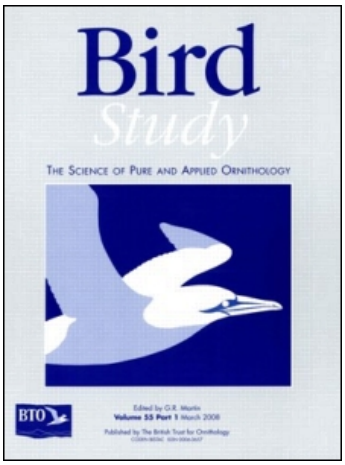

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Avian brood parasitism in a Mediterranean region: hosts and habitat preferences of Common Cuckoos Cuculus canorus

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Avian brood parasitism in a Mediterranean region: hosts and habitat preferences of Common Cuckoos *Cuculus canorus*

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Capsule Cuckoos in Italy support the 'host preference' hypothesis.
Aims To identify the species parasitized in a Mediterranean area, in Italy; to quantify the frequency of parasitism on each host species; and to determine whether some species and/or habitat types are parasitized more than expected from a homogeneous distribution.
Methods Nest records dating from 1865 were compiled from literature, nest card programmes, and personal communication with ornithologists working in the region. Comparisons of parasitism frequencies were made among and within habitats for all cuckoo hosts.
Results The most frequently parasitized hosts were Great Reed Warbler, European Robin, Marsh Warbler, Redstart, and Reed Warbler. The highest number of parasitized species was in anthropic areas (15 host species), whereas wetlands supported the highest number of parasitized nests (471).
Conclusion Cuckoos select a different suite of hosts in Italy from those in continental Europe, but this was not always explained on the basis of different geographical distribution. Results support the 'host preference' hypothesis. We suggest further analyses to avoid over- or underestimates of parasitism on each host species when parasite preferences are examined.

One of the oldest arms races between brood parasites and their hosts is the obligate parasitism of Common Cuckoos *Cuculus canorus*, hereafter cuckoo (Payne 1977). Although most research on interactions between this species of cuckoo and its hosts has been conducted at localized sites (Molnár 1944, Wyllie 1981, Moksnes & Røskaft 1987, Davies & Brooke 1989a, Lindholm & Thomas 2000, Honza *et al.* 2004), analyses on a broader scale have relied on the determination of parasitism frequencies derived from reviews of records of parasitism in the literature, nest record cards, and inspections of clutches of parasitized species in museums (Lack 1963, Wyllie 1981, Glue & Morgan 1972, Glue & Murray 1984, Brooke & Davies 1987, Davies & Brooke 1989b, Moksnes & Røskaft 1995, Sealy *et al.* 1996, Davies 2000). Results of these studies have revealed that some passerine species are clearly favoured as hosts, whereas others are parasitized only occasionally (Glue & Morgan 1972, Glue & Murray 1984, Moksnes & Røskaft 1995, Perrin de Brichambaut 1997, Yom-Tov & Geffen 2005). On the basis of these compilations, hypotheses on the evolution of parasite/host relationships have been formulated which predict, for example, that heavily parasitized species are more likely to evolve the ability to discriminate between parasitic eggs and their own eggs, and eventually reject the foreign eggs (Brooke & Davies 1987, Moksnes & Røskaft 1987, Davies & Brooke 1988, Brooke & Davies 1991).

Although the breeding distribution of Common Cuckoos includes the entire Western Palearctic, reviews of the frequency of parasitism have been focused on host populations in countries of northern Europe (Lack 1963, Wyllie 1981, Glue & Morgan 1972, Glue & Murray 1984, Moksnes & Røskaft 1995, Sealy *et al.* 1996, Davies 2000). Analyses of cuckoo habitat preferences have also been restricted to continental Europe (Glue & Morgan 1972). Few summaries of the frequency of parasitism exist for passerine species in a Mediterranean area (Perrin de Brichambaut 1997), as most studies have been restricted to one or a few sites and have involved anecdotal observations (Claudon 1955), or effects of parasitism on one area or

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on one host species (Alvarez 1993, 1996). Studies of cuckoo habitat preferences are generally lacking. Truffi (1980, 1983, 1986) listed the cuckoo's host species in Italy but he did not quantify the frequency of parasitism on each host.

The aim of this paper is to quantify the frequency of parasitism on each cuckoo host over a Mediterranean region (Italy) by compiling data from nest records dated from 1865 to 2004. We also compared the frequencies of parasitism on species among and within habitats to develop the first quantitative database on which to test hypotheses on cuckoo habitat or host preferences in Mediterranean areas. We compared the parasitism frequencies with data available in the northern portion of the cuckoo's range, in the Western Palearctic.

METHODS

A preliminary list of potential cuckoo hosts nesting in Italy (Fig. 1) was compiled from records that date from 1865 (Bettoni 1865; Giglioli 1889, 1890; Rossi & Di Carlo 1948; Moltoni 1951, 1960, Pazzuconi 1968, Foschi 1978, Realini 1980, Brichetti & Cambi 1981). These reports contained observations of parasitized nests as well as observations of fledged cuckoos being fed by their putative hosts. To verify that all species were the actual cuckoo hosts we searched the literature, using the *BDO 2000* database (Brichetti 2005), which included all articles from ornithological journals, atlases, national, regional and local reports of museums, private and public institutions, and proceedings of conferences published between 1900 and

Figure 1. Area searched for records of avian brood parasitism by Common Cuckoo.

2003, which dealt with the Italian avifauna. From each source, and for each species, we extracted the number of parasitized and unparasitized nests observed, at both the egg and nestling stages, but excluded sources which reported only that a species was parasitized, when only a vague indication was given of the number of nests that had been inspected. We did not include sources that reported adults feeding cuckoo fledglings or adults mobbing cuckoos because these may not reliably indicate host use (Redondo 1993, Sealy & Lorenzana 1997). We excluded records reported in other publications that clearly did not indicate whether the data involved new observations or whether they had been cited by other sources. For 2001–04, we also reviewed nest cards submitted throughout Italy, collected by the Italian Nest Record Scheme and run by the Italian Wildlife Institute (ISPRA, ex-INFS; Zenatello 2004).

Requests for records of parasitized and unparasitized nests of potential cuckoo hosts were published in the ornithological journal *Avocetta* (2005, vol. 29, number 2, p. 107), posted on the website of the Italian Centre for Avian Studies (CISO), and sent to the online mailing list of the European Bird Net-Italy. Additional records were obtained through correspondence from 13 ornithologists and naturalists, four of whom had published papers that also contributed to this review (Pazzuconi 1965, Quaglierini 2002, Caffi 2004, Dicapi & Maestri 2004); five had published papers in Italian journals (Andena 1974, Fracasso 1978, Viganò 1990, Mostini 1992, Grattini 2003), two as nest recorders for the Italian Wildlife Institute (ISPRA, ex-INFS; A. Belosi, C. Mancuso), and two were members of the Italian Association for the Protection of Birds (LIPU; L. Bonetti, A. Cazzaniga). These records were used only when they met the criteria indicated above and if they had not been published previously or were included in Zenatello (2004).

These records permitted us to calculate the number of parasitized and unparasitized nests for each of the species indicated as cuckoo hosts and to determine the frequency of parasitism as the number of parasitized nests out of the total nests observed. We classified cuckoo hosts according to their habitat (Mediterranean mattoral, woodland, mountain, riparian, and anthropic areas) as indicated by Cramp (1992) and Fornasari *et al.* (2004). We used chi-square tests (Zar 1999) to verify whether the number of parasitized species or nests was equally distributed among all hosts in or within habitats.

RESULTS

A list of 70 potential cuckoo hosts was extracted from the first literature reviews (Bettoni 1865; Giglioli 1889, 1890; Rossi & Di Carlo 1948; Moltoni 1951, 1960; Pazzuconi 1968; Foschi 1978; Realini 1980; Brichetti & Cambi 1981). Of 102 additional studies reviewed by us, 65 met the criteria necessary for inclusion in the analysis. We compiled a total of 13 157 nests of 70 species distributed among 16 families in the orders Piciformes and Passeriformes (Appendix 1). Icterine Warbler and Willow Warbler (scientific names given in Appendix 1) were not confirmed as cuckoo hosts: Moltoni (1951) had reported them as parasitized, but because neither species has been confirmed as nesting in Italy, Truffi (1983) suggested that errors had been made in nest identification. Another 24 species, each of which nests in Italy, but not recorded as parasitized, were in the families Motacillidae, Turdidae, Paridae, Passeridae, Fringillidae, and Emberizidae. The other 44 species were confirmed as cuckoo hosts (Table 1). Species in the Sylviidae were the most frequently parasitized, accounting for 41% of the parasitized species. The species parasitized most frequently were Great Reed Warblers (27% of 1416 nests), followed by Wood Warblers (25% of 4), European Robins (23% of 150), and Dunnocks (20% of 35). The four least parasitized were Moustached Warblers and European Goldfinches (0.7% of 151 and 293 nests, respectively), followed by Blackbirds (0.5% of 1083) and Red-backed Shrikes (0.3% of 323). Neither the number of species parasitized ($\chi^2 = 12.7$, df = 5, $P = 0.026$) nor the number of nests parasitized ($\chi^2 = 533$, $P < 0.001$) was equally distributed among the six habitats where hosts nested (Fig. 2).

Riparian habitats supported the fewest parasitized species (2 out of 44; 4.5%), whereas anthropic areas predominated with 15 species (34.1%). Frequency of parasitism on hosts nesting in wetlands was higher than the mean for all habitats (18.4% versus 7.8%, respectively), whereas in anthropic areas, the number of nests parasitized was less than the number expected (3.2% versus 7.8%). There were too few species in riparian habitats to permit a comparable analysis of the frequency of parasitism among hosts. Within the remaining five habitats, the frequency of parasitism was not equally distributed among species. Against a mean of 2.4% among all host nests in the Mediterranean mattoral, Orphean Warblers were the most frequently parasitized (13.2%; $\chi^2 = 42.5$, df = 6, $P < 0.001$). The frequency of parasitism was most

Table 1. Frequencies of parasitism determined as the proportion of nests parasitized out of the total nests reported. Codes are composed by first two letters of the genus and species names and refer to species abbreviations used in Figure 3.

Code	Cuckoo host species	Frequency of parasitism	Nests (*n*)
ACAR	Great Reed Warbler[1]	0.267	1416
PHSI	Wood Warbler	0.250	4
ERRU	Robin[1]	0.227	150
PRMO	Dunnock[1]	0.200	35
ACPA	Marsh Warbler	0.191	131
PHPH	Redstart[1]	0.160	331
SYNI	Barred Warbler	0.158	38
LUAR	Woodlark	0.156	32
SYHO	Orphean Warbler[1]	0.132	38
SYSA	Marmora's Warbler	0.111	27
SYBO	Garden Warbler	0.094	53
SARU	Whinchat	0.091	22
ACSCI	Reed Warbler	0.079	820
TUVI	Mistle Thrush	0.079	38
CIJU	Fan-tailed Warbler	0.071	70
ANSP	Water Pipit	0.057	35
ACSCH	Sedge Warbler	0.054	37
SATO	Stonechat	0.054	186
SYCO	Whitethroat	0.050	159
PHOC	Black Redstart	0.049	123
GACR	Crested Lark	0.047	64
OEOE	Wheatear	0.039	77
TIMU	Wall Creeper	0.036	28
SYCA	Subalpine Warbler	0.030	102
SYCU	Lesser Whitethroat	0.029	34
MOFL	Yellow Wagtail	0.029	69
LUME	Nightingale	0.027	219
MOAL	White Wagtail	0.027	110
EMCI	Cirl Bunting	0.025	204
HIPO	Melodious Warbler	0.023	128
PHBO	Bonelli's Warbler	0.022	45
MUST	Spotted Flycatcher	0.022	226
TRTR	Wren	0.021	191
ANCA	Twany Pipit	0.020	51
SYME	Sardinian Warbler	0.016	124
MICA	Corn bunting	0.014	208
LASE	Woodchat Shrike	0.014	73
HIRU	Swallow	0.012	416
SYAT	Blackcap	0.011	701
SESE	Serin	0.009	229
CACA	European Goldfinch	0.007	293
ACME	Moustached Warbler	0.007	151
TUME	Blackbird	0.005	1083
LACO	Red-backed Shrike	0.003	323

[1]Species whose frequency of parasitism was significantly higher than the mean recorded for all hosts parasitized in the same habitat.

unequal among hosts in woodlands where European Robins were parasitized at 22.7%, compared with 4.4% of the habitat mean (χ^2 = 134, df = 7, $P < 0.001$, Fig. 3a). In high mountains, almost all species were parasitized, with a mean of 7.2%; only Dunnocks were parasitized more frequently, at 20% (χ^2 = 12.6, df = 6, $P = 0.050$, Fig. 3b). The heavy parasitism recorded in wetlands was due mostly to parasitism on Great Reed Warblers (χ^2 = 124, df = 4, $P < 0.001$, Fig. 3c). The unequal parasitism within the anthropic habitat was at the expense of Redstarts, which were parasitized at 16% against the habitat mean of 3.2% (χ^2 = 238, df = 14, $P < 0.001$, Fig. 3d). The unequal frequency of parasitism recorded among hosts within habitats was also due to a parasitism frequency that was lower than the habitat mean for Blackcaps in Mediterranean mattoral, European Goldfinches in woodlands, Wheatears in mountains, Reed Warblers in wetlands, and Blackbirds in anthropic areas (Fig. 3).

DISCUSSION

In Italy, 10 of the 20 most parasitized species (Great Reed Warbler, Robin, Dunnock, Marsh Warbler, Black Redstart, Barred Warbler, Garden Warbler, Whinchat, Reed Warbler, and Whitethroat) were among the hosts most parasitized elsewhere in Europe (Appendix 1), whereas the other 10 species were recorded only as secondary hosts (Moksnes & Røskaft 1995). This was expected for Woodlark, Orphean Warbler, Marmora's Warbler, and Fan-tailed Warbler whose distribution is typically Mediterranean, but not for the other six species (Wood Warbler, Mistle Thrush, Water Pipit, Sedge Warbler, Stonechat, Red Blackstart), which are also abundant in northern Europe (Cramp 1992). The most surprising hosts are Mistle Thrush and Black Redstart, which are considered to be unsuitable species (Moksnes & Røskaft 1995). The latter authors recorded only one and seven parasitized nests of these species, respectively, among 12 000 parasitized clutches examined in museum collections (Moksnes & Røskaft 1995).

Among the 24 species for which we could not confirm their status as hosts, 16 have been considered unsuitable (Moksnes & Røskaft 1995) (see Appendix 1) and parasitized only occasionally elsewhere in the Western Palearctic. By contrast, one of the other eight suitable yet unparasitized species in Italy, Meadow Pipit, is one of the favoured host species in northern Europe (Sealy *et al*. 1996, Davies 2000). Meadow Pipits are scarce and local in Italy (Meschini and Frugis 1993); in fact, during an extensive census, they were recorded in fewer than 20% of the census plots (Fornasari *et al*. 2004). Moreover, Chiffchaffs, one of the most frequently parasitized hosts in Finland (Davies 2000), were similarly not parasitized in Italy. In addition to their scarcity, a different habitat composition of the two areas might account for this difference, as

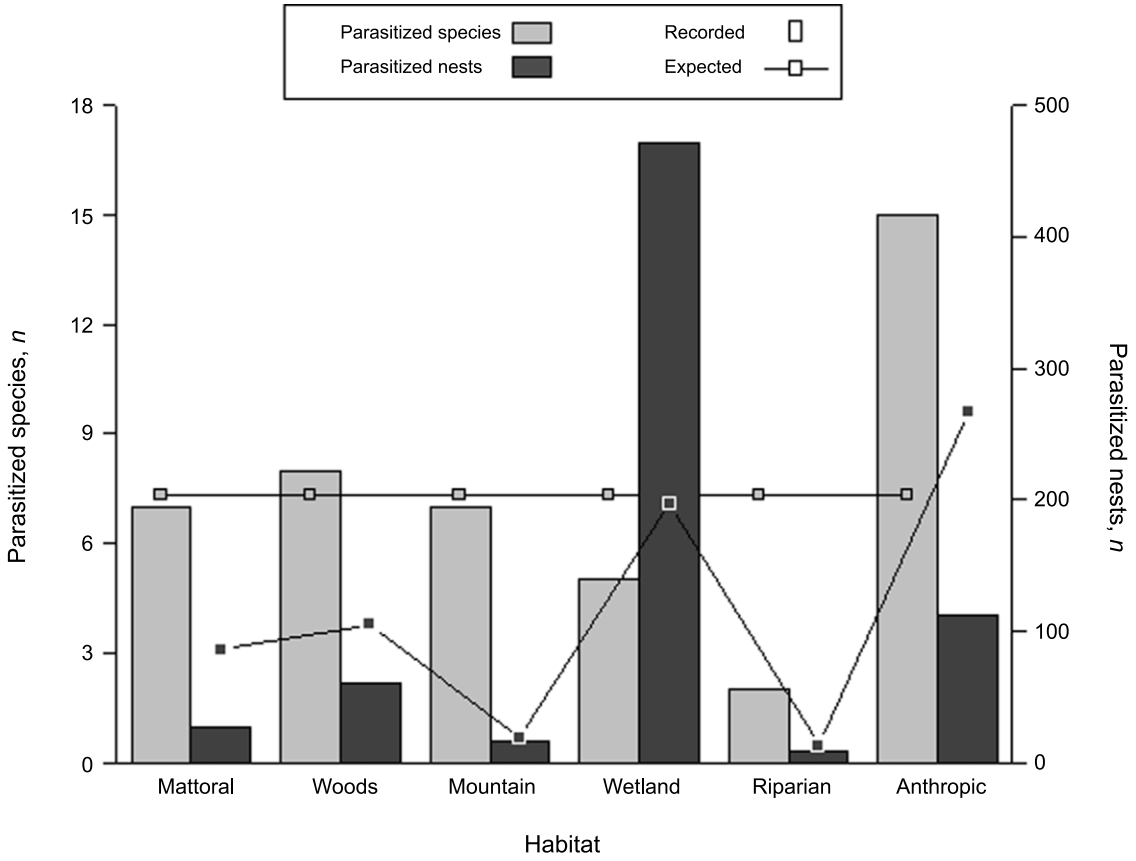

Figure 2. Species and nests parasitized in different habitats of the Italian region as numbers recorded by compiling nest records (bars) and as numbers expected (lines) from an equally distributed parasitism pressure.

Chiffchaffs inhabit open forests, one of the predominant habitat types in Finland, but which is much less extensive in Italy (Enoksson *et al.* 1995, Corona *et al.* 2002).

The degree of host specialization in cuckoos is well known, according to the level of egg mimicry of the different cuckoo *gens* (Brooke & Davies 1988, Moksnes *et al.* 1995). From the tables of data on hosts parasitized, reported by Pazzuconi (1997), some sort of egg mimicry apparently occurs on some of the most frequently parasitized species in Italy, such as Orphean Warbler, European Robin and Great Reed Warbler. Furthermore, a striking similarity with cuckoo *gens* breeding in other parts of Europe is the perfect egg mimicry and absence of egg mimicry of Redstart and Dunnock, respectively, both species that lay immaculate blue eggs (Brooke & Davies 1988, Rutila *et al.* 2002). Nest records that we analysed often did not report the degree of cuckoo egg matching, thus, further studies are necessary to confirm what has been found elsewhere, that egg morphs are laid not only in nests where host-egg mimicry is perfect but also in nests of other species where the match may be poor (Moksnes & Røskaft 1995).

To unravel the mechanisms of the maintenance of egg mimicry, authors have alternatively hypothesed that cuckoos search for a single species to parasitize ('host preference' hypothesis; Baker 1942, Lack 1968) or for the same nest type ('nest-site' hypothesis; Wyllie 1981, Moksnes & Røskaft 1987) or habitat ('natal philopatry' hypothesis; Brooke & Davies 1991) in which they were reared. Our results agree with studies that have provided robust evidence in support of the 'host preference' hypothesis (Marchetti *et al.* 1998, Davies 2000, Gibbs *et al.* 2000). The unequal parasitism pressure among hosts within habitats and with similar nest types is not consistent with the other hypotheses, where a similar parasitism pressure would be expected to have been evenly distributed among all host species breeding in a particular habitat or with a specific nest type, respectively. Recently, results of a study of parasitized Reed Warblers showed that host density predicted the frequency of parasitism of different populations that nest

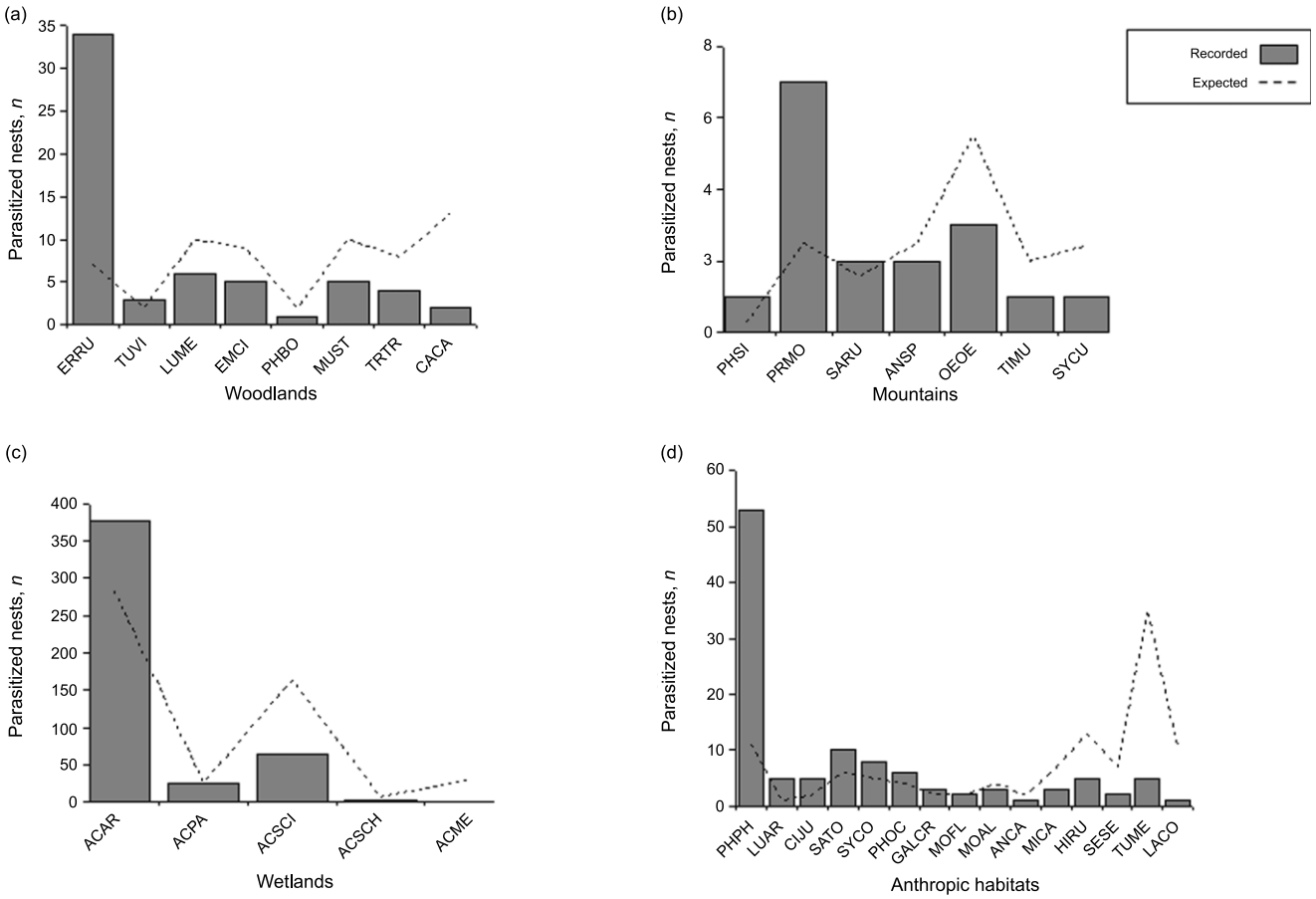

Figure 3. Nests parasitized for each cuckoo host as numbers recorded by compiling nest records and as numbers expected from an equally distributed parasitism pressure within (a) woodlands; (b) mountains; (c) wetlands; and (d) anthropic habitats.

in Europe (Stokke *et al.* 2007). Similarly, it is necessary to determine the abundance of each host to ascertain whether the species most frequently parasitized in this study are selected by cuckoos in proportion to the availability of their nests.

Although analyses on a larger spatial scale have been important in unravelling coevolutionary interactions between cuckoos and their hosts (Brooke & Davies 1987, Lindholm 1999, Soler *et al.* 1999, Soler & Soler 2000, Røskaft *et al.* 2002), some authors (Lack 1963; Glue & Morgan 1972; Brooke & Davies 1987, 1991; Moksnes & Røskaft 1995) correctly noted biases in these methods. Nest cards may reflect the abundance of the species in habitats close to human settlements, whereas communities in more isolated habitats may be neglected, or some species may have been the focus of long-term studies. Only anecdotal observations are available for other species. We have treated our results cautiously because the method we used to present the data, such as the total number of nests, may not have been representative of the sizes of nesting populations available to the cuckoos (Lack 1963; Glue & Morgan 1972; Hurlbert 1984; Brooke & Davies 1987, 1991; Moksnes & Røskaft 1995). In turn, the frequencies of parasitism calculated may be over- or underestimates of local parasitism when simply averaged over a larger geographic area. This has limited our ability to identify a geographical or temporal pattern in host use over the area considered. Nevertheless, as our data were obtained using the same methods as other workers, these results provide additional information on the dynamics of parasitism in a more extended area of the cuckoo's range and, thus, broaden the background against which to propose hypotheses on the coevolutionary interactions between Common Cuckoos and their hosts.

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APPENDIX 1. PARASITIZED AND UNPARASITIZED NEST NUMBERS DETERMINED BY REVIEWING NEST RECORDS FOR 70 SPECIES INDICATED AS CUCKOO HOSTS

Potential cuckoo host species	Number of nests		Sources
	Unparasitized	Parasitized	
Wryneck[1] *Jynx torquilla*	49	0	Zenatello (2004)
Crested Lark *Galerida cristata*	61	3	Truffi (1983), Salvo (1995), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Woodlark *Lullula arborea*	27	5	Di Carlo (1957), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Sky Lark *Alauda arvensis*	90	0	Pasquali & Pasquali (1977), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Swallow[1] *Hirundo rustica*	411	5	Truffi e Giussani (1995), Zenatello (2004). L. Bonetti (Pers. comm.)
Twany Pipit *Anthus campestris*	50	1	Cambi (1982), Tornielli & Ravasini (1982), Alessandria *et al.* (1996), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Tree Pipit *A. trivialis*	50	0	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Meadow Pipit[10] *A. pratensis*	1	0	Vallon (1919)
Water Pipit[2, 4, 5] *A. spinoletta*	33	2	Truffi (1985), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Yellow Wagtail *Motacilla flava*	67	2	Vallon (1919), Truffi (1983), Carlotto (1987), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Grey Wagtail *M. cinerea*	13	0	Di Carlo (1972), Zenatello (2004)
White Wagtail[2, 3, 4, 6, 7, 8 9] *M. alba*	107	3	Truffi (1983), Petraccaro *et al.* (1987), Panzera (1988), Valle & D'Este (1992), Zenatello (2004), L. Andena, A. Belosi, A. Cazzaniga, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Wren[6, 7] *Troglodytes troglodytes*	187	4	Quaglierini *et al.* (1979), Truffi (1985, 1986), Zenatello (2004), L. Andena, A. Belosi, A. Cazzaniga, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Dunnock[2, 6] *Prunella modularis*	28	7	Truffi (1983, 1985), Zenatello (2004), L. Andena, M. Caffi, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Alpine Accentor[1] *P. collaris*	16	0	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Robin[2, 6, 8, 9] *Erithacus rubecola*	116	34	Salvini (1957), Quaglierini *et al.* (1979), Truffi (1983, 1985), Bocca & Maffei (1997), Caffi (2002a), Zenatello (2004), L. Andena, A. Belosi, A. Cazzaniga, C. Dicapi, A Pazzuconi., A. Quaglierini, E. Viganò (Pers. comm.)
Nightingale *Luscinia megarhynchos*	213	6	Truffi (1983, 1985), Caffi (2004), Zenatello (2004), L. Andena, A. Belosi, L. Bonetti, M. Caffi, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Black Redstart[1] *Phoenicurus ochruros*	117	6	Bordignon (1984), Tabarrini (1985), Truffi (1985), Petraccaro *et al.* (1987), Bocca & Maffei (1997), Zenatello (2004), L. Andena, A. Belosi, C. Dicapi, L. Mostini, A. Pazzuconi, E. Viganò (Pers. comm.)
Redstart[4, 8, 9] *P. phoenicurus*	278	53	Banfi (1944), Messedaglia (1948), Cova (1981), Truffi (1981, 1985), Zenatello (2004), L. Andena, A. Belosi, A. Cazzaniga, C. Dicapi, L. Mostini, A. Pazzuconi, E. Viganò (Pers. comm.)
Whinchat *Saxicola rubetra*	20	2	Truffi (1985, 1986), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Stonechat *S. torquata*	176	10	Truffi (1983), Paci (1990), Malavasi (1998), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Wheatear[1] *Oenanthe oenanthe*	74	3	Bocca & Maffei (1997), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Rock Thrush[1] *Monticola saxatilis*	68	0	Cagnucci (1998), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Ring Ouzel[1] *Turdus torquatus*	17	0	Ceccarelli & Foschi (1986), Zenatello (2004), L. Andena, C. Dicapi, L. Mostini, A. Pazzuconi, E. Viganò (Pers. comm.)
Blackbird[1] *T. merula*	1078	5	Vallon (1919), Truffi (1985, 1986), Bocca & Maffei (1997), Caffi (2002b), Zenatello (2004), L. Andena, A. Belosi, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Song Thrush[1] *T. philomelos*	5	0	Zenatello (2004)
Mistle Thrush[1] *T. viscivorus*	35	3	Truffi (1986), Zenatello (2004), L. Andena, A. Pazzuconi, E. Viganò (Pers. comm.)

continued

APPENDIX 1. CONTINUED

Potential cuckoo host species	Number of nests: Unparasitized	Number of nests: Parasitized	Sources
Fan-tailed Warbler *Cisticola juncidis*	65	5	Cambi (1982), Dicapi (1983), Caffi (2002a), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, A. Quaglierini (Pers. comm.)
Moustached Warbler *Acrocephalus melanopogon*	150	1	Quaglierini (2003), Zenatello (2004), C. Dicapi (Pers. comm.)
Sedge Warbler *A. schoenobaenus*	35	2	Pollo (1992), L. Bonetti, A. Pazzuconi, A. Quaglierini (Pers. comm.)
Marsh Warbler *A. palustris*	106	25	Pazzuconi (1965), Truffi (1983), Realini (1984), L. Andena, L. Bonetti, M. Caffi, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Reed Warbler[2, 6] *A. scirpaceus*	755	65	Quaglierini *et al.* (1979), Bocca & Maffei (1997), Quaglierini (2003), Zenatello (2004), L. Andena, C. Dicapi, N. Grattini, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Great Reed Warbler[9] *A. arundinaceus*	1038	378	Petretti (1979), Quaglierini *et al.* (1979), Truffi (1983), Quaglierini (2003), Zenatello (2004), L. Andena, C. Dicapi, G. Fracasso, N. Grattini, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Icterine Warbler *Hippolais icterina*	–	–	–
Melodious Warbler *H. polyglotta*	125	3	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Marmora's Warbler *S. sarda*	24	3	Truffi (1986), C. Dicapi, A. Pazzuconi (Pers. comm.)
Subalpine Warbler *Sylvia cantillans*	98	3	Massa (1981), Cambi (1982), Truffi (1983), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Sardinian Warbler *S. melanocephala*	122	2	Massa (1981), Truffi (1983), Bocca & Maffei (1997), Zenatello (2004), L. Andena, C. Dicapi, C. Mancuso, A. Pazzuconi, A. Quaglierini (Pers. comm.)
Orphean Warbler *S. hortensis*	33	5	Quaglierini *et al.* (1979), Truffi (1985), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Barred Warbler[7] *S. nisoria*	32	6	Cambi (1979), Truffi (1983), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Lesser Whitethroat *S. curruca*	33	1	Truffi (1983), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Whitethroat[4] *S. communis*	151	8	Giglioli (1889), Massa (1981), Cambi (1982), Truffi (1983), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Garden Warbler[7] *S. borin*	48	5	Quaglierini *et al.* (1979), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Blackcap *S. atricapilla*	693	8	Sommani (1976), Canobbio (1979), Quaglierini *et al.* (1979), Truffi (1985), Massa (1997), Caffi (2000), Zenatello (2004), L. Andena, A. Belosi, M. Caffi, A. Cazzaniga, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Weastern Bonelli's Warbler *Phylloscopus bonelli*	44	1	Bocca & Maffei (1997), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Wood Warbler *P. sibilatrix*	3	1	Bonvicini & Farina (1991), L. Andena, E. Viganò. (Pers. comm.)
Chiffchaff[3] *P. collybita*	47	0	Zunino (1969), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Willow Warbler *P. trochilus*	–	–	–
Spotted Flycatcher *Muscicapa striata*	221	5	Pasquali (1991), Zenatello (2004), L. Andena, A. Belosi, A. Cazzaniga, C. Dicapi, L. Mostini, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Coal Tit[1] *Parus ater*	87	0	Messini *et al.* (1997), Zenatello (2004), L. Andena, A. Cazzaniga, C. Dicapi, L. Mostini, A. Pazzuconi (Pers. comm.)
Blue Tit[1] *P. caeruleus*	713	0	Petrassi *et al.* (1998), Fraticelli *et al.* (1989), Ruvolo *et al.* (1991), Minelli *et al.* (1994), Sorace *et al.* (1996), Murgia *et al.* (1997), Tanda *et al.* (2001), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Great Tit[1] *P. major*	1275	0	Di Carlo (1972), Fraticelli *et al.* (1989), Fusco *et al.* (1991), Ruvolo *et al.* (1991), Minelli *et al.* (1993), Sorace *et al.* (1996), Arcamone & Brichetti (1997), Messini *et al.* (1997), Nissardi *et al.* (1997), Petrassi *et al.* (1998), Zenatello (2004), L. Andena, C. Dicapi, L. Mostini, A. Pazzuconi, A. Quaglierini (Pers. comm.)
Wall Creeper[1] *Tichodroma muraria*	27	1	De Franceschi (1981), Dicapi & Maestri (2004), L. Andena, C. Dicapi (Pers. comm.)

continued

APPENDIX 1. CONTINUED

Potential cuckoo host species	Number of nests: Unparasitized	Number of nests: Parasitized	Sources
Red-backed Shrike[7] *Lanius collurio*	322	1	Vallon (1919), Quaglierini *et al.* (1979), Rolando (1979), Favini *et al.* (1995), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Woodchat Shrike *L. senator*	72	1	Truffi (1986), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, A. Quaglierni (Pers. comm.)
Starling[1] *Sturnus vulgaris*	361	0	Brichetti *et al.* (1993), Zenatello (2004), C. Dicapi, A. Pazzuconi (Pers. comm.)
House Sparrow[1] *Passer domesticus*	279	0	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Tree Sparrow[1] *P. montanus*	341	0	Zenatello (2004)
Snow Finch[1] *Montifringilla nivalis*	37	0	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Chaffinch *Fringilla coelebs*	194	0	Zenatello (2004), L. Andena, A. Belosi, C. Dicapi, L. Mostini, A. Pazzuconi, E. Viganò (Pers. comm.)
Serin[1] *Serinus serinus*	227	2	Truffi (1986), Zenatello (2004), L. Andena, A. Belosi, C. Dicapi, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Greenfinch[1] *Carduelis chloris*	319	0	Zenatello (2004), L. Andena, A. Belosi, C. Dicapi, A. Pazzuconi, A Quaglierini., E. Viganò (Pers. comm.)
Goldfinch[1] *C. carduelis*	291	2	Vallon (1919), Truffi (1986), Zenatello (2004), L. Andena, A. Belosi, C. Dicapi, L. Mostini, A. Pazzuconi, A. Quaglierini, E. Viganò (Pers. comm.)
Bullfinch[1] *Pyrrhula pyrrhula*	158	0	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Hawfinch[1] *Coccothraustes coccothraustes*	38	0	L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Yellowhammer *Emberiza citrinella*	41	0	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Cirl Bunting *E. cirlus*	199	5	Truffi (1985), Zenatello (2004), L. Andena, A. Belosi, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)
Rock Bunting[1] *E. cia*	29	0	Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi (Pers. comm.)
Reed bunting *E. schoeniclus*	36	0	Zenatello (2004), L. Andena, C. Dicapi (Pers. comm.)
Corn bunting *Milaria calandra*	205	3	Truffi (1983), Zenatello (2004), L. Andena, C. Dicapi, A. Pazzuconi, E. Viganò (Pers. comm.)

[1]Unsuitable hosts (*sensu* Moksnes & Røskaft 1995); favoured cuckoo hosts reported in [2]Britain, [3]Finland, [4]Sweden, [5]Norway, [6]France, [7]Germany, [8]ex Czechoslovakia, [9]Russia (Davies 2000), [10]Ireland (Sealy *et al.* 1996).