

Do life-history variables of European cuckoo hosts explain their egg-rejection behavior?

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Recently, Brooker and Brooker suggested an equilibrium in the level of host defense and parasite counter-defense despite the passage of sufficient time for the evolution of host defenses through coevolution between brood parasites and their hosts. A long coevolutionary history of brood parasitism and nest predation has favored an adjustment of the host's life-history pattern to the point where total acceptance of a cuckoo egg is now an evolutionarily stable strategy. In a comparative study based on host species as independent observations, some predictions were tested for the European cuckoo (*Cuculus canorus*) and Horsfield's bronze cuckoo (*Chrysococcyx basalis*). In this article I reanalyze the predictions made by Brooker and Brooker using information on the European cuckoo and its hosts in the British Isles while controlling for common phylogenetic descent. Only 1 of the 12 predictions of Brooker and Brooker was supported using the new analyses, and none of the life-history variables was related to rejection behavior of the hosts of the European cuckoo, implying weak support for the hypothesis. Therefore, we conclude that when analyzing life-history variables that have a phylogenetic component, the use of modern comparative analyses is essential. *Key words*: brood parasitism, coevolution, evolutionary equilibrium. [*Behav Ecol* 10:1–6 (1999)]

Brood parasitism is a reproductive strategy in which the parasite lays its eggs in the nests of other species, which incubate the parasite's eggs and take care of the chicks. The high costs imposed by brood parasites on their hosts have been proposed to select for host defenses against the brood parasite (Rothstein, 1990). Host-egg discrimination and rejection is one of the most important defense tactics, which simultaneously selects for parasitic counter-defenses such as egg mimicry (Davies and Brooke, 1988; Rothstein, 1990). Levels of host defense and parasite counter-defense are predicted to change in relation to the duration of sympatry (Davies and Brooke, 1989a; Lotem and Rothstein, 1995; Øien et al., 1995), an aspect that has received some experimental support (Brisson et al., 1992; Soler and Møller, 1990; Soler et al., 1994). This scenario indicates reciprocal selective influences between the parasite and its hosts (Davies and Brooke, 1989b; Moksnes et al., 1990), possibly resulting in a coevolutionary arms race (Dawkins and Krebs, 1979).

Although parasites and hosts have been involved in a coevolutionary process for a long time, not all host species are rejectors, and some host species almost always accept parasitic eggs and raise parasitic chicks (Brooke and Davies, 1988; Brooker and Brooker, 1989; Mason, 1986; Rothstein, 1975; von Haartman, 1981). There are two general explanations for the lack of rejection behavior in hosts: (1) the "evolutionary lag" hypothesis states that rejection behavior has not had time to evolve in the host population (Davies and Brooke, 1989b; Dawkins and Krebs, 1979; Rothstein, 1990), whereas (2) the "evolutionary equilibrium" hypothesis states that, although there has been time for the evolution of rejection behavior in hosts, putative costs of rejection apparently outweigh the benefits, thereby preventing the evolution of rejection (Davies and Brooke, 1989a; Lotem et al., 1992, 1995; Marchetti, 1992; Rohwer and Spaw, 1988). Alternatively, variation in host populations, related to individual host quality, its life history, or

environmental characteristics could allow an equilibrium at the level of host recognition and rejection of cuckoo eggs (Brooker and Brooker, 1996).

Brooker and Brooker (1996) recently analyzed different host life-history and environmental variables in relation to the lack of rejection behavior in the splendid fairy-wren (*Malurus splendens*), a common host of Horsfield's bronze cuckoo (*Chrysococcyx basalis*), concluding that a long coevolutionary history of brood parasitism and nest predation has favored an adjustment of the host's life-history pattern to the point where total acceptance of the cuckoo egg is now an evolutionarily stable strategy. Moreover, a comparative study of both hosts of Horsfield's bronze cuckoo and those of the European cuckoo (*Cuculus canorus*) were used to analyze the relationship between rejection rate, as an index of duration of coevolution and life-history traits of suitable hosts. These researchers found that these two kind of variables were related and that consequently host rejection behavior can be explained only by life-history variables. This information was used to suggest a change in the current paradigm concerning the European cuckoo and its hosts as a classical example of an escalating coevolutionary arms race.

The comparative analysis fails in several respects: (1) the authors did not control for common phylogenetic descent and therefore treated species and different populations of the same species as statistically independent observations. This point is highly important, given that many examples in the literature demonstrate that lack of control for common phylogenetic descent leads to erroneous conclusions (see examples in Harvey and Pagel, 1991) or masks real relationships (Soler and Møller, 1996). (2) The authors used data from different host populations (even from different continents), which may imply differences in the value of life-history traits (Martin and Clobert, 1996) and in the selection pressures suffered by hosts (e.g., parasitism rate; Davies and Brooke, 1989a; Moksnes et al., 1993). Moreover, (3) the authors mixed hosts of the European cuckoo and those of Horsfield's bronze cuckoo in the same analysis, but these are two species that could impose different selection pressures on their hosts. Because of this, the level of host defense against parasitism (e.g., rejection rate) could depend on the particular brood parasite

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species rather than the life history of the host. For example, both dependent (rejection rate) and independent variables (life-history traits, see above) may be affected by confounding factors leading to an erroneous conclusion.

In summary, variables used in the comparative analysis by Brooker and Brooker (1996) may be influenced by (1) common phylogenetic descent of the host species, (2) the geographical area from which the data came, and (3) the brood parasite species. Therefore, further comparative analyses are needed to test the predictions by Brooker and Brooker (1996) for the European cuckoo, while controlling for all confounding factors by using (1) life-history data of hosts from the same area, (2) hosts of only one species of brood parasite, and (3) modern comparative methodology that controls for the effects of common phylogenetic descent. In this article, I report tests of the predictions by Brooker and Brooker (1996) for the European cuckoo and its hosts, while controlling for common phylogenetic descent, using data from hosts in Britain. The predictions based on the Brooker and Brooker's (1996) "evolutionary equilibrium" hypothesis are as follows:

1. Frequency of rejection should increase as host mobility increases.
2. Frequency of rejection should increase as the breeding season becomes shorter.
3. The type of strategy used by hosts (acceptance, desertion, or ejection) should be correlated with the duration of the breeding season.
4. Frequency of acceptance should increase as clutch size decreases.
5. Species with the highest rejection rates should not be those whose eggs are mimicked by the cuckoo.
6. Species with the lowest rejection rates should be those that are most frequently parasitized.
7. The three categories of host strategies (acceptors, deserters, or ejectors) are distinct when plotted against ability to renege, migration status, putative costs of raising a cuckoo, and putative costs of ejection.
8. Acceptor species should be sedentary species with a high probability of renegeing.
9. Rejector species should be migratory species with low probability of renegeing.
10. Acceptor species are those for whom the putative cost of raising the cuckoo is lowest.
11. Ejector species are those for whom the putative cost of ejection is lowest.
12. Deserter species have costs between acceptors and ejectors (higher putative cost of raising a cuckoo than acceptors and higher putative cost of ejection than ejectors).

MATERIALS AND METHODS

Potential host species used in the analyses

To analyze features of potential cuckoo hosts, I used all British passerine species that had been recorded with a cuckoo egg in their nests and for which information was available in the literature for all variables used in the analyses ($n = 22$). However, when testing differences between acceptor, ejector and deserter species, I used only species that had previously been classified in one of these groups by Moksnes et al. (1991), or other host species for which their behavior had been recorded (accepting, ejecting, or deserting) by Davies and Brooke (1989a).

Variables analyzed in the model

I assembled information on the following variables for each potential cuckoo host: (1) body mass: the mean value of those

reported for male and female by Perrins (1987). (2) Clutch size, as the mean of maximum and minimum values reported by Perrins (1987). (3) Number of broods per season, from Perrins (1987). (4) Rejection rate, as the mean value of those reported from various sources (Davies and Brooke 1989a; Moksnes et al. 1990), not only from studies in the British Isles, but also from other European countries. I used the mean value for the rejection rate because Soler and Møller (1996) demonstrated a high repeatability of estimates from different countries (repeatability = 0.73; SE = 0.13; $F = 7.12$; $df = 13,16$; $p = .0002$; from Soler and Møller, 1996). (5) Degree of mimicry of European cuckoo eggs parasitizing different host species as the percentage of cuckoo eggs found in their corresponding host species reported by Moksnes and Røskaft (1995). (6) Bill length, from the values of British populations reported by Cramp and Perrins (1993–1994). (7) Migratory status: as did Brooker and Brooker (1996), I classified host species in seven different groups based on their winter quarters reported by Cramp and Perrins (1993–1994) for the British population: (i) year-round residents, (ii) primarily residents (migrate <50 km), (iii) migrate >50 km but stay in the British Isles, (iv) migrate outside the British Isles but to surrounding countries, (v) migrate to southern Europe or North Africa, (vi) migrate south of the Sahara but not farther than the equator, and (vii) migrate south of the equator. (8) Duration of the breeding season in months, as the season for the occurrence of eggs without the margins for early eggs and late broods reported in annual cycle diagrams by Cramp and Perrins (1993–1994). (9) Degree of renegeing, calculated following Brooker and Brooker (1996), as the duration of the breeding season divided by the clutch size. (10) The putative cost of rejection, calculated following Brooker and Brooker (1996), as $1/(\text{body mass} + \text{bill length})$. (11) The putative cost of raising a cuckoo was defined by Brooker and Brooker (1996) as the relative difference in size between the host and the cuckoo fledgling; therefore we used only host body mass. Finally, (12) when testing differences between acceptor, ejector, and deserter species, using data from Moksnes et al. (1991) and Davies and Brooke (1989a), I classified species as (i) acceptors if they accepted more than 50% of experimental eggs; (ii) ejectors if they rejected more than 50% of the experimental eggs and in more than 50% of the rejector nests the experimental eggs were ejected; and (iii) deserters if they rejected more than 50% of the experimental eggs and more than 50% of the rejector nests were abandoned. See the appendix for the data set.

Statistical procedures

Because it is necessary to distinguish between the value of a trait due to common phylogenetic descent and that due to coevolutionary history of hosts and brood parasites (see Introduction), I used available comparative methods.

I have used the passerine classification given in Howard and Moore (1991) as a phylogeny (Figure 1). Although the use of phylogenies based on morphology (traditional cladistic classification) could involve 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 involved becomes better known (Garland et al., 1991). Moreover, several recent studies have suggested that phylogenies based on molecular changes may also include inaccuracies (Harvey et al., 1992; Nee et al., 1993), and there are many examples in the literature where traditional cladistic classification has been used in comparative studies (e.g., Hartley and Davies, 1994; Keller and Genoud, 1997; Owens and Bennett, 1994).

In performing the analyses, I assumed polytomies between

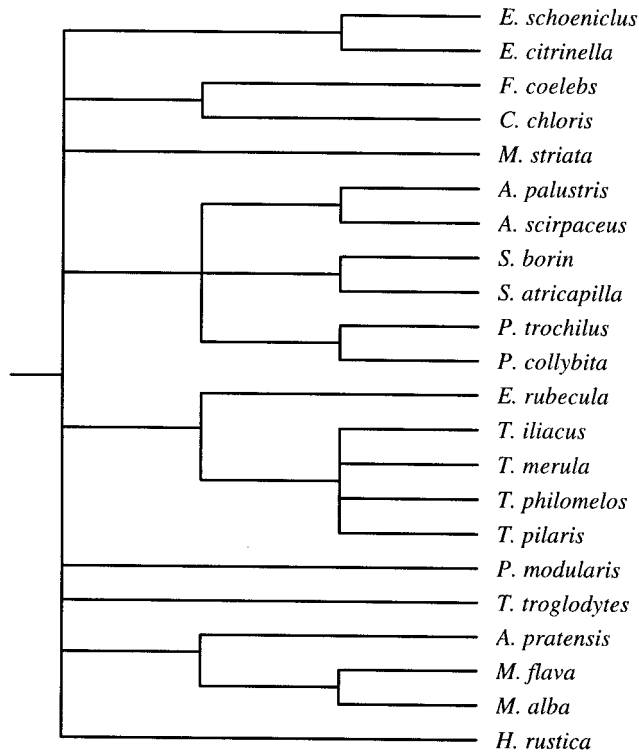


Figure 1
Phylogenetic tree used in the analyses. Cladistic classification from Howard and Moore (1991).

different species within the same genus and between different genera from the same family; i.e., I assumed that all species from the same genus (or all genera from 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, I set branch lengths of all species to the same value (=1) (Garland et al., 1993; Purvis and Garland, 1993). I also used two methods to solve polytomies and assigned branch length, one developed by Grafen (1989) and another developed by Pagel and Harvey (1989). These methods can be applied to imperfectly resolved phylogenies, as might be the case if a taxonomy is used instead of a phylogeny, as in this study. To control for the possible effects of common phylogenetic descent, I used Felsenstein's (1985) independent comparison method as implemented in a computer program developed 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 modeled 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 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). Moreover, by the use of three different methods of assigning branch length, the conclusions are stronger when the results are the same, regardless of assuming polytomies or using methodologies to resolve them.

Some variables in the analyses could be interrelated, and to solve this problem, I previously carried out a principal com-

ponent analysis (PCA; factor rotation: varimax normalized) using the values of contrasts of all dependent variables. However, the variables shared little variance, the eigenvalue of the second factor being less than 2 (eigenvalue factor 2 = 1.66), and the three first axes explaining only 67.5% of the variance. Therefore, for a better understanding of the results, I used the contrast value for each variable instead of the principal component coordinate for each factor.

Some variables introduced in the analyses were transformed to obtain approximately normal distributions of variables: body mass and clutch size were transformed to $\log(n)$; rejection rates and degree of mimicry were transformed to $\arcsin(n)$; the other variables already had approximately normal distributions. All variables with the calculated phylogenetic independent contrasts had approximately normal distributions (Kolmogorov-Smirnov tests, ns). All tests were two-tailed.

RESULTS

With the use of European cuckoo hosts in the British Isles and control for common phylogenetic descent, only prediction number 5 given by Brooker and Brooker (1996) was supported (Table 1). Rejection rates were unrelated to egg mimicry. All other predictions by Brooker and Brooker (1996) were unsupported (Table 1). Therefore, it appears that the use of host species of different brood parasites and the absence of control for common phylogenetic descent confounded the results presented by Brooker and Brooker (1996).

DISCUSSION

The association between brood parasites and their hosts has traditionally been viewed as a classical example of an escalating coevolutionary arms race (Davies and Brooke, 1989b; Dawkins and Krebs, 1979; Rothstein, 1990). Under the arms race hypothesis, differences between host species in rejection behavior reflect different stages of a coevolutionary race (Davies and Brooke, 1989b), with acceptors at an early stage (experiencing evolutionary lag) and rejectors at a later stage. However, Brooker and Brooker (1996) recently reported a correlation between acceptance rates and host life-history traits and environment and a negative relationship between rejection rate and the "resultant" degree of egg mimicry.

Therefore, it seems that acceptance by cuckoo hosts cannot be due to evolutionary lag, and egg rejection behavior cannot be responsible for egg mimicry. Rather, host rejection has forced cuckoos to specialize mainly on those acceptors and partial acceptors whose life-history strategies and habitat allow them to cope with parasitism. Therefore, at least in the *Cuculus* clade of cuckoos, mounting evidence supports a hypothesis of evolutionary equilibrium in brood parasitism (Brooker and Brooker, 1996).

In this study I reanalyzed data and predictions from Brooker and Brooker (1996), while controlling for factors such as common phylogenetic descent, and using data from only one country and only one species of brood parasite, the European cuckoo. This new analysis clearly shows no relationship between any life-history trait of hosts and their level of rejection. Contrary to this prediction, Soler and Møller (1996) showed that the rejection rate was positively related to traits that evolved to facilitate cuckoo-egg recognition, such as a low degree of intraclutch variation and a high degree of interclutch variation, evidence that clearly supports the idea that egg pigmentation is an evolutionary response to brood parasitism and that coevolution took place (Øien et al., 1995).

Brooker and Brooker (1996) also found that acceptors, ejectors, and deserters varied in life-history traits, although none of the predictions were supported when controlling for

Table 1
Results of predictions by Brooker and Brooker (1996)

Prediction no. ^a	Using phylogenetically independent contrasts								Polytomies solved by Pagel and Harvey's (1989) methodology				Polytomies solved by Grafen's (1989) methodology			
	Using real data				Branch length = 1				<i>R</i>	<i>F</i>	df	<i>p</i>	<i>R</i>	<i>F</i>	df	<i>p</i>
<i>R_s</i>	<i>n</i>	<i>t</i>	<i>p</i>	<i>R</i>	<i>F</i>	df	<i>p</i>									
1	.15	22	0.69	.50	.03	0.02	1,20	.88	.07	0.09	1,20	.77	.07	0.09	1,20	.76
2	-.39	22	1.91	.07	-.16	0.53	1,20	.48	.08	0.12	1,20	.74	.07	0.11	1,20	.75
	-.03	22	0.13	.90	-.06	0.06	1,20	.80	-.03	0.02	1,20	.88	.03	0.02	1,20	.89
5 ^b	.21	22	0.95	.35	.01	0.00	1,20	.97	.02	0.01	1,20	.93	.02	0.01	1,20	.92
6	.02	22	0.10	.92	-.38	3.41	1,20	.08	-.34	2.53	1,20	.13	-.33	2.48	1,20	.13
Multiple regression analysis (dependent variable rejection rate; independent variables: migration and reneating ability)																
8, 9	<i>R</i>	df	<i>F</i>	<i>p</i>	<i>R</i>	<i>F</i>	df	<i>p</i>	<i>R</i>	<i>F</i>	df	<i>p</i>	<i>R</i>	<i>F</i>	df	<i>p</i>
	.30	2,19	0.77	.40	.10	0.08	2,18	.92	.08	0.02	2,18	.95	.11	0.11	2,18	.89
Migr.	.06	1,20	0.06	.81	-.07	0.08	1,19	.78	-.08	0.10	1,19	.75	-.07	0.10	1,19	.76
Renest.	-.20	1,20	1.68	.21	-.09	0.14	1,19	.71	-.04	0.03	1,19	.87	-.09	0.14	1,19	.71
Acceptors																
Deserters																
Ejectors																
Kruskal-Wallis test																
Mean																
<i>n</i>																
SE																
H																
<i>n</i>																
<i>p</i>																
3	2.58	6	0.46		2.08	9	0.28		3.31	4	0.56		4.54	19		.10
Discriminant analysis																
Wilks' λ																
<i>F</i> (8,26)																
<i>p</i>																
7													0.418	1.78		.128
Mass	41.9	6	19.3		17.9	9	3.7		51.6	4	26.2					
Migrant	2.83	6	0.85		4.33	9	1.3		4.00	4	1.70					
Costs ej.	0.0041	6	0.0017		0.0093	9	0.0039		0.0046	4	0.0025					
Renest.	0.51	6	0.13		0.39	9	0.06		0.80	4	0.17					
Wilks' λ																
<i>F</i> (4,30)																
<i>p</i>																
10, 11, 12													0.713	1.38		.263
Mass	41.9	6	19.3		17.9	9	3.7		51.6	4	26.2					
Costs ej.	0.0041	6	0.0017		0.0093	9	0.0039		0.0046	4	0.0025					

^a Prediction 1: frequency of rejection should increase as host mobility increases. Prediction 2: frequency of rejection tends to increase as the breeding season becomes shorter. Prediction 3: species with a long breeding season tend to be acceptors, those with a short breeding season tend to be deserters, while those with a very limited breeding season are ejectors. Prediction 4: the frequency of acceptance should increase as clutch size decreases. Prediction 5: species with the highest rejection rate should not be those whose eggs are mimicked by the cuckoo. Prediction 6: species with the lowest rejection rate should be those that are more frequently parasitized. Prediction 7: the three host-strategy groups (acceptors, deserters, and ejectors) are distinct when based on reneating potential (Renest.), migration, putative cost of raising a cuckoo (mass) and putative cost of ejection (Costs ej.). Predictions 8 and 9: acceptors should be sedentary species with high reneating ability, while rejecter species should have low reneating ability. Predictions 10, 11 and 12: acceptor species should be those for which the putative cost of raising a cuckoo is lowest; ejector species should be those for which the cost of ejection is lowest while deserter species should be intermediate. I show how the results of the different tests varied when using real data or contrasts estimated with different methodologies.

^b Prediction 5 was the only prediction supported by the analyses in the present study.

confounding factors. On the contrary, Davies and Brooke (1989a) found that species with smaller bills suffered greater rejection costs (own eggs damaged; see also Moksnes et al., 1991; Rohwer and Spaw, 1988) and that these species were more likely to reject model eggs by desertion than species with larger bills, which tended to reject by ejection. Therefore, the apparent relationship between host life-history traits and whether they are acceptors, ejectors, or deserters could be simply because this kind of behavior is related to bill length, which is a trait with a strong phylogenetic effect (closely related species have similar bill lengths and, therefore, similar costs of rejecting cuckoo eggs and life-history traits).

The only one of Brooker and Brooker's predictions supported by the new analysis is number 5: species with the highest rejection rate should not be those whose eggs are mimicked by the cuckoo. If the cuckoo egg mimicry appears as a counter-defense mechanism against the ability of hosts to reject cuckoo eggs, we should expect a positive relationship be-

tween these two variables. However, because egg coloration and patterns have a phylogenetic component (closely related species have similar kind of eggs compared with nonrelated species), it is difficult to know which host species is mainly responsible for the evolution of cuckoo egg mimicry. In this scenario, it is possible to detect cuckoo egg mimicry in a group of species not responsible for the evolution of that parasite counter-defense. Then, to test that relationship it is first necessary to detect host species potentially responsible for cuckoo egg mimicry. However, even in this case, a change in cuckoo host selection to a closely related species will make the interpretation of the results difficult because (1) although degree of mimicry will be the same, the former host may gradually lose its capability of such rejection behavior (see Cruz and Willey, 1989), and (2) the new host, not responsible for the cuckoo egg mimicry, will have a low rejection rate. Moreover, if cuckoos select similar nesting sites (Moksnes and Røskaft, 1987, 1995; Wyllie, 1981), or seek nests completely at

random in the habitat where they were born and reared (Brooke and Davies, 1991; Moksnes and Røskaft, 1995), it will be difficult to interpret the results. Therefore, to make clear predictions of cuckoo-host coevolution, it is first necessary to clarify the mechanisms governing cuckoo host selection and subsequently make predictions.

In conclusion, in a new analysis of the predictions by Brooker and Brooker (1996), I found weak support for the evolutionary equilibrium hypothesis described by the authors between the European cuckoo and its hosts. However, Brooker

and Brooker's hypothesis might still be correct, but they were not allowed to argue this based on current data. Moreover, it is clear that when analyzing life-history variables, which have a phylogenetic component, the use of modern comparative analyses is essential.

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APPENDIX

Information on body mass (g), clutch size, rejection rate (%), classification of host species, degree of mimicry (from Moksnes and Roskaft, 1995), bill length (mm), winter quarters (from Cramp and Perrins 1993–1994), migratory status, duration of the breeding season (months), reneating ability (duration of breeding season divided by clutch size), and cost of rejection (inverse of body mass multiplied by bill length)

	Body mass	Clutch size	Rejection rate ^a	Type of host	No. of clutch-ees	Mimicry	Bill length (mm)	Winter quarter	Migratory status	Breeding season	Re-neating ability	Cost of ejection
Hirundinidae												
<i>H. rustica</i>	18.6	5	0.0 ^{1,2}		2	0.0	5.7	S. Africa	7	3.00	0.600	0.009
Motacillidae												
<i>M. alba</i>	22.6	6	73.17 ^{1,2}	Deserter	2	54.2	9.0	England, Spain, Morocco	5	3.50 ^b	0.583	0.005
<i>M. flava</i>	16.8	6	80.00 ²	Deserter	2	64.0	9.8	Tropics	6	3.00 ^b	0.500	0.006
<i>A. pratensis</i>	18.2	5	26.83 ^{1,2}	Acceptor	2	74.9	8.5	Resident	1	3.50 ^b	0.700	0.006
Troglodytidae												
<i>T. troglodytes</i>	9.4	6	0.00 ¹		2	0.0	8.2	50–250 km	3	3.00	0.500	0.013
Prunellidae												
<i>P. modularis</i>	20.8	5	3.13 ^{1,2}	Acceptor	2	0.4	8.1	30 km	2	4.00	0.800	0.006
Turdidae												
<i>T. pilaris</i>	98.5	5	9.09 ²	Acceptor	1	0.0	15.7	S. Europe	5	2.50	0.500	0.001
<i>T. philomelos</i>	73.4	4	62.75 ^{1,2}	Ejector	2	0.0	14.0	Residents	1	4.25	1.063	0.001
<i>T. merula</i>	106.0	4	63.89 ^{1,2}	Ejector	3	0.0	17.3	3/4 residents	2	4.00	1.000	0.001
<i>T. iliacus</i>	67.2	6	34.88 ²	Acceptor	2	0.0	14.6	O. Europe below Scotland	4	1.75	0.292	0.001
<i>E. rubecula</i>	18.1	5	20.00 ¹	Acceptor	2	4.4	7.6	Largely resident	2	2.50	0.500	0.007
Sylviidae												
<i>P. collybita</i>	7.5	6	100.00 ²	Deserter	2	0.0	5.7	Spain	5	2.25	0.375	0.023
<i>P. trochilus</i>	8.8	5	90.00 ²	Deserter	1	0.0	6.2	S. Africa	7	2.00	0.400	0.018
<i>S. atricapilla</i>	17.0	5	76.92 ²	Deserter	2	65.0	7.2	France and Switzerland	4	2.00	0.400	0.008
<i>S. borin</i>	19.4	5	66.67 ²	Deserter	2	86.9	7.3	S. Africa	7	2.25	0.450	0.007
<i>A. scirpaceus</i>	12.0	4	61.82 ¹	Ejector	2	47.4	9.3	South Sahara	6	2.75	0.688	0.009
<i>A. palustris</i>	12.0	5	86.84 ³		1	19.1	8.6	S. Africa	7	2.00	0.400	0.010
Muscicapidae												
<i>M. striata</i>	15.0	5	72.22 ^{1,2}	Ejector	2	33.0	8.5	South Equador	7	2.25	0.450	0.008
Fringillidae												
<i>C. chloris</i>	28.6	5	24.14 ^{1,2}	Acceptor	2	8.2	10.2	Partially in Britain	3	1.25	0.250	0.003
<i>F. coelebs</i>	22.7	5	61.29 ^{1,2}	Deserter	1	11.8	9.7	10% migratory	2	1.25	0.250	0.005
Emberizidae												
<i>E. citrinella</i>	26.9	4	100.00 ²	Deserter	2	4.1	8.8	Sedentary	1	1.25	0.313	0.004
<i>E. schoenichus</i>	19.4	5	95.00 ²	Deserter	2	4.2	7.2	Chiefly sedentary in Britain	2	1.25	0.250	0.007

^a Sources: ¹Davies and Brooke (1989a), ²Moksnes et al. (1990), ³Cramp (1985) (when more than one reference was available for species I calculated the mean value).

^b No diagram was available in Cramp, but information for northwestern Europe. I used maximal period (in months minus 0.5).

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