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## A comparative study of host selection in the European cuckoo *Cuculus canorus*

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**Abstract** Certain kinds of hosts are commonly regarded as being more suitable than others for rearing European cuckoos (*Cuculus canorus*) – insectivores that lay small eggs and have open, shallow nests – although empirical tests of cuckoo host selection are lacking. We analysed host use by the European cuckoo in 72 British passerines that are potential hosts and for which there was information available on life-history variables and variables related to cuckoo-host coevolution, such as rate of parasitism, rejection rate of non-mimetic model eggs and degree of cuckoo-egg mimicry of host eggs. The relative population size of the host species affected parasitism rate most strongly, followed by relatively short duration of the nestling period, and the kind of nest, with cuckoos selecting open-nesting hosts. However, the effect of the nestling period could be related to host body size and the kind of nest used, because hole-nesting species normally have longer nestling periods than open-nesters. We re-analysed the data excluding hole nesters and corvid species (species with larger body mass), but the results remained identical. The European cuckoo may benefit from selecting hosts with short nestling periods because such hosts provide food for their nestlings at a very high rate. When only those species known as cuckoo hosts were analysed, the variable that best accounted for the parasitism rate was duration of the breeding season. Therefore, availability of potential hosts in both time and space is important for cuckoos in selecting hosts.

**Key words** Brood parasitism · Cuckoo Host abundance · Host characteristics · Host-parasite coevolution

### Introduction

Studies of specialisation by parasites on particular hosts have expanded our understanding of host-parasite coevolution (Price 1980). Haldane (1949) pointed out that the abundance of hosts should be important in host selection by a parasite, and when an exploited host genotype evolved a high degree of immunity against the parasite, this should result in a change in the preference of the parasite to more abundant and less immune host genotypes. Although Haldane (1949) specifically considered particular genotypes of hosts in his arguments, these could readily be applied to selection by parasites of particular host species. Work by parasitologists has identified some of the factors responsible for variation in host specificity. One such rule is that the more specialised the host group, the more specialised are its parasites (Eichler 1948). The degree of specialisation by parasites may provide information on the relative phylogenetic age of hosts (Noble and Noble 1976). Therefore, to gain a good understanding of host selection, it is important to know the phylogenetically independent values of the characters that make hosts suitable for exploitation by parasites. Here we study such characteristics of the hosts of a generalist brood parasite, the European cuckoo (*Cuculus canorus*).

Interspecific brood parasitism is a reproductive strategy which consists of laying eggs in the nests of another species, known as the host, which usually provides care for the eggs and chicks of the parasite. This reproductive strategy is used by approximately 1% of all birds species (Payne 1977), and many bird species suffer from being hosts of brood parasites. For example, the shiny cowbird (*Molothrus bonariensis*), an American obligate brood parasite, has been known to parasitise more than 180 host species (Friedmann et al. 1977). The

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European cuckoo is also known to parasitise a large number of host species, with a few main hosts (Glue and Morgan 1972; Wyllie 1981). Different strains of cuckoos (*gentes*) have evolved eggs that mimic those of their hosts in appearance, and there is thus clear evidence of specialisation on particular host species (Brooke and Davies 1988; Mason 1986; Moksnes and Røskaft 1995). Species which reject cuckoo eggs have been regarded as unsuitable hosts on the basis of this single criterion (Rothstein 1982). Egg mimicry could have evolved a posteriori as a counter-defence against the parasite, and if this were so, rejecter hosts would then be the agents selecting for mimetic cuckoo eggs, through natural selection (Brooke and Davies 1988; Øien et al. 1995; but see Brooker and Brooker 1996). The main hosts may have particular characteristics, other than similar eggs, that make them suitable as foster parents for the European cuckoo nestling.

The function of host preferences remains unknown, but it is likely that cuckoos prefer hosts that provide suitable food for parasite offspring, or that build nests from which the cuckoo nestling is able to eject host offspring, or that do not physically attack the female cuckoo when she is laying. Some potential host characteristics that are traditionally accepted as important for cuckoos were summarised by Payne (1977) as follows:

1. The food regime of the host species should facilitate proper development of the parasite. However, the growth rate of some brood-parasite nestlings is similar when fed by different host species (Payne 1977).
2. Parental behaviour of the parasite and the foster parents should be compatible, e.g. there should be some similarity between the begging behaviour of host and parasite nestlings.
3. Host egg size may be decisive, because eggs are incubated by contact with the hosts' brood patch, and contact may be poor if parasite eggs are smaller than those of the host; hence the cuckoo has evolved a small egg relative to its body size.
4. Hosts or their nests must be readily available.
5. Host size must be compatible with that of the parasite.

Since the review by Payne (1977) was published, more characteristics have been added to this list, such as the type of host nest and duration of sympatry with the parasite. However, no study has yet analysed host characteristics, other than those related to host-parasite coevolution such as host defences, in relation to parasitism by any brood parasite.

More detailed studies are needed on parasitism of different hosts, because the use of parasitism rate as an index of host suitability may cause a major error – that is, apparently unparasitised nests may earlier have held a cuckoo egg that has already been ejected by the host. Thus, it can be difficult to estimate the real parasitism rate of each species with available information. Therefore, although parasitism and rejection rates are clearly interrelated (they are not really independent variables),

the only accurate way to estimate the parasitism rate is to compensate for the ejection rate of the species as determined from field experiments simulating parasitism (Rothstein 1982). On the other hand, there are some problems with using such parasitism rates corrected for experimental rejection rates because:

1. The rate of rejection is determined by the degree of mimicry of the cuckoo egg and, therefore, we should correct for rejection rates measured in the same populations as the rates of parasitism. However, such data are not available in the literature, which more often reports information only on experimental rejection rates of non-mimetic model eggs.
2. Parasitism rates are likely to be underestimates for common hosts (because mimetic eggs will be missed by observers), while parasitism rates for uncommon hosts are likely to be overestimates.

These arguments suggest that it is more convenient simply to use data on parasitism rate as a measure of host suitability.

We attempted to tackle the problem of using the parasitism rate in two ways. Firstly, we corrected the parasitism rate for the rejection rate of the host species based on rejection of experimentally introduced non-mimetic cuckoo eggs (see Appendix 1) by forcing the entry of this variable into the final multiple regression model. However, most of the species for which this information is available are hosts of the European cuckoo, and, therefore, it can only be used to analyse differences in parasitism rates of known host species. Secondly, we used the parasitism rate directly in the comparative analyses.

In this paper:

1. We analyse biological features of potential hosts in order to pinpoint those that may be important in the process of host selection by the European cuckoo.
2. We also analyse this question by excluding hole nesters as potential hosts of the European cuckoo, because some features of the host could be related to the type of nest used by potential hosts, and also by excluding corvids, which, due to their great body mass, are outside the range of potential hosts.
3. Finally, we reanalyse the data using only species that have been found parasitised by the European cuckoo, both forcing and not forcing the entry of the rejection rate into the final multiple-regression model, in order to determine which variables are able to explain variance in parasitism rate of European cuckoo hosts.

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## Materials and methods

### Potential host species used in the analyses

To analyse possible features of potential cuckoo hosts, we used as potential hosts of the European cuckoo all British passerine species for which there was information available in the literature ( $n = 72$ ); 16 of these potential hosts were hole nesters. We found data in the literature on rejection rate of experimental non-mimetic

eggs for 19 host species with a known duration of breeding season in Britain (Appendix 1).

#### Variables analysed in the model

We assembled information on the following variables for each potential cuckoo host:

1. Rate of parasitism in Great Britain collected from different sources (Davies and Brooke 1989b; Glue and Murray 1984; Lack 1963; Wyllie 1981).
2. For a measure of host abundance, we used the number of breeding pairs during 1988–1991 in Britain, reported by Gibbons et al. (1993). When a minimum and a maximum number of breeding pairs were reported, we used mean values.
3. For a measure of host geographic range size we used number of 10 km × 10 km squares where the species was found breeding between 1988 and 1991 in Britain (Gibbons et al. 1993). This estimate also provides a relative measure of population size, since overall abundance and distribution of birds are generally positively correlated (Brown 1984; Maurer 1994; Blackburn et al. 1997). However, for the study of cuckoos selecting hosts, it could be of interest to distinguish between these two variables, because, while host density is a local feature, host geographic range size would be an index of availability of hosts at different locations. Local abundance and geographic range size have been shown to be positively related (Blackburn et al. 1997).
4. Body mass (g): the mean value of those reported for male and female by Perrins (1987).
5. Clutch size, as the mean value of the maximum and the minimum reported by Perrins (1987).
6. Duration of incubation period, as a mean value of the maximum and the minimum reported by Perrins (1987).
7. Duration of nestling period, as a mean value of the maximum and the minimum reported by Perrins (1987).
8. Number of broods raised per breeding season (data from Perrins 1987).
9. Duration of breeding season, as the season for the occurrence of eggs without the margins for early eggs and late broods reported in annual cycle diagrams by Cramp (1985–1992) and Cramp and Perrins (1993–1994).
10. Hatching asynchrony: whether the duration of the hatching period exceeded 1 day (data from Clark and Wilson 1981; Cramp 1985–1992; Cramp and Perrins 1993–1994).
11. Type of nest (open, semi-open or hole nest) from Cramp (1985–1992) and Cramp and Perrins (1993–1994).
12. Sociality (solitary, semi-colonial or colonial) from Cramp (1985–1992) and Cramp and Perrins (1993–1994).
13. Type of food that the potential host brings to the nestlings, from Cramp (1985–1992) and Cramp and Perrins (1993–1994).
14. Rejection rate, as the mean value of those reported from various sources (Davies and Brooke 1989a; von Haartman 1981; Järvinen 1984; Moksnes et al. 1990) not only from studies in the British Isles, but also from other European countries. We used the mean value for the rejection rate because Soler and Møller (1996) demonstrated a high repeatability between values from different studies (repeatability = 0.73;  $SE = 0.13$ ;  $F = 7.12$ ;  $df = 13,16$ ;  $P = 0.0002$ ; Soler and Møller 1996).
15. Degree of mimicry of European cuckoo eggs parasitising different host species as the percentage of cuckoo egg found in museum collections (in England, Sweden, Germany, Denmark, Switzerland, Finland, United States, The Netherlands, The Czech Republic, Hungary, Austria, Serbia (Vojvodina) and Norway) that mimics those of each host species reported by Moksnes and Røskaft (1995).

#### Statistical procedures

Because we were interested in the characteristics that make passerines suitable as hosts of the European cuckoo (features inde-

pendent of common phylogenetic ancestry), we used available comparative methods. In a previous article we calculated the repeatability of parasitism and rejection rate variables for species for which there were data available in the literature from at least two different countries, and both repeatability values were statistically significant (Soler and Møller 1996), thereby being candidates for comparative analyses.

No comparative method allows analysis of potential relationships of more than a single discrete variable with continuous variables (Harvey and Pagel 1991). On the other hand, in analyses of the possible relationship between discrete variables and parasitism rate (one by one), because the phylogeny of the hosts is poorly known, only a few contrasts were calculated (hatching asynchrony: 9; type of nest: 5; sociality: 5; type of food that the potential host brings to the nestlings: 3). Moreover, the contrasts were estimated for different nodes for each variable (depending on whether the character changed), and thus the contrast values for each variable cannot be combined and used in multivariate analyses. To solve problems with discrete variables in the analyses, we carried out a canonical correspondence analysis for the discrete variables (ter Braak 1987), which produced a continuous canonical axis representing the values of the discrete variables. We introduced four discrete variables into the correspondence analysis: (1) hatching asynchrony (yes or no), (2) type of nest (hole-, semi-open, or open nests), (3) sociality (colonial, semi-colonial, or solitary), and (4) kind of food brought to the nestlings (insects, mixture of insects and seeds, or seeds). The analysis provided us with three axes that explained 100% of the variance (total eigenvalue = 0.12, percentage of variance explained: first axis = 55.1%, second axis = 26.0%, third axis = 19.0%), and one coordinate for each species on each axis. To identify the relationships between each axis and the different variables, i.e. to interpret the canonical axes, we carried out Spearman rank correlation analyses between the categorised data and the coordinates for all three axes (see Table 1 for the values of the Spearman coefficients for each axis). We performed one correspondence analysis for all species, another that excluded hole nesters and corvids, and a third one for European cuckoo host species for which we found data on experimental rejection rate and duration of breeding. In this way, we were able to calculate contrasts for each of the canonical axes. Because we did not find information on duration of the breeding season for all 72 species, we analysed the data including and excluding this variable. For all canonical analyses performed, the resulting axes explained 100% of the variance.

Although Sibley and Ahlquist (1991) published a bird phylogeny based on DNA sequences, many of the passerine species for which we found data on the previously described variables are not in this phylogeny, and thus it was not possible to use that phylogenetic information in this study. Therefore, we used the passerine classification given in Howard and Moore (1991) as a phylogeny. Although the use of phylogenies based on morphology (traditional taxonomic classification) could cause some problems, it is preferable to use the most available complete information rather than making no analyses at all, although analyses should be revised when the phylogeny becomes better known (Garland et al. 1991). Moreover, several recent studies have suggested that phylogenies based on molecular changes may also include inaccuracies such as branching patterns (Harvey et al. 1992; Nee et al. 1993) and there are many examples in the literature where traditional morphological classification has been used in comparative studies (e.g. Hartley and Davies 1994; Keller and Genoud 1997; Owens and Bennett 1994).

In the analysis, we assumed polytomies among different species within the same genus, and among different genera within the same family; i.e. we assumed that all species in the same genus (or all genera in the same family) evolved simultaneously from a common ancestor (multiway speciation events; see Purvis and Garland (1993) for problems with polytomies, their implications, and possible solutions). Hence, we have set branch lengths of all species to the same value (=1) (Garland et al. 1993; Purvis and Garland 1993). We also used two methods to solve polytomies and assign branch lengths, one method developed by Grafen (1989) that gives

**Table 1** Relationships between the discrete variables and the value of each canonical axis from the correspondence analysis for **A** all species in the analysis, **B** all species excluding hole nesters and corvids, and **C** only species known to be cuckoo hosts and with information on experimental rejection rate. Values are Spearman rank order correlation coefficients. Open nesters were assigned a value of 1, semi-open nesters a value of 2, and hole nesters a value of 3. Insectivorous nestlings were assigned a value of 1, semi-insectivorous nestlings a value of 2, and seed eating nestlings a value of 3. Synchronous species were assigned a value of 1, and asynchronous species a value of 2. Solitary species were assigned a value of 1, semi-colonial species a value of 2, and colonial species a value of 3

	Axis 1	Axis 2	Axis 3
<b>A</b> All species in the analysis ( $n=72$ )			
Hatching asynchrony	0.067	0.593	0.200
Type of nest	-0.860	-0.260	-0.200
Sociality	0.262	-0.516	0.456
Type of food	0.662	-0.310	-0.271
<b>B</b> Non-hole nesters and non-corvids ( $n=51$ )			
Hatching asynchrony	-0.725	-0.396	
Sociality	0.491	0.275	
Type of food	0.709	-0.390	
<b>C</b> Cuckoo host species ( $n=22$ )			
Hatching asynchrony	-0.098	0.653	0.576
Type of nest	-0.891	0.051	-0.196
Sociality	0.408	0.472	-0.381
Type of food	0.625	-0.488	-0.121

greater weight to those species or nodes whose data points are not well explained by the phylogeny or by the other predictor variables under consideration, and another developed by Pagel and Harvey (1989) which relies on the assumption that the  $X$  (or  $Y$ ) variable can provide useful information about the hidden phylogenetic structure in the multiple node. These methods can be applied to imperfectly resolved phylogenies, such as might be the case if a taxonomy were used instead of a phylogeny, as in the present work.

To control for the possible effects of common phylogenetic descent we used the independent-comparison method of Felsenstein (1985) as implemented in a computer program written by Garland et al. (1993). This method finds a set of independent pairwise differences or contrasts, assuming that changes along the branches of the phylogeny can be modelled by a Brownian motion process (successive changes are independent of one another), and that the expected total change added together over many independent changes is zero (Harvey and Pagel 1991). Therefore, pairwise differences in the phylogenetic tree are independent of each other (Harvey and Pagel 1991). The advantage of the independent-comparison approaches is that, by partitioning the variation appropriately, all contrasts can be used to assess a hypothetical comparative relationship (Harvey and Pagel 1991). We calculated Felsenstein's independent contrasts for all the potential confounding variables, including those non-continuous variables. For the calculation of contrasts, we used normalised values of continuous variables and the coordinates on the axes from the correspondence analysis for non-continuous variables. Thus, we obtained a set of contrasts for each variable estimated from the same node or species pair.

To study the possible relationships between the level of parasitism that each host is suffering by the European cuckoo (parasitism rate) and different life-history variables of the potential hosts, we used the standardised independent contrasts (from the independent-contrast method of Felsenstein 1985) in a forward stepwise multiple regression analysis ( $F$  value to enter in the model additional independent variables = 3.00) forced through the origin, where parasitism rate was the dependent variable and all the others were independent variables.

Some variables in the analysis could be interrelated, and, in order to solve this problem, we carried out a principal component analysis (PCA) with the values of contrasts of all dependent variables derived from a phylogeny with all branch lengths equalling one. However, the variables shared little variance, the eigenvalue of the second factor being less than 2 (eigenvalue factor 2 = 1.68) and the three first axes explaining only 58.7% of the variance. Therefore, for a better understanding of the results, we used the contrast value for each variable instead of the principal-component coordinate for each factor. It is known that the kind of nest used by potential hosts is one of the most important physical constraints on parasitism by the European cuckoo, because the opening of a nest hole is usually too small to allow the young cuckoo to fledge (Øien et al. 1995). Furthermore, hole-nesting birds have a reduced risk of predation that has resulted in evolution of a long nestling period (Bosque and Bosque 1995; Lack 1968) and large clutches (Lack 1968). Corvids are not potential hosts of the European cuckoo (although *Cyanopica cyana* is a cuckoo host in Japan: Nakamura 1990). Therefore, we analysed the data including and excluding hole nesters and corvids from the analysis. To identify variables explaining differences in parasitism rate suffered by species known as a hosts, we used those for which information was available for all variables ( $n = 19$ ), and in order to control for problems related to host ejection of cuckoo eggs before nests were checked, we forced, the rejection rate in the multiple-regression analyses as an independent variable.

All variables introduced in the analyses were normalised (Kolmogorov-Smirnov tests, n.s.): parasitism rate was transformed to  $\log(n + 0.001)$ , population density of the host species was fourth-root transformed. Host geographic range size and duration of breeding season were already normally distributed, body mass, clutch size and incubation period were  $\log(n)$  transformed, the duration of the nestling period was  $\log_{10}(n)$ , rejection rates and degree of mimicry were transformed to  $\arcsin(n)$ , axes 1 and 3 were already normally distributed, and axis 2 and number of broods raised per breeding season were binomial. All tests were two-tailed.

## Results

### Variables explaining cuckoo host selection

The analysis of the relationship between the standardised contrasts of the different life history variables of the potential hosts and the standardised contrasts of the parasitism rate showed that only three variables explained a significant proportion of the variance: host geographic range size (positively related), the duration of the nestling period (negatively related), and the kind of nest selected (first canonical axis) (selecting open nesters). This was the case regardless of the method used to estimate branch length (Table 2). These three variables explained more than 28.1% of the variance (multiple  $R > 0.52$ ,  $F > 8.7$ ,  $df = 3,68$ ,  $P < 0.00006$ ; Table 2). When duration of the breeding season was used as an additional independent variable (thereby reducing sample size, see Methods), the result was similar and only geographic range size of the hosts and the duration of the nestling period explained a significant proportion of the variance independently of the method used to estimate branch length ( $R^2 > 0.39$ ,  $F > 14.5$ ,  $df = 2,45$ ,  $P < 0.000011$ ; Table 2; Fig. 1).

Because the duration of the nestling period could be related to the kind of nest used, and corvids fell outside the body-size range of potential hosts, we re-

analysed the data for non-hole nesters and non-corvids only. The results were similar, showing that, regardless of the method used to estimate branch length, the most important predictor of parasitism rate was host density (partial correlation coefficients,  $R > 0.41$ ,  $t > 3.19$ ,  $df = 49$ ,  $P < 0.0024$ ; Table 2) and the duration of the nestling period (partial correlation coefficients,  $R < -0.327$ ,  $t > 2.4$ ,  $df = 49$ ,  $P < 0.02$ ; Table 2) (only these two variables were statistically significant). Both variables explained more than 24% of the variance in the parasitism rate (multiple  $R > 0.49$ ,  $F > 7.69$ ,  $df = 2, 48$ ,  $P < 0.0013$ ; Table 2). When the duration of the breeding season was used as an additional independent variable, geographic range size of the hosts, but not host density, and duration of the nestling period were the variables that best accounted for the parasitism rate (geographic range size, partial correlation coefficient,  $R > 0.56$ ,  $t > 4.1$ ,  $df = 38$ ,  $P < 0.00017$ ; duration of the nestling period,  $R < -0.45$ ,  $t > 3.12$ ,  $df = 38$ ,  $P < 0.0034$ ; Table 2).

Therefore, host population size (geographic range size or density) and the duration of the nestling period explain why some passerine species are more suitable hosts of the European cuckoo than others.

#### Variables explaining differences in parasitism rate of known European cuckoo hosts

In this analysis of 19 species of hosts of the European cuckoo, we introduced the level of mimicry of cuckoo eggs and the rejection rate as additional variables. The results of a stepwise multiple-regression analyses of the phylogenetically independent contrasts showed that the European cuckoo preferentially selects hosts with a longer breeding season, and those with eggs that the cuckoo can mimic. No other variables were statistically significant (Table 3). However, when rejection rate was forced to enter into the final model (see Methods), thereby controlling the final model for this variable, duration of breeding season was the only significant variable (Table 3).

## Discussion

Although the European cuckoo is able to parasitise a large number of passerine species, it has evolved clear preferences for particular species. For example, the number of hosts reported in Britain exceeds 50, but only three species, duncock (*Prunella modularis*), reed warbler (*Acrocephalus scirpaceus*) and meadow pipit (*Anthus pratensis*) accounted for 77% of all cases of parasitism (Glue and Morgan 1972). These host preferences must be related to differences in fitness obtained by parasitism of different hosts, and particular host characteristics may be responsible for such differential parasite fitness. One of the most obvious host characteristics, directly related to parasite fitness, is whether the host is able to

recognise and reject cuckoo eggs. Although it has been shown that cuckoos have decreased their use of some rejector species, because of the great costs for the brood parasite of host rejection of foreign eggs (Rothstein 1990), brood parasites are still using particular host species rather than switching to acceptor species. A fundamental question regarding host use by cuckoos is whether host use is genetically inherited or arises by imprinting. However, an analysis of genetic differentiation of host race using mitochondrial and microsatellite DNA variation found no significant differences among cuckoos from different hosts (Gibbs et al. 1996).

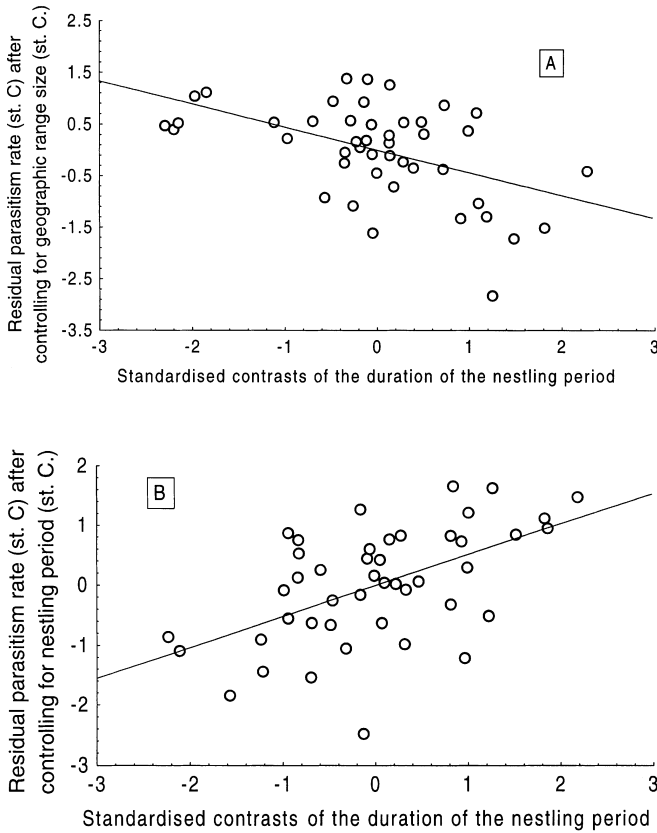
Recognition of foreign eggs by common cuckoo hosts is a non-intrinsic host characteristic resulting from host-parasite interactions possibly depending on the duration of coevolution between parasite and host populations (Davies and Brooke 1989a,b; Øien et al. 1995; Soler and Møller 1996; but see Brooker and Brooker 1996). Moreover, different populations of the same species can be rejectors or acceptors depending on the duration of sympatry between parasite and host, such as meadow pipit and pied/white wagtail (*Motacilla alba*) (Davies and Brooke 1989a) or magpies (Soler and Møller 1990). Therefore, the fact that the parasite does not dramatically change host species, despite the high costs of egg rejection, may be because of beneficial host characteristics that are important for the proper development of the offspring of the parasite, but perhaps also because cuckoos have a genetically based host choice.

Some host characteristics that did not explain a significant proportion of the variance in parasitism could still be important in the process of host selection by the cuckoo. The low variance of these variables among hosts, and the relationships between different life-history variables of hosts, may mask their importance in the comparative analyses. For example, all hole nesters in the analyses feed their chicks with insects, and all seed-eaters are non-hole nesters. Since the European cuckoo rarely parasitises hole nesters (see Appendix 1), a preference of the brood parasite for non-hole-nesting hosts would be confirmed by the comparative analyses. Due to the relationship between hole-nesting and the kind of food brought to nestlings, the analysis could even detect an apparent relationship between parasitism and food provided for nestlings. Other important interrelated variables are (1) the body mass of the potential host species and the duration of the incubation and the nestling periods, and clutch size (Lack 1968), (2) the duration of the nestling period, clutch size and incubation period (Siikamäki 1995), and (3) relative population size and degree of sociality.

Our results showed that host population size (mostly geographic range size) and the duration of the nestling period of the host were related (positively and negatively, respectively) to parasitism rate suffered by different potential host species. The relatively large importance of the population size of potential hosts as a predictor of parasitism by the European cuckoo makes intuitive sense. This result is consistent with the predic-

**Table 2** Results of the forward stepwise multiple regression analyses forced through the origin between standardised contrasts of parasitism rate (dependent variable), standardised contrasts of life-history variables [population density, population geographic range, body mass, clutch size, duration of incubation period, duration of nestling period, number of broods per season, hatching asynchrony, type of nest (open, semi-open or hole nests), sociality (solitary, semi-colonial or colonial), and type of food brought to the nestlings] and standardised contrasts of host variables related to coevolution (mimicry of cuckoo eggs to those of the host and host rejection-rate of non-mimetic egg) of potential host species calculated using three different methods to assign branch lengths.  $R^*$  is the multiple regression coefficient of the variables included in the model

	All branch lengths equal to 1 method			Using the method of Pagel and Harvey (1989)			Using the method of Grafen (1989)		
	$R$	Test	$P$	$R$	Test	$P$	$R$	Test	$P$
<u>Analysis of all potential host species</u>									
Dependent variable:	$R^* = 0.534$	$F_{(3,68)} = 9.02$	0.00004	$R^* = 0.531$	$F_{(3,68)} = 8.92$	0.000046	$R^* = 0.528$	$F_{(3,68)} = 8.76$	0.000055
Parasitism rate									
Independent variables:									
Geographic range size	$R = 0.427$	$t_{(69)} = 3.90$	0.0002	$R = 0.429$	$t_{(69)} = 3.91$	0.0002	$R = 0.427$	$t_{(69)} = 3.89$	0.00023
Duration of the nestling period	$R = -0.299$	$t_{(69)} = 2.59$	0.012	$R = -0.271$	$t_{(69)} = 2.33$	0.023	$R = -0.276$	$t_{(69)} = 2.37$	0.021
Preference for open nesters	$R = 0.235$	$t_{(69)} = 2.00$	0.0498	$R = 0.241$	$t_{(69)} = 2.05$	0.044	$R = 0.240$	$t_{(69)} = 2.04$	0.045
Including duration of the breeding season in the analyses									
Dependent variable:	$R^* = 0.630$	$F_{(2,45)} = 14.8$	0.000011	$R^* = 0.632$	$F_{(2,45)} = 15.0$	0.00001	$R^* = 0.631$	$F_{(2,45)} = 14.9$	0.000011
Parasitism rate									
Independent variables:									
Geographic range size	$R = 0.569$	$t_{(46)} = 4.64$	0.00003	$R = 0.579$	$t_{(46)} = 4.77$	0.00002	$R = 0.577$	$t_{(46)} = 4.75$	0.000021
Duration of the nestling period	$R = -0.509$	$t_{(46)} = 3.98$	0.00025	$R = -0.492$	$t_{(46)} = 3.79$	0.00044	$R = -0.491$	$t_{(46)} = 3.78$	0.00045
<u>Analysis of potential non-hole nester and non-corvid host species</u>									
Dependent variable:	$R^* = 0.493$	$F_{(2,48)} = 7.69$	0.0013	$R^* = 0.507$	$F_{(2,48)} = 8.28$	0.0008	$R^* = 0.507$	$F_{(2,48)} = 8.32$	0.0008
Parasitism rate									
Independent variables:									
Population density	$R = 0.422$	$t_{(49)} = 3.22$	0.0023	$R = 0.424$	$t_{(49)} = 3.24$	0.0022	$R = 0.419$	$t_{(49)} = 3.20$	0.0024
Duration of the nestling period	$R = -0.327$	$t_{(49)} = 2.40$	0.02	$R = -0.342$	$t_{(49)} = 2.52$	0.015	$R = -0.347$	$t_{(49)} = 2.57$	0.013
Including duration of the breeding season in the analyses									
Dependent variable:	$R^* = 0.602$	$F_{(2,37)} = 10.5$	0.00025	$R^* = 0.613$	$F_{(2,37)} = 11.1$	0.00016	$R^* = 0.613$	$F_{(2,37)} = 11.1$	0.00016
Parasitism rate									
Independent variables:									
Geographic range size	$R = 0.565$	$t_{(38)} = 4.17$	0.00017	$R = 0.576$	$t_{(38)} = 4.28$	0.00012	$R = 0.575$	$t_{(38)} = 4.26$	0.00013
Duration of the nestling period	$R = -0.456$	$t_{(38)} = 3.12$	0.003	$R = -0.457$	$t_{(38)} = 3.12$	0.0034	$R = -0.459$	$t_{(46)} = 3.15$	0.0032



**Fig. 1** Relationships between residuals of parasitism rates and **A** duration of the nesting period and **B** geographic range size of species for which we found information on duration of the breeding season. Standardised contrasts (*st. C.*), estimated with all branch lengths equal to 1 and polytomies (see Methods), were used in the analyses

tion of Haldane (1949) that parasites should specialise on the commonest host genotype. Host availability must be an important factor for the cuckoo choosing hosts because one European cuckoo female lays more than 12 eggs per season (Payne 1977), presumably to compensate for rejection and predation rates, and, if the host is not sufficiently widespread and/or abundant, it could be difficult for a female cuckoo to find nests in which to lay all eggs. The scarcity of individual potential host species has been proposed as an important factor affecting the use of secondary host species (Riddiford 1986).

When species known to be hosts of the European cuckoo were analysed, variation in parasitism rate was explained by the duration of the breeding season. Species with a long breeding season were frequently parasitised. These two results suggest that availability of potential hosts both in time and space is important for cuckoos selecting hosts.

The second variable explaining cuckoo host selection is the duration of the nestling period. That was the case when analysing all potential host species, but not when only known host species were used in the analyses. One of the possible factors explaining why the European cuckoo selects hosts with relatively short nestling peri-

**Table 3** Result of stepwise regression analyses between parasitism rate (dependent variable) and life history, and other variables related to coevolution (mimicry by cuckoo eggs of those of the host and host rejection-rate of non-mimetic eggs) of 19 host species, using standardised contrasts calculated according to different methods to resolve polytomies. We also controlled for the possibility of hosts ejecting the cuckoo egg before checking the nest by forcing standardised contrasts of rejection rate to enter in the final model. *R* is the multiple regression coefficient of the variables included in the model

	All branch lengths equal to 1 method			Using the method of Pagel and Harvey (1989)			Using the method of Grafen (1989)		
	<i>R</i>	Test	<i>P</i>	<i>R</i>	Test	<i>P</i>	<i>R</i>	Test	<i>P</i>
<b>Final model</b>									
Dependent variable: Parasitism rate	$\hat{R} = 0.652$	$F_{(2,16)} = 5.90$	0.012	$\hat{R} = 0.671$	$F_{(2,16)} = 6.56$	0.008	$\hat{R} = 0.672$	$F_{(2,15)} = 6.58$	0.008
Independent variables:									
Duration of the breeding season	$R = 0.588$	$t_{(17)} = 2.91$	0.01	$R = 0.592$	$t_{(17)} = 2.94$	0.009	$R = 0.590$	$t_{(17)} = 2.93$	0.009
Mimicry	$R = 0.464$	$t_{(17)} = 2.1$	0.05	$R = 0.470$	$t_{(17)} = 2.13$	0.048	$R = 0.472$	$t_{(17)} = 2.14$	0.047
Forcing entry of rejection rate into the model									
Dependent variable: Parasitism rate	$R = 0.716$	$F_{(3,15)} = 5.26$	0.011	$\hat{R} = 0.730$	$F_{(3,15)} = 5.71$	0.008	$\hat{R} = 0.729$	$F_{(3,15)} = 5.68$	0.008
Independent variables:									
Duration of the breeding season	$R = 0.584$	$t_{(16)} = 2.79$	0.013	$R = 0.611$	$t_{(16)} = 2.99$	0.009	$R = 0.610$	$t_{(16)} = 2.98$	0.009
Mimicry	$R = 0.466$	$t_{(16)} = 2.04$	0.06	$R = 0.435$	$t_{(16)} = 1.87$	0.08	$R = 0.434$	$t_{(16)} = 1.87$	0.08
Rejection rate	$R = -0.392$	$t_{(16)} = 1.65$	0.12	$R = -0.388$	$t_{(16)} = 1.63$	0.12	$R = -0.383$	$t_{(16)} = 1.60$	0.13

ods is the low risk of nest predation compared to species with longer nestling periods (Bosque and Bosque 1995; Lack 1968). However, nestlings of the European cuckoo spend around 17 days in the nest, independently of the host species (Wyllie 1981), and therefore, the predation risk of a nest with a cuckoo nestling would be independent of the host species. However, species with a relatively short nestling period also have high growth rates (Lack 1968), and, therefore, the food requirements by the chicks of such species are higher than for species with a low growth rate. Hence, the growth rate may reflect a trade-off between selection for rapid growth to escape predation and selection for slow growth to reduce food requirements (Lack 1968). An example of this effect is the low growth rate of hole nesters (Gill 1990). The family Cuculidae, which contains both brood parasites and non-parasitic species, has a short nestling period for their body mass (Lack 1968). This means that their chicks need a large amount of food per day to support their fast growth rate. Therefore, brood-parasitic cuckoos should select hosts based on their growth rate and, because they need foster parents that are able to provide chicks sufficiently for a high growth rate, they should select hosts with relatively short nestling periods.

The duration of the nestling period is also related to clutch size, and larger clutches are commoner in species with low predation rates (hole nesters) and long nestling periods (Gill 1990; Lack 1968). However, clutch size did not enter the final models explaining variation in parasitism rates, but it was related to other life-history variables such as duration of the breeding season (independently of the method used to resolve polytomies,  $R < -0.29$ ,  $n = 47$ ,  $P < 0.05$ ). Therefore, clutch size could also be an important factor per se due to the ejection behaviour of the cuckoo chick (Wyllie 1981), and it would be beneficial for the brood parasite to select hosts with a small clutch size, thereby reducing the cost of ejecting host eggs and/or chicks for the cuckoo nestling. This activity is very costly (the eggs or the chicks of the host are very heavy, normally more than half the mass of the cuckoo chick), and sometimes the cuckoo chick is exhausted after ejecting one host egg or chick (Palomino, personal communication). For example, it has been proposed that their deep nests explain the low parasitism rate suffered by thrushes (*Turdus* spp., Moksnes et al. 1990), because of the difficulty for the cuckoo chick of ejecting the eggs and chicks of the host.

Another possible reason why the cuckoo prefers host species with small, fast-growing broods is that such

species are more likely to be able to reneest the same season and, therefore, are better able to cope with the costs of parasitism (Brooker and Brooker 1996) and offer new opportunities for the parasite. Although the number of broods raised during the breeding season did not significantly improve the model explaining parasitism rate, the number of broods is significantly related to the duration of the breeding season, given that species with more than one breeding attempt have longer breeding seasons than those with only one attempt. Thus, both the number of breeding attempts and the duration of the breeding season are related to temporal availability of hosts.

Recently, Blackburn et al. (1996) showed that the abundance of British birds correlated with life-history variables corresponding to rate of offspring development: more abundant species are those that develop faster. This suggests an interrelationship between the two principal factors influencing host choice in cuckoos. However, because both host availability (geographic range size or density) and duration of the nestling period are included in the same multiple regression model, the partial correlation coefficients are by definition controlled for each other's effects. Therefore, although interrelationships among these two variables were not investigated, the detected effects of geographic range size (or density) of potential hosts and the duration of the nestling period on parasitism rate are independent of the relationship between those variables.

With respect to the discrete variables such as hatching asynchrony, type of nest, sociality, and type of food that the potential host brings to the nestlings, we found no significant relationship with parasitism rates. However, we do not exclude the possibility that they are important for cuckoo host selection because (1) the phylogeny of potential hosts is poorly known and, therefore, the number of independent contrasts is very small, and (2) the relationships between the discrete variables and other life-history variables are sometimes strong.

In conclusion, we provide comparative evidence suggesting that host availability (in time and space) and the duration of the nestling period of potential hosts explain host selection by the European cuckoo.

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**Appendix 1** Information on parasitism rate (%) (sources: *a* Davies and Brooke 1989b, *b* Lack 1963, *c* Glue and Murray 1984, and *d* Wyllie 1981), rejection rate (%) (sources: *e* Davies and Brooke 1989a, *f* Moksnes et al. 1990, *g* Järvinen 1984, *h* von Haartman 1981, *i* Cramp 1985; when more than one reference was available for a species we calculated the mean value), geographic range size, population density (number of pairs breeding in Britain), body mass (g), clutch size, incubation period (days), nestling period (days), hatching asynchrony, type of nest, sociality, and type of food that the potential hosts bring to the nest to feed their chicks

Species	Parasitism rate	Rejection rate	Geographic range	Population density	Body mass	Clutch size	Incubation period	Nestling period	No. of broods	Hatch asynchrony	Nest type	Sociality	Food type	Duration of the breeding season	Egg mimicry
<b>Alaudidae</b>															
<i>Alauda arvensis</i>	0.04(c)		2571	2000000	38.6	4	12	19	2	Sync	Open	Solitary	Insects	3	
<i>Lullula arborea</i>	0.01(b)		162	350	27.2	4	14	12	2.5	Sync	Open	Solitary	Insects	4	
<b>Hirundinidae</b>															
<i>Riparia riparia</i>	0.00(c)		991	250000	13.4	5	14	19	2	Sync	Hole	Colonial	Insects	2.25	
<i>Hirundo rustica</i>	0.01(d)	0.0(ef)	2457	570000	18.6	5	15	21	2.5	Sync	Semi-open	Semi-col	Insects	3	0.0
<i>Delichon urbica</i>	0.00(c)		2227	375000	17.0	5	14	21	2.5	Sync	Hole	Colonial	Insects		
<b>Motacillidae</b>															
<i>Anthus trivialis</i>	0.74(c)		1215	120000	21.6	5	14	13	1.5	Sync	Open	Solitary	Insects		
<i>A. pratensis</i>	2.66(a)	26.8(ef)	2261	1900000	18.2	5	14	14	2	Sync	Open	Solitary	Insects		74.9
<i>Motacilla flava</i>	0.13(c)	80.0(f)	759	50000	16.8	6	13	13	2	Sync	Open	Solitary	Insects		64.0
<i>M. cinerea</i>	0.03(c)		1657	34000	18.4	5	14	12	2	Sync	Semi-open	Solitary	Insects		
<i>M. alba</i>	0.42(a)	73.2(ef)	2467	300000	22.6	6	14	15	2	Sync	Semio-pen	Solitary	Insects		54.2
<b>Laniidae</b>															
<i>Lanius collurio</i>	0.01(b)		2	2	28.2	6	15	14	1	Async	Open	Solitary	Insects	2	
<b>Cinclidae</b>															
<i>Cinclus cinclus</i>	0.00(c)		1097	14000	63.1	5	16	23	2	Sync	Semi-open	Solitary	Insects	4	
<b>Troglodytidae</b>															
<i>Troglodytes troglodytes</i>	0.04(a)	0.0(e)	2650	7100000	9.4	6	15	17	1.5	Async	Semi-open	Solitary	Insects	3	0.0
<b>Prunellidae</b>															
<i>Prunella modularis</i>	1.93(a)	3.1(ef)	1317	2000000	20.8	5	12	12	2.5	Sync	Open	Solitary	Insects	4	0.4
<b>Turdidae</b>															
<i>Erithacus rubecula</i>	0.29(a)	20.0(e)	2536	4200000	18.1	5	14	14	2.5	Sync	Open	Semi-col	Insects	2.5	4.4
<i>Luscinia megarhynchos</i>	0.01(b)		303	5500	20.7	5	14	13	1	Async	Open	Solitary	Insects	1	
<i>Phoenicurus ochruros</i>	0.00(c)		57	100	16.4	5	13	17	2	Sync	Hole	Solitary	Insects	1.75	
<i>P. phoenicurus</i>	0.03(a)	31.5(efgh)	1019	90000	14.3	6	14	15	1.5	Sync	Hole	Solitary	Insects	1.75	
<i>Saxicola rubetra</i>	0.01(b)		1062	21000	16.9	6	13	13	1.5	Sync	Open	Solitary	Insects	1.75	
<i>S. torquata</i>	0.12(c)		850	15000	14.4	6	15	15	2.5	Sync	Open	Solitary	Insects	3	
<i>Oenanthe oenanthe</i>	0.00(a)	5.9(ef)	1341	55000	25.9	6	14	15	1.5	Sync	Hole	Solitary	Insects	2.75	
<i>Turdus torquatus</i>	0.11(c)		401	8250	112.0	5	14	14	2	Sync	Open	Solitary	Insects	2.25	
<i>T. merula</i>	0.01(a)	63.9(ef)	2583	4400000	106.0	4	14	14	2.5	Async	Open	Solitary	Insects	4	0.0
<i>T. pilaris</i>	0.00(c)	9.1(f)	18	25	98.5	5	14	14	1.5	Async	Open	Colonial	Insects	2.5	0.0
<i>T. philomelos</i>	0.01(b)	62.7(ef)	1491	990000	73.4	4	13	14	2.5	Sync	Open	Solitary	Insects	4.25	0.0
<i>T. iliacus</i>	0.00(c)	34.9(f)	46	60	67.2	6	13	13	2	Sync	Open	Solitary	Insects	1.75	0.0
<i>T. viscivorus</i>	0.00(c)		2153	230000	125.0	4	14	15	2	Sync	Open	Solitary	Insects	2.5	

## Appendix I (contd.)

Species	Parasitism rate	Rejection rate	Geographic range	Population density	Body mass	Clutch size	Incubation period	Nestling period	No. of broods	Hatch asyn-chrony	Nest type	Sociality	Food type	Duration of the breeding season	Egg mimicry
<b>Sylviidae</b>															
<i>Cettia cetti</i>	0.00(c)		57	450	14.2	5	16	15 <sup>a</sup>	1	Sync	Open	Solitary	Insects		19.1
<i>Acrocephalus palustris</i>	1.88(c)	86.8(f)	8	12	12.0	5	12	12	1	Async	Open	Solitary	Insects	2	
<i>A. scirpaceus</i>	5.54(a)	61.8(e)	638	60000	12.0	4	12	12	2	Sync	Open	Solitary	Insects	2.75	47.4
<i>Phylloscopus sibilatrix</i>	0.09(c)		859	17200	8.9	6	13	12	1	Sync	Semi-open	Solitary	Insects	1.5	
<i>P. collybita</i>	0.00(c)	100(f)	1662	640000	7.5	6	13	14	1.5	Sync	Semi-open	Solitary	Insects	2.25	0.0
<i>P. trochilus</i>	0.06(c)	90.0(f)	2446	2300000	8.8	5	13	14	1	Sync	Semi-open	Solitary	Insects	2	0.0
<i>Sylvia atricapilla</i>	0.17(c)	76.9(f)	1757	580000	17.0	5	11	12	1.5	Sync	Open	Solitary	Insects	2	65.0
<i>S. borin</i>	0.32(c)	66.7(f)	1477	200000	19.4	5	12	10	1.5	Sync	Open	Solitary	Insects	2.25	86.9
<i>S. communis</i>	0.07(c)		1934	660000	14.7	5	12	12	1.5	Sync	Open	Solitary	Insects	2.5	
<i>S. curruca</i>	0.01(b)		978	80000	11.9	5	11	11	1.5	Sync	Open	Solitary	Insects	2.5	
<i>S. undata</i>	0.00(c)		40	950	9.5	4	13	14	2	Sync	Open	Solitary	Insects	2.75	
<i>Regulus ignicapillus</i>	0.00(c)		48	165	5.5	8	15	20	2	Async	Semi-open	Solitary	Insects	1.75	
<i>R. regulus</i>	0.01(b)		1930	560000	5.6	8	16	19	2	Async	Semi-open	Solitary	Insects	1.75	
<b>Muscicapidae</b>															
<i>Muscicapa striata</i>	0.12(c)	72.2(ef)	2097	120000	15.0	5	13	14	2	Sync	Semi-open	Solitary	Insects	2.25	33.0
<i>Ficedula hypoleuca</i>	0.00(a)	0.0(ef)	547	37500	12.1	7	13	16	1	Sync	Hole	Solitary	Insects		
<b>Panuridae</b>															
<i>Panurus biarmicus</i>	0.00(c)		52	400	15.5	6	13	12	2	Sync	Open	Semi-col	Insects	2.75	
<b>Aegithalidae</b>															
<i>Aegithalos caedatus</i>	0.00(c)		1868	210000	9.0	10	14	16	1	Sync	Semi-open	Solitary	Insects	2.25	
<b>Paridae</b>															
<i>Parus palustris</i>	0.00(c)	0.0(f)	858	60000	10.5	7	13	17	1	Async	Hole	Solitary	Insects		
<i>P. montanus</i>	0.00(c)		789	25000	10.3	8	13	18	1	Async	Hole	Solitary	Insects		
<i>P. major</i>	0.00(c)	16.7(e)	2317	1600000	18.8	8	13	20	1.5	Async	Hole	Solitary	Insects		
<i>P. caeruleus</i>	0.00(a)	0.0(ef)	1382	3300000	10.8	9	14	19	1	Async	Hole	Solitary	Insects		
<b>Sittidae</b>															
<i>Sitta europaea</i>	0.00(c)		1063	130000	22.7	7	15	24	1	Sync	Hole	Solitary	Insects		
<b>Certhiidae</b>															
<i>Certhia familiaris</i>	0.00(c)		1675	200000	8.7	6	15	15	1.5	Async	Hole	Solitary	Insects		
<b>Ploceidae</b>															
<i>Passer domesticus</i>	0.00(c)		1431	3600000	28.2	5	13	15	2.5	Sync	Hole	Colonial	Some seed		
<i>P. montanus</i>	0.00(c)		1040	110000	22.4	5	13	13	2.5	Sync	Hole	Colonial	Some seed		



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