsin varhain. Käen saapuminen osui yhteen leppälinnun muninnan alkamisen kanssa (kuva 2).

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