

# Co-evolution of the Cuckoo *Cuculus canorus* and a regular Cuckoo host

LARS VON HAARTMAN

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The reaction of the Redstart *Phoenicurus phoenicurus* to foreign eggs was studied experimentally in an area in SW Finland. Foreign eggs were ejected by a minority of the Redstarts (1—2 out of 8—9 pairs). Ejection took place during the laying, incubation, and nestling phases of the host. When ejection occurred, it invariably took place between the introduction of the foreign egg and the next check, usually within c. one day. The same pair repeatedly ejected introduced eggs. Acceptor Redstarts incubated the foreign egg and fed the foreign young developing from it, at least until it fledged (three nests with introduced Great Tit eggs).

The cause of the dimorphic reaction to foreign eggs is discussed. It is suggested (A) that the dimorphism either may be a steady state, caused by the Cuckoos having evolved effectively mimicking eggs, so that the ejector behaviour is no longer selected for in the Redstart and has ceased to spread, or (B) that it is the consequence of both the Redstart and Cuckoo populations having decreased strongly, causing parasitism to end and selection for rejection to slacken.

The Redstart Cuckoo is common in the European parts of the USSR, in Finland and parts of the Scandinavian peninsula. Extralimital occurrences also exist. Among the causes of the rarity of Redstart Cuckoos in Central and W Europe may be competition with other Cuckoo demes parasitizing hosts with a longer breeding season, which allows the parasite to lay more eggs.

The breeding season of the Redstart in Finland allows the Cuckoos about a fortnight of regular laying, with a chance of laying single eggs later.

*Lars von Haartman, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland*

## Introduction

Evolution never takes place in a vacuum, and co-evolution, therefore, exists among all living beings. In its usual form it appears as diffuse co-evolution affecting species at least partly occupying the same niche and connected with each other to varying degrees through an intricate plexus of relations. Sometimes, however, co-evolution is restricted to a small number of species, and the extreme cases involving only a couple of them

serve to visualize the working of the evolutionary process. Certain forms of symbiosis belong here, as between flowering plants and pollinating animals or between fruit-producing plants and animals dispersing seeds. So do also the relations between exploiter and victim, as in the cases of predators and their prey or of parasites and their hosts.

This co-evolution has parallels in the development of many human relations. The evolution of warfare is, perhaps, the most striking example;

attack and defence weapons develop in close dependence of each other. There is, however, apart from the time scale and other obvious discrepancies one principal difference between this "cultural" evolution and the evolution of animals and plants. The cultural evolution may well overshoot its goal; that of organisms may not. In the latter, natural selection tests the fitness of phenotypes in every generation. When fitness is complete, evolution stops. In the cultural evolution a certain innovation may not be tried in practice for a considerable time, if at all, and this may cause painful failures or expensive excesses. In the last-mentioned category we may place certain fortresses constructed by Vauban, master constructor of fortifications to the *Roi soleil*, which could not be conquered during World War II, though those built about 250 years later by his compatriot Maginot were not equally impregnable.

I propose the name Vaubanism for this concept of overshooting or unnecessarily perfect evolution. It has not always been clearly appreciated that evolution cannot produce Vaubanism. For instance, the Leaf-butterfly *Kallima* has been claimed to be more similar to a leaf than would be strictly necessary to cheat all its potential predators, but, as has been pointed out, this assertion is disproved by its presence in numerous entomological collections.

Even prolonged retention of once adaptive traits after they have become useless is unlikely, as such traits are costly and are, therefore, disadvantageous rather than neutral. At most one may expect them to remain as vestiges during a transition period, which, admittedly, may sometimes be surprisingly long.

Under these circumstances it was somewhat perplexing when, as reported earlier (v. Haartman 1977), I found indications that the Cuckoo lays mimicking eggs in nests of the Redstart *Phoenicurus phoenicurus*, although all the Redstarts tested accepted non-mimicking eggs. However, the explanation of this apparent Vaubanism had to be postponed until more data were available.

Experimental studies have revealed that most birds do not discriminate between their own eggs and those of foreign species or even artificial objects very unlike eggs (e.g. Goethe 1937, Lorenz & Tinbergen 1938, Poulsen 1953, Baerends 1964). The female Pied Flycatcher *Ficedula hypoleuca* (a species which, like the Redstart, breeds in holes, though with a narrower entrance, and has eggs very similar to Redstart eggs) was found to incubate an incredible variety of strange eggs, including an egg of the Eider Duck *Somateria mollissima*, on top of which she had certain difficulties in keeping her balance (v. Haartman 1952). Of course, the female will finally desert such a nest, influenced not by visual but by tactile stimuli, coming from her brood-patch. In this way, incubation of an empty nest will be discontinued within a reasonable time.

There is, of course, little danger that the Pied Flycatcher will have an opportunity to incubate strange eggs. Single eggs of other hole-nesting species are only occasionally found in its nest. The Cuckoo does not normally lay eggs in the nest of the flycatcher, as the entrance to the nest hole is usually too narrow. The observations of Cuckoo young reared successfully in nest-boxes with a narrow entrance (Väisänen 1974, Homoky-Nagy 1978) are certainly exceptional. As shown by Löhrl (1979), Cuckoo young may weigh

only as much "as Starlings" *Sturnus vulgaris* when fledged, increasing strongly in weight afterwards.

In species which for one reason or another are in danger of incubating strange eggs, mechanisms of egg discrimination may evolve. Razorbills *Alca torda* and Guillemots *Uria aalge* breeding in dense colonies, where eggs of different individuals may easily be confused, learn to recognize their own eggs (Wahlin 1943, Tschantz 1959). So do also small song-birds which are regular hosts of avian nest-parasites (Swynnerton 1916, Rensch 1924, 1925, Rothstein 1975a, b). Rensch has shown that in Cuckoo hosts this learning takes place during the egg-laying phase. When the eggs of a Cuckoo host were replaced immediately after laying with eggs of another species, the female learned to recognize the foreign eggs as her own and to reject those she had laid herself.

Both the densely breeding auks and the hosts of nest parasites are perfect examples of a genetically controlled capacity to learn something at a certain time and in a certain place, one of the "preformed" learning processes so important in the theory of ethology (see Tinbergen 1951, Lorenz 1978).

Small song-birds have three main strategies for coping with the situation "parasite's egg in nest". They may abandon the clutch, which, though a rather expensive strategy, is that chosen, for example, by warblers of the genus *Phylloscopus*<sup>1</sup>, they may bury the foreign egg by building over it, or they may eject the foreign egg, which is the usual reaction among Cuckoo hosts.

The fact that Cuckoos laying in the nests of Redstarts have mimicking eggs implies selection for this feature, and what other selective impetus can there have been than rejection of strange eggs by the Redstarts? There is, admittedly, another explanation, which to the best of my knowledge has never been presented before, and which I give here, for what it is worth: (1) Numerous species breeding in holes lay blue or white, unspotted eggs. This colouration must, then, be adaptive (v. Haartman 1956a). (2) What is adaptive for hole-breeders in general ought to be so for hole-breeding Cuckoos as well. Therefore, Cuckoos parasitizing hole-nesting birds such as the Redstart should lay unspotted blue or white eggs, even though the host is not a rejector.

The same explanation would, *mutatis mutandis*, apply to all cases of apparent mimicry in the eggs of avian nest-parasites. Instead of mimicry, convergency would be the cause of the similarity of Cuckoo and host eggs. However, as it is evident that the selective forces promoting this evolutionary process would be very much weaker than those exerted by egg-rejecting hosts, this explanation will not be considered any further here.

The singularly small size of the Cuckoo egg could, instead of mimicry, be a strategy to increase the number laid (cf. the copious small eggs produced by tapeworms).

## Experiments

In 1974 a study was started of the reaction of the Redstart to foreign eggs. The study area was Lemsjöholm in SW Finland (60°30' N, 21°27' E). On theoretical grounds, I believed that the species would be rather particular about the appearance of eggs. Now,

<sup>1</sup> If there is no special documentation, the reader is referred to the general texts by Braestrup (n.d.), v. Haartman et al. (1963—72), Löhrl (1979) and Glutz von Blotzheim & Bauer (1980).

seven years later, the results have turned out to contradict my expectations.

The foreign eggs introduced into Redstart's nests differed from the host's blue, unspotted eggs in at most three characteristics: (1) size, (2) ground colour, (3) presence of spots. Subtler qualities, such as differences in the gloss of the egg-shell and minute differences in form and size were not considered. Fresh or briefly incubated eggs were taken from whatever passerine nests were available, but in more recent years, eggs of the Great Tit *Parus major* were preferred in order to standardize the experiments. The foreign egg was introduced into the Redstart nest at any time, except at night and early morning. Cuckoos are known often to swallow one or two of the host's eggs when laying their own, but I never removed any Redstart egg, as the Cuckoo's behaviour is now considered feeding rather than an attempt to keep the number of host eggs unchanged. The studies of Koehler and his circle (e.g. Koehler 1955) make it seem highly improbable that small song-birds have any idea about the number of their eggs. Birds learn to "count" without symbols, but only in experimental situations and extremely slowly.

As Redstarts were few in my area, the number of experiments remained restricted. Experiments with 4 pairs in 1974—76 have been described in an earlier account (v. Haartman 1977), to which the reader is referred. The experiments listed below have been undertaken since; both sets of experiments will be considered in the discussion. Abridgements: R = Redstart, GT = Great Tit.

1977 (Pair 5): 8 June 1st R egg; 10 June 3 R eggs, 1 GT egg added; 11 June 3 R eggs,

the GT egg had disappeared, the R pair had deserted the nest, which was checked several times during the following days.

1978 (Pair 6): 26 May 1st R egg; 27 May 2 R eggs, 1 GT egg added; 31 May 6 R + 1 GT egg; 14 June 6 R young + 1 GT young; 22 June ditto; 1 July all young (R and GT) fledged.

1978 (Pair 7): 26 May 1st R egg; 27 May 2 R eggs, 1 GT egg added; 30 May 5 R + 1 GT egg; 15 June 6 R young + 1 GT young (a Cuckoo on the roof of the nest-box!); 2 July all fledged.

1979 (Pair 8): 21 May 1st R egg; 27 May 3 R eggs, 1 GT egg added; 30 May 6 R eggs + 1 GT egg; 1 and 5 June ditto; 15 June 6 R young + 1 GT young; 26 June ditto; 4 July all young (R and GT) fledged.

1980 (Pair 9), exp. A: 4 June 1st R egg; 11 June 8 R eggs; 12 June 8 R eggs, 1 GT egg added; 13 June 8 R eggs, GT egg removed.

1980 (Pair 9), exp. B: 13 June 8 R eggs, 1 new GT egg added; 15 June 8 R eggs, GT egg removed.

1980 (Pair 9), exp. C: 24 June 7 R young + 1 added R egg, 1 dwarf egg of GT added; 25 June 7 R young + 1 added R egg, the dwarf GT egg removed.

### Egg rejection and the breeding phase

Before turning to the experiments on egg recognition, it is necessary to establish at what phases of their breeding cycle Redstarts remove eggs. It is conceivable that the longer the female has incubated, the easier she will recognize her eggs. On the other hand, rejection of Cuckoo eggs is meaningful only during the egg-laying phase and, perhaps, during the very beginning of the incubation phase. Cuckoo eggs laid later than this will not hatch, or will hatch too late. Besides, as a rule Cuckoos lay their eggs during the laying phase of their hosts, not later (Glutz von Blotzheim & Bauer 1980).

Removal of strange eggs (Table 1), though rare, is evidently not restricted to a definite phase of the host's breeding period. Among a number of hosts of the Cowbird *Molothrus ater*, Roth-

TABLE 1. Rejection in relation to the breeding cycle of the Redstart

	Foreign eggs introduced during			
	egg-laying phase	1st half of incubation	2nd half of incubation	nestling phase
Foreign egg accepted	4	1	2	2
Foreign egg rejected	1	2	0	1

stein (1975b) found only one, the Cedar Waxwing *Bombycilla cedrorum*, which "showed variation in response that was dependent on nest stage".

### Acceptor and rejector Redstarts

If a foreign egg was rejected, this always took place between the introduction of the egg and the next check, usually within 24 hours. Ejection of foreign eggs did not, however, necessarily follow immediately upon their introduction. Once, I waited for more than one hour, but the female, although incubating for several periods, did not remove the foreign egg; the male did not visit the nest. The next day the egg had disappeared.

If not ejected before my next check, the foreign egg was not ejected later. In three Redstart nests Great Tit's eggs were incubated together with the Redstart's own eggs, the tit's eggs hatched, the young tits were fed by the

Redstarts, and fledged together with their step brothers and sisters. Acceptance or rejection of foreign eggs by Redstarts is shown in Table 2.

Eggs differing from Redstart eggs in two or three traits may be rejected or accepted. The "standard" Cuckoo egg is spotted, has a non-blue ground colour and is a trifle larger than a small song-bird's egg. Its degree of difference, as compared with a Redstart egg, could perhaps best be scored 2+. The three eggs shown in Table 2 as deviating from Redstart eggs in size were much larger (*Wryneck Jynx torquilla*, Redwing *Turdus iliacus*) or much smaller (Great Tit dwarf egg) than Redstart eggs.

In all but two nests the introduced egg was accepted. Of these nests, one represents an unclear case. A Great Tit egg was introduced, but had disappeared by the next day, whereas the Redstart eggs remained. The adult Redstarts were not seen and the nest was deserted, this being confirmed by

TABLE 2. Acceptance or rejection of foreign eggs in 9 different Redstart nests. In some of them several successive experiments were carried out so that the total number of experiments was 13. Seven of the females were acceptors, two (or one?) rejectors.

Dissimilar traits	Ground colour and size	Ground colour and spots	Ground colour, size and spots
Dissimilarity score	2	2	3
Foreign egg accepted	1	7	1
Foreign egg rejected	0	3	1

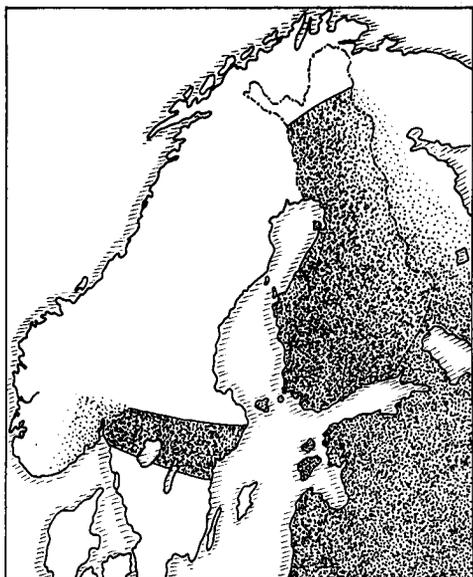


FIG. 1. The main distribution of Cuckoo eggs of the Redstart type in N and NE Europe. Extralimital occurrences are not mapped. Data from Rosenius (1929), Wasenius (1936), Malchevsky (1960), and Vilks (1972).

further checks. Does the Redstart perhaps possess two ways to reject foreign eggs (removal of egg and desertion of nest), or had something unexpected happened? In the other case of rejection, foreign eggs were introduced thrice, and were always removed. This repeated egg rejection shows that the removal was not "accidental" (e.g. a consequence of varying threshold values, as discussed by Fabricius 1951, p. 58 in another connection) but individually constant. Redstarts are evidently dimorphic with respect to acceptance or rejection.

### The geographical distribution of Redstart Cuckoos

The Redstart is (or was, see below) considered the commonest Cuckoo host

in Finland. According to Wasenius (1936), about 45% of all Finnish Cuckoo eggs were found in Redstart nests. In adjacent areas its status is almost the same. In the Baltic parts of the USSR it is second only to the White Wagtail *Motacilla alba* (Malchevsky 1960), and in Latvia even holds the first position (Vilks 1972). It is also frequently parasitized in the other European parts of the USSR. In Sweden the Redstart comes only fourth, after the White Wagtail and two *Sylvia* species (Rosenius 1929). The Redstart Cuckoos mainly occur within a strip traversing Central Sweden (Fig. 1). In Central and W Europe Redstart Cuckoos are much rarer. In Switzerland, it is true, the Redstart shares 5—6th position (Glutz von Blotzheim 1962), but in England it is very rarely parasitized. Lack (1963) does not mention a single case and Glue & Morgan (1972) list only one Cuckoo's egg in 1487 Redstart clutches. This should be compared with 3—4% parasitized clutches in the most severely afflicted species. All these figures are given with the reservation that the more quickly a strange egg is ejected by a certain species, the fewer will be the parasite eggs found in its nests (Rothstein 1975b). Further, host species whose nests are easy to find will have their share of Cuckoo eggs artificially increased.

It is puzzling that Redstart Cuckoos are restricted to N and E Europe, although both host and parasite are widespread and to a great extent sympatric. There may, of course, be competition between different Cuckoo demes. Certain Cuckoo hosts (e.g. the Reed Warbler *Acrocephalus scirpaceus*) that are numerous in Central and W Europe are too rare in N and E Europe to play an important role as hosts. Further, the Cuckoo demes with

superior reproduction (largest number of eggs, highest proportion of fledglings) will probably exclude less productive demes. Features that should make Redstarts favourable hosts are their relatively safe nests (of 37 clutches found at Lemsjöholm during the egg-laying phase, 26 = 70% produced one or more fledglings) and their relatively large clutches (average clutch size, mainly in S Finland = 6.5), which indicate good feeding ability. A less favourable feature is their relatively short breeding season.

#### Length of breeding season of the Redstart

No attempt has been made in the Nordic countries to calculate the number of eggs laid by the Cuckoo. This number will necessarily be restricted by the length of the breeding season of the host. Table 3 shows the commencement of laying in the Redstart.

The first Cuckoo egg found in Finland dates from 19 May. In many years Cuckoos arrive too late to breed as early as this (v. Haartman & Söderholm-Tana 1981). On the other hand, a clutch commenced on 5 June can still be parasitized 5 days later, if the clutch size is 6 (average of June clutches) and if parasitizing may take place on any day during the laying phase of the host. Thus, a scrutiny of Table 3 suggests that a Cuckoo starting about 23 May could continue to lay regularly in Redstart nests until about 10 June. This period is, however, a compound season, including data from a third of a century, and from both early and late years. The single season will inevitably be shorter by several days. This will give the Cuckoo about a fortnight of continuous laying. Cuckoos lay eggs every second day with longer

TABLE 3. Commencement of laying in Redstarts at Lemsjöholm in 1947—80.

Date (May)	No. of clutches	Date (June)	No. of clutches
8	1	1	2
9—14	—	2	2
15	2	3	1
16	—	4	2
17	2	5	1
18	1	6	—
19	2	7	—
20	1	8	1
21	3	9	1
22	5	10	—
23	3	11	1
24	2	12—14	—
25	3	15	1
26	3	16	2
27	1	17	—
28	—	18	2
29	2	19	1
30	2	20—25	—
31	2	26	1

pauses intercalated (Glutz von Blotzheim & Bauer 1980). In some years, a Cuckoo may still be able to lay an egg or two after the main breeding season of the Redstart. Dutch Redstarts are reported by Ruiter (1941) to have a main laying season of 17 days (4—20 May) with a marked peak of 10 days (9—18 May). This was a compound period of four single seasons. Again, the single season will be shorter and will hardly offer the Cuckoo better conditions than at Lemsjöholm. In the Pied Flycatcher, whose breeding season has been thoroughly studied, it is not unusual for 80—97% of the clutches to be commenced within a period of only 11 days (for graphs, see v. Haartman 1956b).

Payne (1973) claimed that his otherwise valuable data on the number of post-breeding follicles (*calyces*, Stieve 1919) in tropical parasitic Cuckoos were also valid in the temperate zone with its incomparably shorter breeding seasons. In a later paper (1974) he accuses me (v. Haartman 1971) of accepting the theory

that clutch size is adjusted to compensate for mortality. This is untrue. I have used the small number of eggs probably laid by the Cuckoo to disprove this very theory. It is often maintained that parasites lay large numbers of eggs to compensate for high mortality in their early developmental stages. If Cuckoos lay numerous eggs, this agrees with the theory, if they lay few eggs, this does not. The chapter on clutch size in my treatise (1971, p. 430) is summarized in its last sentence: "I agree with Lack that there is an overproduction of young. A smaller number would probably be enough to cover the inevitable losses of adult birds".

It is evident that, for instance, the Reed Warbler, the White Wagtail, and the Dunnock *Prunella modularis* have longer breeding seasons than the Redstart (for data see v. Haartman 1969). All these species, in one part or another of Central and W Europe, substitute for the Redstart as the main Cuckoo host.

#### A discussion of the rejector dimorphism in the Redstart

In my Redstart population there was a minority (1—2 pairs out of 8 or 9) rejecting foreign eggs. This situation, odd as it may seem, is not unique. According to Rothstein (1975b), most North American song-birds may be classified as acceptors or ejectors, but a few species are dimorphic. Among certain European song-birds there are indications of dimorphism (Glutz von Blotzheim & Bauer 1980). The Black Redstart *Phoenicurus ochruros*, however, rejects all eggs which are not blue or white and unspotted (op. cit.).

Dimorphism in rejection behaviour may, theoretically, be final or transitory.

*A. Dimorphism as a steady state.* Evolution of egg mimicry in the Cuckoo will start only after egg rejection has evolved among at least some individuals in the host population. There is,

however, a chance that mimicry will then spread more rapidly than rejection. The gene(s) for mimicry are now believed to be situated in the Y-chromosome (Punnett 1933, Ford 1964), promoting rapid evolution. Egg rejection, again, will probably be coded for in the autosomes, provided that it has evolved from ejection of egg shells and/or faecal sacs, behaviour common among male song-birds as well.

Now, if the parasite is the first to reach more or less complete adaptation, the selection pressure upon the host will slacken, and spread of ejector genes will cease. It seems possible, though far from certain, that the dimorphism has arisen in this way.

*B. Transitory dimorphism.* Rothstein (1975b) has shown that ejector dimorphism in American song-birds may be transitory in species only recently parasitized by the Cowbird and still developing a defence. With respect to Cuckoo Redstarts, the opposite could be true. In Finland, the population of both species has decreased strongly. Decrease in host numbers will finally make regular parasitism impossible, removing the selection pressure on the host and allowing it to abandon its antiparasite behaviour.

The decrease of the Cuckoo is not easy to demonstrate precisely as Cuckoos are shy, mobile and relatively rare — a combination of qualities that makes a species a real headache for the census taker. But the information available points to the general conclusion that the population has decreased, especially in W Finland (v. Haartman et al. 1963—72). In my study area there is no doubt about the reality of the decrease. In the diaries of my earlier years there are entries reporting three Cuckoo males heard simultaneously. Today, it is almost sensational to hear

as many as two. Also, older persons living in the area have observed the decrease. A 91-year-old farmer's widow on Palva in Velkua, 5 km from my area, told me that the Corncrake *Crex crex*, the Partridge *Perdix perdix*, the Starling *Sturnus vulgaris* and the Cuckoo had become extinct or rare. A list, testifying to a good memory and an equally remarkable capacity for observation!

The decrease of the Redstart has been easier to follow. Censuses in the archipelago around Lemsjöholm show a steady decline in this species during the last 44 years, now assuming the dimensions of a catastrophe (Fig. 2).

The present rarity of the Redstart in my study area may well have eradicated the Cuckoo deme that is its parasite. With about one Redstart pair per square kilometre, there is not much chance of a female Cuckoo finding enough clutches. The Cuckoos still existing in the area probably mainly parasitize White Wagtails. We even ought to consider the possibility that there never have been any Redstart Cuckoos in this area. Antiparasite Redstart behaviour could have spread here from adjacent areas.

If Redstart rarity has restricted Cuckoo parasitism, egg rejection should be more widespread in Redstarts in other areas. There is no definite evidence of this, but in Latvia Vilks (1972) found a high number of Cuckoo eggs in Redstart nests, most of them mimicking the host eggs. No less than 40 per cent of the Cuckoo eggs lay outside the nest depression. The author assumes that this was the Redstart's way to reject the parasite egg. If so, in a healthy population of Cuckoos and Redstarts, the Redstarts showed powers of discrimination and a frequency of rejection far above those in the dwindling population studied by me.

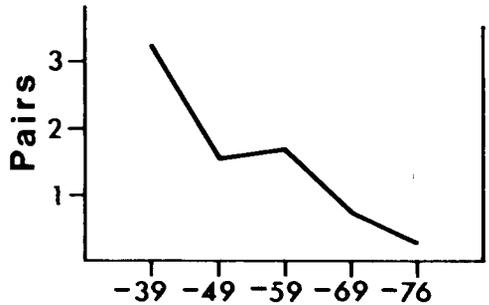


FIG. 2. Decline of the Redstart population in an archipelago in SW Finland. Average yearly numbers of pairs. From v. Haartman (1978). In 1980 not a single pair bred on the islands.

### Selostus: Käen ja sen säännöllisen isäntälajin rinnakkaisevoluutiosta

Leppälinnun suhtautumista sen pesään asetettuihin vieraisiin muniin tutkittiin Askaisten Lempisaaressa 1974—80. Vain 1 tai 2 paria 8—9:stä heitti ulos vieraan munan pöntöstä, yhtä hyvin muninta- ja haudontavaiheessa kuin poikaskaudella (taul. 1). Joka kokeessa muna oli poistettu seuraavaan tarkastuskäyntiin mennessä, yleensä vuorokauden kuluessa. Pääosa leppälinnuista hyväksyi vieraan munan (talitaisen) ja ruokki siitä kuoriutunutta poikasta omiensa joukossa lentokykyiseksi asti.

Leppälinnuilla loisiva käkityyppi on yleinen Neuvostoliiton Euroopan puoleisessa osassa, Suomessa ja osassa Skandinaviaa (kuva 1). Syynä tämän tyypin harvinaisuuteen Keski- ja Länsi-Euroopassa saattaa olla kilpailu sellaisten käkityyppien kanssa, jotka käyttävät isäntänä pitempään pesiviä lajeja ja pystyvät näin tuottamaan enemmän muniä. Suomessa leppälinnun pesimäkauti mahdollistaa käen säännöllisen loismuninnan noin kahden viikon ajan (taul. 3), minkä jälkeen siihen on enää harvoin tilaisuuksia.

Leppälintujen kahdenlaisen reaktion taustaa pohditaan. Yksi mahdollisuus on se, että käytäytymisen dimorfismi olisi pysyvä tilanne: käen muna on sopeutunut niin täydellisesti isäntälinnun munien ulkonäköön, ettei valinta enää pysty yleistämään vieraiden munien ulosheittämismisreaktiota. Toinen vaihtoehto on, että dimorfismi olisi seurausta leppälinnun viimeaikaisesta jyrkästä vähentymisestä (kuva 2), mikä olisi johtamassa tähän lajiin kohdistuvan loispesinnän käymiseen kannattamattomaksi ja siten vieraiden munien poistamista suosivan valinnan heikentymiseen. Myös käki on harvinaistunut tutkimusalueella, ja jäljellä oleva kanta loisi luultavasti pääasiassa västäräkin pesissä.

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