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Should the redstart *Phoenicurus phoenicurus* accept or reject cuckoo *Cuculus canorus* eggs?

Abstract Hole-nesting habits of redstarts *Phoenicurus phoenicurus* make laying difficult for parasitic cuckoo *Cuculus canorus* females and eviction of host eggs difficult for the cuckoo hatchling, causing fitness costs of cuckoo parasitism to be lower than those reported for open nesting hosts. Redstarts have recognition problems when confronted with real cuckoo eggs showing a perfect mimicry with their own eggs since they never eject when parasitized with perfect mimetic cuckoo eggs but instead desert the nest. Here we use a cost-benefit model to assess the effects of parasitism costs and the probability of being parasitized to estimate the reproductive success of redstarts when accepting or rejecting in the presence or absence of parasitism. Baseline data for model calculations come from this and a previous study on a cuckoo parasitized redstart population in Finland. When desertion implies a loss of 50%, we found that below a threshold value of 20% parasitism redstarts should accept cuckoo eggs since the costs of rejection exceed the benefits, whereas above this threshold they should reject. Interestingly, as the cost of desertion increases the threshold value, it should pay the redstart to reject increasingly at an exponential rate. Our field observations on natural parasitism and experiments with artificial cuckoo eggs confirmed the predictions from the model when hatching failures of the cuckoo were taken into account. Therefore, the low cost imposed by cuckoo parasitism in the system, and the presumably high cost of desertion as a response to parasitism favours acceptance over rejection for a wide range of parasitism pressures. This finding could explain the low rejection rate of real cuckoo eggs found in the redstart despite the presumably long history of a coevolutionary relationship with the cuckoo in Finland.

Keywords Common cuckoo · Cost-benefit model · Hole nesting · Recognition errors · Redstart

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Introduction

Recognition and rejection of parasitic eggs is the most common and effective host defence against interspecific brood parasitism in birds (Rothstein 1990). The evolutionary origin of this defensive mechanism is the high fitness losses suffered by hosts when successfully parasitized by cuckoos (Payne 1977a, b; May and Robinson 1985; Røskaft et al. 1990). Egg rejection protects host chicks from competition with the parasite chick or from being evicted, and it consequently has a high selective advantage. Therefore, rejection should rapidly increase in frequency if genes coding for it are present when a population is parasitized (Rothstein 1975a; Kelly 1987).

The absence of rejection behaviour may be due to an evolutionary lag in the development of defensive mechanisms by the host (e.g. Rothstein 1975b; Dawkins and Krebs 1979; Davies and Brooke 1988; Moksnes et al. 1990; Hoover 2003). Lag may be due to an absence of genetic variants (Rothstein 1975a) or to the time it takes for it to spread in a host population (Kelly 1987). Alternatively, it has been proposed that rejection of parasitic eggs may be costly for hosts (Davies and Brooke 1988; Marchetti 1992), and that such costs may sometimes exceed the benefits of rejection. Acceptance of the cuckoo egg might be adaptive

according to this scenario (Zahavi 1979; Rohwer and Spaw 1988; Lotem et al. 1992, 1995; Brooker and Brooker 1996; Lotem and Nakamura 1998).

Several studies have focused on factors affecting the proneness of hosts to reject parasitic eggs (reviewed in Davies 2000). Host discrimination of foreign eggs is crucial before taking a rejection decision. It has been suggested that hosts may learn how their eggs look like and recognize those with an appearance different from that of their own eggs (Victoria 1972; Rothstein 1975c; Lotem et al. 1992). Studies of natural cuckoo parasitism and experiments on parasitism have shown that the probability of rejection of cuckoo eggs is higher when the level of mimicry between cuckoo egg and host egg is poor (e.g. Davies and Brooke 1989a; Soler and Møller 1990; Moksnes et al. 1993; Moskát and Honza 2002; Rutila et al. 2002). However, hosts sometimes accept the cuckoo egg even when mimicry is poor (e.g. Davies and Brooke 1989a; Soler and Møller 1990; Moksnes et al. 1993; Rutila et al. 2002). Moreover, some experiments in which a stuffed cuckoo has been presented at host nests have shown an increase in the frequency of rejection (e.g. Davies and Brooke 1988; Moksnes et al. 1993), suggesting that other cues than appearance of cuckoo eggs are being considered by hosts, when rejecting a cuckoo egg.

Once the host has recognized the parasitic egg, the costs caused by the parasite and those of rejecting the cuckoo egg may influence the payoff of rejection. When parasites lay their eggs in the nest of a host, they usually cause laying damage (by removal, pecking or accidental breakage of host eggs), these costs varying among host and parasite species (e.g. Payne 1977a, b; Wyllie 1981; Soler 1990). In addition, if the host accepts the parasite egg, it may suffer a loss in reproductive success because of successful parasitism (parasitism costs). These costs usually range from the loss of the entire clutch of the host, when the cuckoo chick evicts all host eggs, to no cost at all (Payne 1977a, b). Alternatively, if the host rejects, it faces two main costs that might reduce the payoff of this decision. First, rejection costs occur when a rejecter individual accidentally breaks some of its own eggs when trying to eject the cuckoo egg, or when the host deserts the nest in response to the parasitic egg, because it is unable to evict it (*sensu* Davies et al. 1996). Second, recognition errors occur when a host erroneously rejects one of its own eggs instead of the parasite egg, or when it deserts a nest because it is unable to recognize the parasite egg (*sensu* Davies et al. 1996; for a different definition, see Røskaft et al. 2002). Costs by recognition errors at unparasitized nests are the only kind of costs that are able to counteract the benefits of rejection for common cuckoo host (Davies et al. 1996; Lotem and Nakamura 1998). Finally, the host may base its rejection decision on its perception of the risk of being parasitized (Davies and Brooke 1988; Moksnes et al. 1993), since the probability of parasitism determines the occurrence of parasitism and rejection costs (Davies and Brooke 1989b; Takasu et al. 1993; Lotem et al. 1995; Davies et al. 1996; Lotem and Nakamura 1998).

Here, we study a redstart *Phoenicurus phoenicurus* population that is currently being parasitized by the common cuckoo *Cuculus canorus* in Finland. The redstart is the only hole-nesting passerine that is a suitable host of the cuckoo in Europe (Moksnes and Røskaft 1995), and it is being parasitized in Finland by a cuckoo race laying blue eggs that perfectly mimic redstart eggs as assessed by the human eye (Rutila et al. 2002). In addition, our own analyses based on ultraviolet visible spectrophotometry reveal a consistent colour matching between cuckoo and redstart eggs both in the ultraviolet and the human visible regions of the spectra (JM Avilés and AP Møller unpublished), suggesting that birds may also perceive a high degree of mimicry in this cuckoo–host system. Also, rejection of non-mimetic cuckoo eggs by redstarts has been widely reported in Fennoscandia (von Haartman 1976, 1981; Järvinen 1984; Rutila et al. 2002, 2005), suggesting that redstarts and cuckoos are involved in a long-term coevolutionary relationship in this region. The hole-nesting habits of redstarts make laying difficult for parasitic cuckoo females and eviction of host eggs difficult for the cuckoo hatchling, causing fitness costs of cuckoo parasitism to be lower than those reported for open nesting hosts (Rutila et al. 2002). Therefore, the expected payoff of a rejection decision for hole-nesting redstarts may differ from that for open nesting hosts. Here we explore this possibility by using a cost-benefit model to use the cost of parasitism and rejection, and the probability of being parasitized to estimate reproductive success of the redstart from acceptance and rejection. Similar approaches have previously been used to explain rejection behaviour among open nesting hosts of the common cuckoo (e.g. Davies and Brooke 1989b; Davies et al. 1996; Lotem and Nakamura 1998; Lindholm 1999; Røskaft and Moksnes 1998), but overlooked the importance of cuckoos' laying and hatching failures in their calculations. This is the first study in which the dynamic of a hole-nesting cuckoo host has been modelled and cuckoo failures at laying and hatching have been taken into account.

Methods

Logic of the model

We consider that a host may behave as accepter or rejecter and its nest may be either parasitized or not. Consequently, a redstart nest belongs to any of the following four situations: (1) acceptor parasitized by a cuckoo; (2) acceptor not parasitized by a cuckoo; (3) rejecter parasitized by a cuckoo; or (4) rejecters not parasitized by a cuckoo (Table 1). Each of these four situations has different fitness consequences for redstarts leading respectively to the payoffs A, B, C and D (Table 1).

If we consider p to be the probability that a redstart nest is parasitized by a cuckoo, then $(1-p)$ is the probability of a redstart not being parasitized. The payoff from acceptance is then given by $P_a = p(A) + (1-p)(B)$ and from rejection by $P_r = p(C) + (1-p)(D)$.

Since we are mainly interested in knowing the probability of parasitism that determines the host strategy against cuckoo parasitism that is stable, we can set the two payoffs equal to each other and calculate the value of p above which

Table 1 Outcome (number of eggs producing fledglings) resulting from host decisions to accept or reject in parasitized and unparasitized redstart nests. A redstart nest belongs to either of the four situations: (A) Acceptor parasitized by a cuckoo; (B) acceptor not parasitized by a cuckoo; (C) rejecter parasitized by a cuckoo; or (D) rejecters not parasitized by a cuckoo. Each of these four situations has different fitness consequences for redstarts since costs of parasitism and rejection vary

Host decision	Nest	
	Unparasitized (six redstart eggs)	Parasitized (six redstart eggs + one cuckoo egg)
Accept	6.00 (B)	2.12 (A)
Reject	5.77[1] (D)	3.00[1] (C)
	5.89[2] (D)	4.50[2] (C)

A, B, C and D are the corresponding payoffs for these situations. The superscripts [1] and [2] apply to the 50 and 25% loss scenarios respectively. Payoff calculations are based on values reported in Table 2

it should pay to reject.
Then

$$p = 1/\{[(C - A)/(B - D)] + 1\} \qquad (1)$$

We can define

$$[(C - A)/(B - D)] = X \qquad (2)$$

Then we can simplify Eq. (1) to

$$p = 1/(X + 1) \qquad (3)$$

By knowing the payoff for each of the four possible situations in which a redstart may be involved, we can identify the fitness consequences of rejecting a cuckoo egg at different parasitism pressures.

Sources of data

Information that we use for our calculations is summarized in Table 2 and comes from a previous study on the relationship between the redstart and the cuckoo in an old forest of Scots pine (*Pinus sylvestris*) in North Karelia (see Rutila et al. (2002)) and from additional unpublished experiments performed in the same area in 2002 (Table 2).

Natural holes are scarce in this forest. Therefore, rejection behaviour of cuckoo eggs by redstarts was studied using specially designed nest-boxes. They are situated 1.5–1.8 m above ground at a similar height to that reported for natural redstart nests (Cramp and Perrins 1994). Although some open nesting attempts have been reported (Pulliainen and Saari 2002), most suitable natural nesting sites for redstarts

Table 2 Assumptions of the model and values used for payoff calculations in Table 1. Sample size and source of data are also provided. The numbers in brackets in the first column refer to the order in which assumptions are cited in the methods section

Assumption	Value used for calculations	Sample size and source of data
(1) Redstart median clutch size is six eggs	6	196 nests (Rutila et al. 2002)
(2) Predation equally affects parasitized and unparasitized redstart nests	–	196 nests (Rutila unpublished)
(3) Rejection is always by desertion	–	97 naturally parasitized nests (Rutila et al. 2002), 26 experimentally parasitized nests with cuckoo egg (J Rutila unpublished)
(4) Cuckoo eggs found outside the next-boxes are inaccurately laid	–	26 redstart nests artificially parasitized with natural cuckoo eggs (present study)
(5) Desertion is linked to cuckoo parasitism	–	143 unparasitized nests (Rutila et al. 2002, 2005) 54 naturally parasitized nests (Rutila et al. 2002) 77 artificially parasitized nests (Rutila et al. 2002, present study)
(6) Desertion implies a continuous variable cost from 0 to 100	0–100	
(7) Effective parasitism in the system is 0.34 × percentage of redstart nests with a cuckoo egg	0.34 ×% of parasitized nests	102 cuckoo eggs (Rutila et al. 2002)
(8) Proneness for rejection does not vary with season	–	54 nests (present study)
(9) Cuckoos do not remove host eggs when laying	0	10 nests (Rutila unpublished)
(10) Some cuckoo eggs laid fail to hatch	10.3%	39 cuckoo eggs (Rutila et al. 2002)
(11) Some cuckoo chicks are unable to evict host offspring	41.0%	39 cuckoo eggs (Rutila et al. 2002)
(12) Some cuckoo chicks successfully evict host offspring	48.7%	39 cuckoo eggs (Rutila et al. 2002)
(13) Some host eggs are lost when cuckoo chicks are unable to evict host offspring	38.3%	16 nests (Rutila et al. 2002)
(14) Desertion occurs at unparasitized nests due to recognition errors	7.9%	143 unparasitized nests (Rutila et al. 2002)
(15) Rejection costs are negligible	0	14 ejectors pairs (Rutila et al. 2002, present study)

in Finland are holes made by three-toed woodpecker *Picoides tridactylus* and great spotted woodpecker *Dendrocopos major* (Pulliainen and Saari 2002). Mean cavity size of holes used by redstarts in nature was rather similar to that of our nest-boxes (nest-boxes: 100 mm × 130 mm × 250 mm vs. 100–125 mm × 100 mm–125 mm × 200 mm–300 mm for three-toed woodpecker nests and 125 mm × 125 mm × 300 mm for great spotted woodpecker nests (Pulliainen and Saari 2002; Harrison and Castell 2002)). In addition, mean size of the entrance hole of nest boxes was slightly larger than those reported for natural redstart nests (77.0 mm in our nest-boxes vs. 25–40 mm in three-toed woodpecker nests and 56 mm in great spotted woodpecker nests (Pulliainen and Saari 2002; Harrison and Castell 2002)). Hence, we can reasonably assume that a cuckoo female can remove host eggs and lay, and that the cuckoo nestling can eject with similar ease at natural holes and our nest-boxes.

Redstarts in North Karelia usually lay six or seven eggs (mean = 6.66, SD = 0.95, range 3–8 eggs, Rutila unpublished). The female usually starts to incubate after laying the last egg, being fed by the male during the incubation stage (Cramp and Perrins 1994). Redstarts in North Karelia are typically used as a host by the cuckoo (mean parasitism rate = 20.0% (Rutila et al. 2002)), and they reject model cuckoo eggs (rejection rate = 26.4%, Rutila et al. 2002).

Assumptions and peculiarities of the redstart–cuckoo system

We measure redstart fitness to equal the number of their eggs producing fledglings, and we assume that clutch size of the redstart is six eggs since this is the modal clutch size in our population (Table 2, assumption 1).

To simplify the analysis we assume that predation equally affects parasitized and unparasitized clutches (see also Davies et al. 1996). We believe that this is justified since no differential predation linked to occurrence of natural parasitism has been revealed in our population (Table 2, assumption 2).

We assume in our analyses that all rejections were by desertion. This is justified by the fact that no ejection was reported in naturally parasitized redstart nests, or in redstart nests artificially parasitized with natural cuckoo eggs (Table 2, assumption 3). It is important to mention that some cuckoo eggs were found on the ground or outside the nest-cup (Rutila et al. 2002). Evidence suggests that these eggs were not ejected by redstarts, but inaccurately laid by cuckoo females (Table 2, assumption 4). We have tested this assumption by experimentally introducing natural cuckoo eggs into 26 redstart nests and checking host response. No ejection was recorded, and, more importantly, no cuckoo egg was found outside the nest cup or on the ground (present study). Second, in our study area cuckoo eggs were sporadically found outside the nest-cup of a non-rejecter species, the pied flycatcher *Ficedula hypoleuca*, and outside the nest-box of unoccupied redstart nests (Rutila unpublished).

A major assumption of our model is that desertion is linked to cuckoo parasitism in the redstart (Table 2, assumption 5). Evidence that desertion of nests is a specific host response to cuckoo parasitism may be provided if desertion occurred more often at parasitized than unparasitized nests. Redstarts deserted 6 (12.5%) of the 54 artificially parasitized nests in the present study, whereas no desertion was reported in 10 unparasitized control nests by Rutila et al. (2002). Furthermore, in a 500 km north of Joensuu redstart population in Rovaniemi, we reported a similar pattern since desertion did not occur at a control group of 7 nests but was frequent in artificially parasitized nests (8 of 23 nests deserted, Rutila et al. 2005). Finally, 13% of 54 naturally parasitized redstarts deserted their nests, whereas natural desertion of unparasitized nests just occurred in 7.9% of cases ($N=126$, Rutila et al. 2002). Since we were interested in knowing whether nest desertion was effectively induced by brood parasitism, we pooled all the above 274 nests and classified them with respect to desertion (deserted vs. non-deserted, Factor 1), type of parasitism (natural vs. artificial, Factor 2) and occurrence of parasitism (parasitized vs. non-parasitized, Factor 3) and performed log-linear models (Sokal and Rohlf 1995). Specifically, we tested a model that hypothesizes independence between occurrence of desertion and occurrence of parasitism in each nest (Model 1,3; StatSoft 1998). The analysis revealed that the occurrence of parasitism predicts the occurrence of desertion in the redstart (three-factor log-linear analysis, $\chi_5^2 = 103.05$, $P<0.001$). Moreover, to estimate expected frequencies from the null hypothesis, we should also take into account whether nests were tested with natural or artificial cuckoo eggs. Thus, we introduced the factor type of parasitism (Factor 2) and tested the model 12,3 (StatSoft 1998) and found that the results remained when controlling for kind of parasitism (three-factor log-linear analysis, $\chi_3^2 = 74.09$, $P<0.001$). Thus, we can reasonably assume that desertion is a specific response to brood parasitism in our system irrespective of whether nests were naturally or artificially parasitized.

A critical parameter in our model is the cost of nest desertion. Deserting a nest may often incur a cost resulting from the loss of time and energy, smaller clutch size and lower fledgling survival during re-nesting (Rohwer and Spaw 1988; Davies and Brooke 1989b; Lotem and Nakamura 1998). Redstarts may re-nest after the loss of a first clutch (personal observation), although we have no quantitative estimates, nor does the literature provide then. Hence, we estimate the expected payoff of a rejecter individual for a continuous range of desertion costs (Table 2, assumption 6).

We consider parasitism rate to be the number of nests with cuckoo eggs irrespective of hatching success. However, Rutila et al. (2002) have documented that just 35 of 102 (34.4%) cuckoo eggs laid in Finland hatched. Therefore, we calculated an effective parasitism rate to be $0.344 \times$ parasitism rate when analyzing the fit of the model predictions to our data (Table 2, assumption 7). The use of effective parasitism rate accounted for loss of cuckoo eggs and thus provided us with a more reliable estimate of cuckoo parasitism pressure in our population.

Because cost of desertion may increase with season due to a lower chance of re-nesting, we would expect desertion to occur more readily early in the season. To test this possibility, responses to artificial cuckoo parasitism were studied in 54 nests found at different stages of building and artificially parasitized with non-mimetic cuckoo eggs (Table 2). The model eggs used in this new experiment were the same as previously described by Rutila et al. (2002). Since the cuckoo always parasitizes the redstart during the laying period and rarely removes a redstart egg, we added experimental eggs to redstart nests at the four eggs stage, and we did not remove any host eggs. All nests were checked every second day and response to parasitism was finally assessed 6 days from artificial parasitism as rejection (eggs ejected or nest deserted) or acceptance of parasitic eggs (all others). Because it is possible that small puncture-ejectors such as the redstart attempt to eject artificial eggs, but they cannot do so because they are made of plaster of Paris, we checked accepted artificial eggs for peck marks. We failed to find peck marks on any of the accepted artificial cuckoo eggs in this study, and hence rejection frequency was not underestimated by using artificial eggs. We performed a logistic regression analysis with response to artificial parasitism (rejection vs. acceptation) as the dependent variable and laying time as the independent variable. Analysis failed to reveal seasonal trends in rejection behaviour by the redstart (mean data $\pm$ SD = 15.35$\pm$11.11 (where 1=1 June) in acceptors vs. 16.80$\pm$12.44 in rejecters, logistic regression: χ^2=0.02, df=1, P=0.88); hence, we can reasonably assume that our results are not affected by differential costs of rejection during the season (Table 2, assumption 8).

Costs of parasitism

Laying damage

The common cuckoo usually removes one egg as a minimum while laying when parasitizing open nesting hosts (e.g. Wyllie 1981). However, host egg numbering and daily monitoring of nests revealed that laying damages seemed to be negligible in the redstart–cuckoo system since in the 10 cases in which natural parasitism has been reported during the laying period of the redstart, no losses of host eggs were reported after a cuckoo visit (Table 2, assumption 9). We think that the absence of egg removal is due to difficulties for the cuckoo when laying in holes, causing a reduction in the benefits of removing host eggs because it would increase the duration of laying, we have no data, however, to evaluate this assumption.

Losses caused by the cuckoo nestling

When hatching in an open nest common cuckoo chicks usually evict all host eggs or chicks, reducing the payoff of a parasitized acceptor host to zero (e.g. Wyllie 1981; Cramp 1985). However, Rutila et al. (2002) have revealed that eviction of a redstart egg or chick from a hole is more difficult for a cuckoo hatchling than eviction from an open nest. Four (10.3%) of 39 cuckoo eggs found inside the redstart's nest failed to hatch. When hatching, 16 out of 35 cuckoo chicks (41.0% of the total number of cuckoo eggs) were unable to evict all foster siblings. In these cases redstarts still succeeded in raising a mean of 3.7 fledglings of their own, which represented a loss of 38.3% of eggs laid by the redstart assuming the modal clutch size of six eggs. The remaining 19 cuckoo eggs (48.7%) hatched and the nestlings successfully evicted the nest mates (Table 2, assumptions 10, 11, 12 and 13).

Costs of rejection

Recognition errors

Recognition errors are expected to be larger when hosts are being parasitized with cuckoo eggs that perfectly mimic host eggs (Davies et al. 1996). However, Rutila et al. (2002) report for 26 experiments using mimetic blue eggs one ejection without egg loss by the host.

Desertion may also be attributed to recognition problems when hosts are aware of being parasitized, but unable to recognize parasite eggs. Rate of desertion in the redstart is unrelated to level of mimicry between artificial cuckoo eggs and host eggs (Rutila et al. 2002). However, artificial mimetic blue eggs may show a poor level of mimicry with host eggs compared to natural cuckoo eggs. With perfect mimicry the best option for the redstart should be to desert (rather than eject an egg at random) and start re-laying. Accordingly, ejection was not reported in 97 naturally parasitized redstart nests (Rutila et al. 2002). However, naturally parasitized redstart pairs deserted more frequently than unparasitized redstart pairs (13% vs. 7.9%, see above). The fact that redstarts desert more, when it is naturally parasitized, suggests that they do have recognition problems (otherwise they should eject as a defense since it is not costly (see below)).

For unparasitized nests we were interested in the payoff for a redstart that assesses that it is parasitized, but, in fact, there is no cuckoo there ('False alarm', Davies et al. 1996). This situation may be simulated in nature by showing the hosts a cuckoo, without adding a cuckoo egg, and investigating rejection of host eggs at unparasitized nests without exposure to the cuckoo. Although theoretically intuitive, this approach may be heuristically unsuitable due to the often low rejection rate of mimetic egg by hosts which makes a sufficient number of experiments difficult to perform to detect small effect sizes as the expected for such a comparison (see for instance Davies et al. 1996). Here we assume that all desertion of unparasitized nests was caused by a 'false alarm' (Table 2, assumption 14). We believe this is valid since cuckoos are commonly present in North Karelia since at least 1984 (Rutila et al. 2002), which should increase proneness of redstarts to reject cuckoo eggs. This assumption makes the model somewhat more conservative in predicting the threshold for rejection (i.e. it makes rejection less likely to be adaptive). However,

since the desertion rate was extremely low at unparasitized nests, even when it presumably yielded the effect of other factors that may potentially induce desertion (i.e. disturbance and predation of adults), we assumed that it has a negligible effect on the threshold for rejection. Hence, for our calculation we used 7.9% as the desertion rate of unparasitized nests due to recognition errors.

Rejection costs

Rutila et al. (2002) reported 12 ejections of artificial cuckoo eggs in which no damage to redstart eggs occurred. Moreover, in two of eight rejections reported in this study ejection occurred, but no costs of ejection were recorded in terms of damage to redstart eggs. Therefore, rejection costs are considered to be negligible (Table 2, assumption 15), since we failed to detect any by using artificial cuckoo eggs that overestimates real rejection costs of ejecting the less heavy cuckoo eggs (Martín-Vivaldi et al. 2002).

Results

Fitness consequences of redstart strategies against parasitism

Redstarts as acceptors

If the redstart is an acceptor, it may face two situations. If the nest is not parasitized, the host obtains the reproductive success from six eggs, since this is the modal clutch size in our population (Table 1). However, if it is parasitized, the nest contains seven eggs, six of the redstart plus the cuckoo egg, since the cuckoo never replaces a host egg by its own (see above). Hence, if it is parasitized, we have to consider hatching failures of the cuckoo. In addition, losses of reproductive success by the redstart are caused by cuckoo parasitism due to the cuckoo nestling evicting its nest mates, and due to the cuckoo chick being raised with the host chicks (Table 2). Consequently, the payoff of an acceptor redstart when parasitized should be $0.103(6)+0.410(6-(6\times0.383))+0.487(0)=2.12$ (Table 1).

Redstarts as rejecters

A rejecting host faces two possible situations. First, if the redstart is parasitized, we should consider that redstarts always reject a parasitized nest by deserting the nest (Table 2). Consequently, the payoff should be $[(6)-(6\times \text{cost of desertion})]$. Thus, if we assume that desertion implies a loss of 50%, the expected payoff should be $[(6)-(6\times0.5)=3]$, and it should be $[(6)-(6\times0.25)=4.5]$, if the loss by desertion is of 25% (Table 1).

Second, if the nest is not parasitized, redstarts desert 7.9% of their nests (Table 2). Thus the payoff should be $0.079(6-(6\times0.5)+0.921(6)=5.77$, if losses by desertion are of 50%, and $0.079(6-(6\times0.25)+0.921(6)=5.89$, if losses by desertion are of 25% (Table 1). Note that for heuristic purposes

Table 1 only includes payoff calculations corresponding to the 25 and 50% loss scenarios. However, in Fig. 2 we provide calculations for a range of desertion costs from zero to 60%.

### Effect of the probability of cuckoo parasitism

Next, we summarize the expected payoff for each of the four possible situations in which a redstart may be involved (Table 1). If we substitute the corresponding payoffs in Eq. (2), we get $X=[(4.50-2.12)/(6-5.89)]=21.63$, so the critical value of p is $1/(21.63+1)=0.044$ when desertion implies a loss of 25%. However, we get a value of $X=[(3.00-2.12)/(6-5.77)]=3.82$, and thus the critical value of p is $1/(3.82+1)=0.20$ when desertion implies a loss of 50%.

In Fig. 1 we show the fitness consequence of acceptance and rejection for redstarts at different probabilities of cuckoo parasitism, assuming that desertion implies respectively a loss of 50 and 25% of a redstart clutch. The higher the probability of a redstart nest being parasitized, the more prone it is to reject the cuckoo egg (Fig. 1). In addition, a lower cost of desertion makes rejection more stable than acceptance at a lower rate of parasitism (Fig. 1).

In Fig. 2 we solve the above calculations and plot the critical value of p for a continuous range of desertion costs. Interestingly, as the cost of desertion increases the threshold value of p above which it should pay the redstart to reject increases exponentially (Fig. 2). Thus, when the cost of desertion is low, variation in the cost of desertion has a low
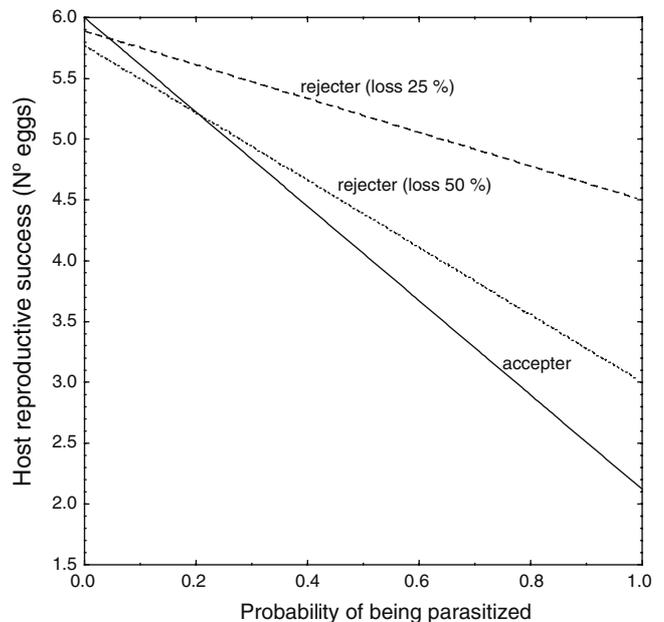
Fig. 1 Reproductive success of redstarts (number of eggs producing fledglings) after accepting (*solid line*) or rejecting (*discontinuous line*) a cuckoo egg at different probabilities of cuckoo parasitism, assuming the payoff in Table 1. The *lower discontinuous line* assumes that desertion implies a loss of 50% of fitness for the redstart whereas the *upper discontinuous line* assumes that desertion implies a loss of 25% of fitness for the redstart (see text for explanations)
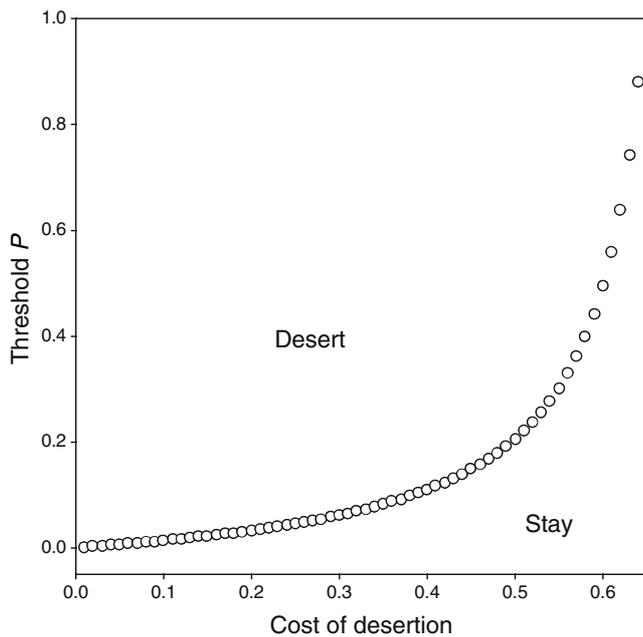
Fig. 2 The critical probability of parasitism, *p*, above which it pays the redstart to reject and below which it pays to accept as a function of the cost of desertion (see text for calculations)

impact on the critical probability of parasitism *p* (Fig. 2). Instead, as desertion costs increase, variation in desertion cost has a major influence on the threshold probability of parasitism (Fig. 2).

Fit of the model

Parasitism rate estimated as the number of nests with cuckoo eggs in our study population varied among years from 0.0% in 1985 and 1997 to 55.9% in 1995 (Fig. 3; Rutila et al. (2002)). Generally these rates fall below the estimated threshold of 0.20 for rejection, assuming a cost of desertion of 50% (Fig. 3). However, if we consider cuckoo failures, effective parasitism rates are consistently below this threshold (Fig. 3). This fits with the observation that most mimetic model eggs (92.3%, Rutila et al. 2002) and real cuckoo eggs were accepted (87%, Rutila et al. 2002).

Discussion

A main prediction arising from the signal detection model applied to avian brood parasitism is that if the parasite evolves perfect mimicry so that the appearance of eggs of host and parasite overlaps completely, then the best rejection behaviour is to desert rather than eject at random (Davies et al. 1996). Here we test this prediction by using the redstart–cuckoo system in which the parasite has evolved a perfect mimetic egg as judged by human and bird vision. In accordance with the prediction, we found that naturally parasitized redstart nests are deserted at higher rates than unparasitized nests (Table 2). Moreover, we failed to demonstrate ejection of cuckoo eggs in naturally
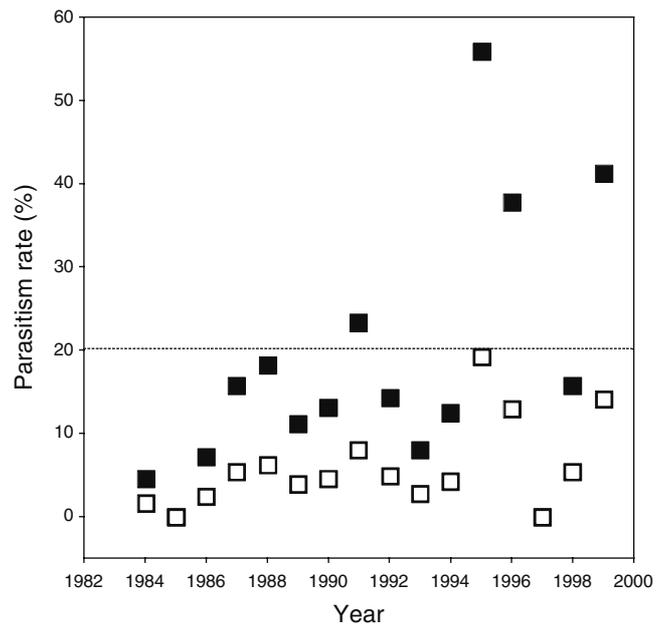
Fig. 3 Parasitism rate (percentage of redstart nests with a cuckoo egg, *filled symbols*) and effective parasitism rate (percentage of redstart nests with a cuckoo egg × proportion of hatched cuckoo eggs causing a cost; *open symbols*) during 1984–1999. The use of effective parasitism rate accounted for loss of cuckoo eggs and thus provided us with a more reliable estimate of cuckoo parasitism pressure. The *dashed line* assumes the payoff in Table 1 and represents the parasitism thresholds above which it should pay the redstart to reject, if desertion implies a loss of 50% of fitness for the redstart

parasitized redstart nests, although ejection was frequent when redstart nests were parasitized with artificial model eggs that showed a poorer degree of mimicry with host eggs than real cuckoo eggs (Rutila et al. 2002). Therefore, current evidence suggests that redstarts in Finland have recognition problems when attempting to identify natural cuckoo parasitism, and that they prefer to desert their nests rather than eject.

Several theoretical studies have proposed that the costs of recognition errors are the only ones that may counteract the benefits of rejection and thereby explain equilibrium stages in the coevolutionary arms race between hosts and parasites (Davies et al. 1996; Lotem and Nakamura 1998). Therefore, hosts should behave differently when confronted with different risks of being parasitized, since the probability of suffering parasitism should determine the costs and benefits of rejection as compared to acceptance (Davies and Brooke 1989b; Takasu et al. 1993; Lotem et al. 1995; Davies et al. 1996; Lotem and Nakamura 1998; Rodríguez-Gironés and Lotem 1999). Here we have assessed the costs of parasitism and rejection in the redstart–cuckoo system. We found that reproductive success of the redstart from acceptance and rejection depended on the probability of parasitism. Our field observations on natural parasitism and experiments with artificial mimetic cuckoo eggs confirmed the predictions from the model when hatching failures of the cuckoo were taken into account. Hence, the low costs imposed by cuckoo parasitism in the system, and the presumably high cost of deserting a redstart nest as a response to cuckoo

parasitism makes acceptance a better choice than rejection for a wide range of parasitism pressures. This fits well with the fact that most of redstarts accepted cuckoo parasitism despite the presumably long-time interaction between redstarts and cuckoos in the region.

The existence of reproductive failures in the cuckoo is an important peculiarity of the redstart–cuckoo system that may prevent parasitism from reaching the threshold probability p that benefits the host by changing its behaviour to rejection. This finding agrees with the fact that all studies in which rejection behaviour of the redstart was tested reported rejection levels below 50% (Davies and Brooke 1989a; Moksnes et al. 1990; von Haartman 1981; Järvinen 1984; Rutila et al. 2002). Previous theoretical models based on open nesting hosts in which host reproductive outcome from acceptance and rejection were calculated assumed that all cuckoo eggs were successful. Interestingly, Rutila et al. (2002) found that just one in three cuckoo eggs laid within the cup of a redstart nest caused any cost. Consequently, the sight of an odd-looking egg may not be a reliable signal of costly cuckoo parasitism for a redstart, since there is a large probability that this foreign egg is unsuccessful. Cuckoo reproductive failures were due to (i) eggs laid outside the nest cup, (ii) cuckoo chicks being unable to evict nest-mates from the nest, and (iii) cuckoo eggs failing to hatch (Rutila et al. 2002). The two first causes of cuckoo failure are due to nesting habits of the redstart making it difficult for the cuckoo to lay eggs in the nest of the host and for the cuckoo to eject host eggs and nestlings (Rutila et al. 2002). However, 10.3% of cuckoo eggs laid in the nest cup still failed to hatch in this system without any apparent causal link to the kind of nests used by host. Information on hatching failures of cuckoo eggs when parasitizing open nesting hosts is rare. Wyllie (1981) reported that just 4 out of 176 (2.27%) cuckoo eggs laid in the nests of the reed warbler *Acrocephalus scirpaceus* failed to hatch. However, future studies modeling cuckoo–host interactions should assess to what extent cuckoo failures may determine the outcome of the interaction between cuckoos and their hosts.

The threshold p value above which it pays redstarts to reject was also influenced by the existence of desertion costs: As costs of deserting a redstart clutch increase, the threshold value of p increases exponentially favouring acceptance of cuckoo parasitism (Fig. 2). The incidence of cuckoo parasitism in our population during the last 15 years was around 20% (Rutila et al. 2002). Assuming this parasitism rate, and following the calculations from the model, it would pay a redstart to reject a cuckoo egg only when the costs of desertion are less than 50% (Fig. 2). However, when desertion implies a loss exceeding 50%, a more stable strategy for the redstart would be to accept cuckoo parasitism. A major goal should be to determine whether it is high desertion costs and/or the low parasitism pressure that determine the redstarts' acceptance of natural cuckoo parasitism in our population. We cannot definitively preclude either of these two possibilities, but we have obtained tentative support for the hypothesis that the high cost of desertion could play a major role in this host. First, a study of the meadow pipit *Anthus pratensis* at a similar latitude has revealed that deserting a nests often implies a total loss due to the short time period available for breeding (Moksnes et al. 1993). Second, as the parasitism rates reported in Rutila et al. (2002) did not account for the low breeding success of the cuckoo, the cost of desertion should presumably exceed 50% to arrive at the current situation in which most redstarts in our population are accepters.

The low costs of parasitism reported in the redstart–cuckoo system as compared to other species parasitized by the cuckoo are expected to reduce the selective advantage of rejection. Surprisingly, the level of mimicry between cuckoo and host eggs is nearly perfect. How did mimicry evolve in this system, if the costs of parasitism are so low? At least three possible explanations exist. Firstly, redstarts and cuckoos may have experienced a long-lasting coevolutionary relation, and mimicry has evolved very slowly since costs of parasitism and levels of rejection are very low. Second, the appearance of cuckoo eggs may not have evolved because of redstart rejection behaviour, and similarity between host and parasite eggs may simply be due to chance. Third, the low costs of parasitism described here may be a consequence of recent adaptation by redstarts to reduce such costs. This adaptation would make the redstart the current winner in the evolutionary arms race against the cuckoo.

According to the first explanation, perfect mimicry evolved after a very long time of coevolution between cuckoo and redstart. Theoretical studies have shown that parasitism rate has a major influence on the speed at which rejection and mimicry evolve, with low parasitism pressures delaying the evolution of these traits (Kelly 1987). The average parasitism rate in our population was 20% (Rutila et al. 2002). However, the realized parasitism rate may well be below 10%, since we detected a very high proportion of cuckoo hatching failures and problems for cuckoo chicks of evicting redstart eggs and chicks. If we assume that 10% is the real parasitism level in the population, at least 474 years should be needed for the frequency of the allele of rejection to reach 0.5 in the population once it appeared (Table 3 in Kelly 1987). We have good evidence that the redstart was already the main host of the cuckoo in Finland in the last quarter of the nineteenth century (Wasenius 1936), but it remains unknown whether current parasitism pressure is representative of the situation in the recent historical past. Thus, since older information is lacking, we cannot test this possibility.

The second possibility is that the colour of cuckoo eggs may just be an apomorphic trait closely related to ancestral egg coloration of the genus *Cuculus*. This explanation is unlikely since cuckoos lay very different eggs depending on the host, and because the appearance of cuckoo eggs correlates with that of their hosts (Davies and Brooke 1988; Moksnes and Røskaft 1995; Avilés and Møller 2004). Furthermore, Rutila et al. (2002) found clear evidence of a selective advantage of mimetic cuckoo eggs in the redstart, since they were significantly less likely to be rejected than non-mimetic eggs.

Third, the low costs of parasitism may be a consequence of a recent adaptation by the redstart, and thus mimicry

was selected before that adaptation appeared. The main peculiarity of the redstart among all hosts of the European cuckoo is its hole-nesting habits. However, this might be a novel situation since von Haartman (1969) reported that nesting on the ground was common in this species. Moreover, Siivonen (1935) suggested that ground nesting is the most common site in natural habitats, although nests are difficult to find. In addition, mapping nesting habits within the *Phoenicurus* genus on the phylogeny reported by Ertan (2002) suggests that hole-nesting habits appeared late in the group. We retrieved information on nesting habits for the 12 *Phoenicurus* species from sources in the literature (Etchecopar and Hüe 1983; Flint et al. 1984) and found that hole-nesting habits only appeared among four relatively recent species of the genus including the common redstart (i.e., *Phoenicurus auroreus, P. phoenicurus, P. schisticeps and P. fuliginosus*). Natural cavities on the ground might make it easier for female cuckoos to lay their eggs and for cuckoo chicks to evict host eggs and chicks. Thus, apparent current preferences for holes by redstart could be a consequence of past strong selection by cuckoos forcing redstarts to change their main nest site preferences. Moreover, hole nesting may give redstarts a clear advantage in their arms race against the cuckoo since parasitism rate may be reduced. Cuckoos have very low breeding success in holes as compared to open nests (0.18 cuckoos fledged per laid egg in the redstart, Rutila et al. 2002). However, information concerning costs caused by cuckoos for ground nesting redstarts is needed to accurately test this possibility.

In conclusion, acceptance of cuckoo eggs may be the most beneficial choice by redstarts against cuckoo parasitism for a wide range of parasitism pressures because of the particularly low cost imposed by cuckoo parasitism when parasitizing a hole-nesting host. It is important to note that this study was conducted on a nest-box population with a low availability of natural nesting sites. Nest-box studies may artificially increase host densities and thus increase the risk of cuckoo parasitism that may have induced higher proneness for rejecting. Therefore, further work on other redstart populations, which use natural sites, is clearly needed to further test our predictions.

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