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Avian brood parasitism in Italy: another perspective

Daniela Campobello[1,*], Spencer G. Sealy[2]

[1] *Università degli Studi di Palermo, Department STEBICEF, Italy*
[2] *University of Manitoba, Department Biological Sciences, Canada*
* *Corresponding author: daniela.campobello@unipa.it*

Abstract – We present a quantitative analysis of the data reported in the only published review of parasitism frequency on hosts of Common Cuckoo *Cuculus canorus* in a Mediterranean area. We first eliminated a bias potentially introduced by the method by which data were recorded. Of the initial potential 70 species parasitized in Italy, only 44 were confirmed as host species, of which only 10 species had more than 10% of their total nests parasitized. We highlighted differential parasitism on host species according to geographic area, but the analysis suggested results were strongly biased because nest location was generally not reported and the number of records steeply decreased from North to South.

Key-words: avian brood parasitism, *Cuculus canorus*, coevolution, host use, meta-analysis.

INTRODUCTION

One of the best examples of coevolutionary adaptations is the interaction between avian brood parasites and their hosts (Payne 1977). Obligate avian brood parasites lay eggs in nests of other species, and divert all parental care to the host species. Hosts generally incur high reproductive costs because they rear few, if any, of their own young (Soler 2017).

The Common Cuckoo (*Cuculus canorus*, hereafter Cuckoo) is the most studied species of brood parasite in the Palearctic (Soler 2017). With its peculiar reproductive strategy, the Cuckoo is one of the most virulent brood parasites, because within a day or two of hatching its chick evicts the host's eggs and nestlings (Grim et al. 2009). Interactions between the Cuckoo and its hosts has long attracted interest among researchers as a seminal example of coevolution (Davies and Brooke 1988), but recently attention to this species has arisen on another front, its decline in numbers (Hewson et al. 2016). This is unfortunate because the Cuckoo has been denoted as a biodiversity indicator (Morelli et al. 2017). As an obligate parasite whose successful reproduction hinges upon the availability of other species, the Cuckoo's absence has been proposed as an indicator of the absence of its potential hosts.

Causes of the Cuckoo decline, however, remain uncertain. Identifying host use and its frequency, and quantifying Cuckoo reproductive success has become important in the design of future conservation measures (Massa & Borg 2018). Over the Cuckoo's entire breeding range, the species' reproductive success has been regularly quantified only in the United Kingdom (Davies 2000). Ten years ago, we assessed host status in Italy by compiling records of parasitism (Campobello & Sealy 2009). We quantified the parasitism frequency of 70 potential host species by compiling records from 1865, but these records were heterogeneous, which possibly biased the results and their interpretation.

Here we re-analyse our previous records using a meta-analytic approach to determine whether parasitism frequency calculated from records derived from the literature, nest cards, and personal communications were affected by the heterogeneity of the sources of the data. Having established the reliability of determining parasitism frequency in the previous analysis, on the actual and most parasitized species, we provided descriptive statistics related to nesting habits, ecology and behaviour. Finally, as species decline is usually global but causes may be local, in the attempt to list parasitism records for five main areas of the Italian peninsula, we revealed the need to acquire more data to reveal local parasitism frequency and host preferences.

MATERIAL AND METHODS

Verifying potential bias

We reviewed records compiled by Campobello & Sealy (2009) to identify potential biases in the calculation of par-

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asitism frequency that may be related to methods by which records were originally reported. Following a summary of methods used to report the records, we listed potential hosts suggested by the literature from the end of 1800s, searching the BDO 2000 database (Brichetti 2005) specifically for records in the Italian avifauna. In addition to reviewing nest cards filed in the Italian Nest Record Scheme (ISPRA, ex-INFS; Zenatello 2004), we appealed to the readers of *Avocetta* (2005, vol. 29, number 2, p. 107) for records of parasitized and unparasitized nests of potential cuckoo hosts and also corresponded with well-known ornithologists and naturalists. The resulting records allowed us to compute the frequency of parasitism among the species.

We used a meta-analytical technique to evaluate whether parasitism frequency calculated from published records, reported in nest record schemes, and derived from personal communications was affected by the heterogeneity of data and sources. Following Gurevitch and Hedge (1993), we quantified the parasitism frequency per species as an "effect size", *d*, that is the difference between the number of parasitized and unparasitized nests divided by a pooled Standard Deviation (SD). For each species, we used mean plus SD derived from the number of parasitized and unparasitized nests reported for each record. Therefore, *d* was a measure of the parasitism frequency on each species weighted by the species' abundance (parasitized and unparasitized nest mean) and by the variability (SD of parasitized and unparasitized nest) of results due to the different methods of obtaining the data. We hypothesized that if records were homogenous, parasitism frequency would correlate with effect size, or possibly was affected by pseudoreplication (i.e. number of records artificially inflated). If so, frequency of parasitism on a given species may be an artefact that reflects an experimental design consistent with all observations. Parasitism frequency and effect size data sets were log transformed to meet the condition of a normal distribution. Gurevitch & Hedges (1983) showed that their statistic *d* is able to take into account the strong imbalance of the numbers of records often present in databases obtained from detailed literature sampling. Their data treatment and statistics (Electronic Supplementary Materials, **ESM 1**) are, in other words, a way to weigh the collected results in relation to the sample size. Formula applied to the database and data treatment are reported in **ESM 1**.

Descriptive statistics

Referring to the original list of host species (Campobello & Sealy 2009), we arbitrarily selected species whose frequency of parasitism was higher than 10%. We characterized these species according to data compiled from Cramp (1992) on nest site (i.e. on the ground, low, high), nest type (i.e. hole, semi-open, open), diet (i.e. insects, other invertebrates, omnivore), mating system (i.e. monogamous, polygamous, promiscuous) and contiguity of territories (contiguous, mixed, dispersed). We reported the most frequently parasitized species for each of five Italian areas (Figure 1).

Figure 1. The five areas that divided the Italian peninsula for reporting the frequency of parasitism. North (blue): regions of Aosta Valley, Piedmont, Liguria, Lombardy, Emilia-Romagna, Friuli-Venezia Giulia, Trentino, Veneto; Centre (orange): Tuscany, Umbria, Lazio, Marche; South (red): Abruzzo, Apulia, Basilicata, Molise, Campania, Calabria; and the two largest islands Sardinia (grey) and Sicily (azure) were treated as separate areas.

RESULTS

It was not possible to compute effect size, *d*, for six of the 70 potential host species, because there was only one record either for parasitized or unparasitized nests (**ESM 2**). For the remaining 64 species, parasitism frequency was significantly correlated with effect size (N=64, r_s=-0.27, P=0.029, Figure 2), which indicates no bias was introduced when the frequency of parasitism was calculated for each species. Among the 64 potential host species, 20 were not parasitized (**ESM 2**), whereas 44 species were confirmed as host species. Parasitism frequency among these species ranged from 0.3% to 26.7% of the total nests parasitized (Table 1). From these 44, only 10 species were parasitized at frequencies higher than 10% (Figure 3A, Table 1). Among the latter hosts, Cuckoos used mainly species that nested low in the vegetation or on the ground (Figure 3B), built open-cup nests (Figure 3C), foraged on invertebrates (Figure 2D), mated both monogamously and polygamously (Figure 3E), and established contiguous territories (Figure 3F). The 10 most frequently parasitized hosts were single- or doubled-brooded that laid four- or five-egg clutches, whereas most species were solitary with incubation periods of 13-15 days. The Great Reed Warbler is the only heavily parasitized host that exhibits all these characteristics, except its social system is described as semi-colonial.

From the total of 13,157 nests, of which 1,860 were parasitized (Campobello & Sealy 2009), we uncovered references to nest location for 4,170 nests, of which 656 were parasitized. The most frequently parasitized species per area are shown in Table 2.

DISCUSSION

Our results confirmed the status of host for some species, whereas excluded it for others. Reviews often are biased due to the lack of an *a priori* design of the way experimental data are collected (Gurevitch & Hedges 1983). From the preliminary list of potential hosts in Italy suggested by early records (e.g. Bettoni 1865, Giglioli 1890, but see complete list in Campobello & Sealy 2009), we were unable to confirm the status of either host or non-host for only six species, because of small sample sizes. Of these six species, three (Wryneck, Song Thrush, Tree Sparrow) were reported as unsuitable hosts (*sensu* Moksnes & Røskaft 1995), two (Icterine and Willow warblers) were not reported parasitized elsewhere, whereas the Meadow Pipit was reported not only as a Cuckoo host (Moksnes & Røskaft 1989) but also as one of the most frequently parasitized species in Ireland (Sealy et al. 1996).

In describing the main ecological and behavioural aspects of the most frequently parasitized hosts, we identified characteristics similar to those described elsewhere (Soler 2017). An exception was the semi-colonial system, rather than the more common solitary system, for the most heavily parasitized species, the Great Reed Warbler. This system is suggested to turn a frontline nest defence into a more effective group defence such as that adopted by the Reed Warbler (Campobello & Sealy 2011, 2018; Feeney et al. 2012). A semi-colonial breeding system also promotes defensive learning, which was amply exhibited by Reed Warblers. This species refines its antiparasite and antipredator responses by watching conspecifics defend their nest when under attack. The semi-colonial nesting system makes learning opportunities more probable, given nest vicinity (Davies & Welbergen 2009, Campobello et al. 2017).

Frequency of parasitism on each host species in each

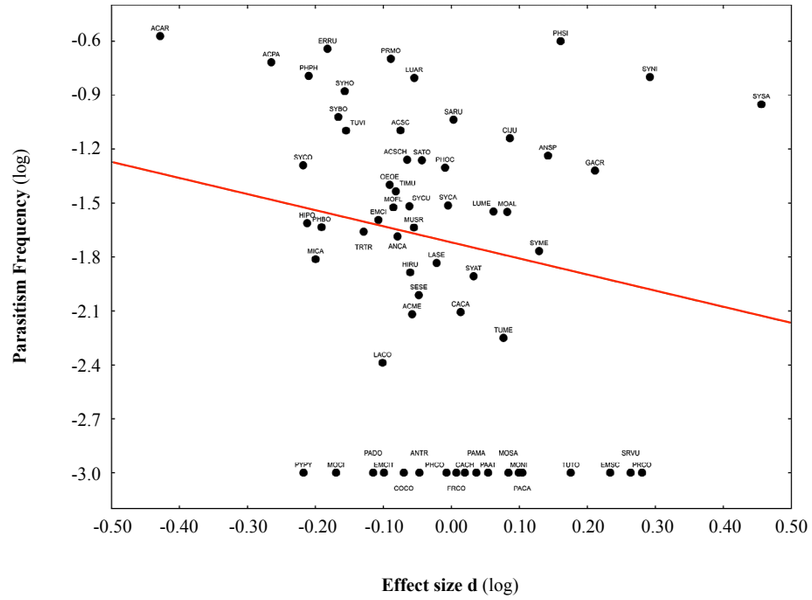

Figure 2. Correlation between parasitism frequency and effect size, *d*, indicating no bias was introduced due to differences in the method of data collection, from literature and nest records. For most species, acronyms are the first two letters of the genus and species whereas in some ambiguous cases, the acronyms include the first three letters of the species. The solid line shows the linear fit between frequency of parasitism and effect size (both log transformed).

Table 1. The species confirmed as Cuckoo hosts whose parasitism frequency is ≥ 0.05; in bold, species parasitized with a parasitism frequency > 0.10. **ESM 2** for a complete list of all the other species suggested by literature as hosts but not confirmed together with values of s pooled and d effect size.

Potential host species		Number of reports	# PARA nests	PARA mean	PARA SD	Parasitism frequency
Acrocephalus arundinaceus	**Great Reed Warbler**	**12**	**378**	**31.50**	**91.3**	**0.27**
Phylloscopus sibilatrix	**Wood Warbler**	**3**	**1**	**0.33**	**0.6**	**0.25**
Erithacus rubecula	**Robin**	**14**	**34**	**2.43**	**5.2**	**0.23**
Prunella modularis	**Dunnock**	**8**	**7**	**0.88**	**1.0**	**0.20**
Acrocephalus palustris	**Marsh Warbler**	**9**	**25**	**2.78**	**6.1**	**0.19**
Phoenicurus phoenicurus	**Redstart**	**13**	**53**	**4.08**	**8.9**	**0.16**
Sylvia nisoria	**Barred Warbler**	**5**	**6**	**1.20**	**1.3**	**0.16**
Lullula arborea	**Woodlark**	**5**	**5**	**1.00**	**1.4**	**0.16**
Sylvia hortensis	**Orphean Warbler**	**5**	**5**	**1.00**	**1.7**	**0.13**
Sylvia sarda	**Marmora's Warbler**	**3**	**3**	**1.00**	**1.0**	**0.11**
Sylvia borin	Garden Warbler	5	5	1.25	2.5	0.09
Saxicola rubetra	Whinchat	6	2	0.29	0.5	0.09
Acrocephalus scirpaceus	Reed Warbler	10	65	6.50	8.5	0.08
Turdus viscivorus	Mistle Thrush	5	3	0.60	1.3	0.08
Cisticola juncidis	Fan-tailed Warbler	8	5	0.63	0.9	0.07
Anthus spinoletta	Water Pipit	5	2	0.40	0.9	0.06
Acrocephalus schoenobaenus	Sedge Warbler	4	2	0.50	1.0	0.05
Saxicola torquata	Stonechat	6	10	1.11	2.6	0.05
Sylvia communis	Whitethroat	10	8	0.80	1.6	0.05
Phoenicurus ochruros	Black Redstart	12	6	0.50	1.0	0.05
Galerida cristata	Crested Lark	6	3	0.50	0.8	0.05

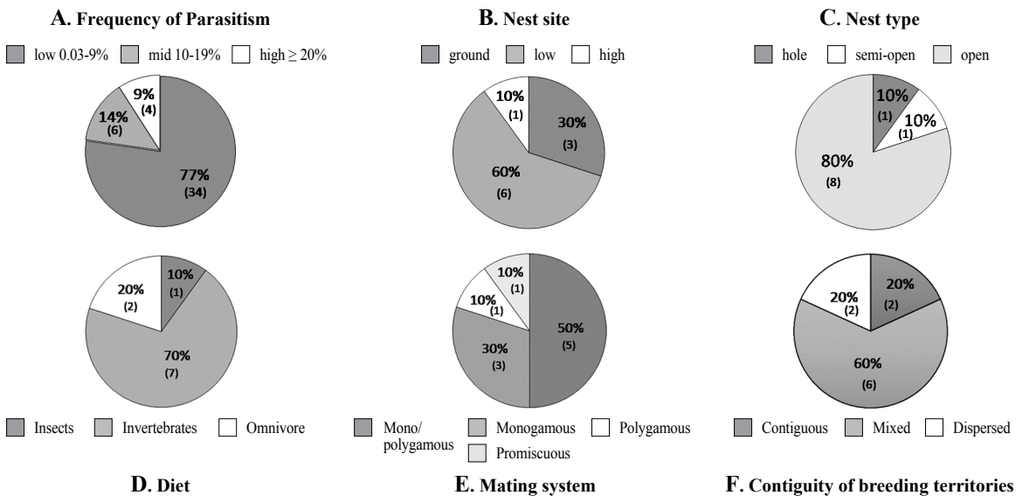

Figure 3. A) Percentages of the confirmed 44 host species according to their parasitism frequencies; numbers in parentheses are the number of species. Percentages of the 10 species parasitized at frequencies higher than 0.10, sorted by B) nest site, C) nest type, D) diet, E) mating system, and F) contiguity of breeding territories. 'Invertebrates' is the short term for 'Other invertebrates'.

Table 2. Parasitism frequency (%) of each Cuckoo host in five Italian regions, North, Centre, South, Sardinia and Sicily, as recorded in a subsample where nest location was indicated. Total nests (*n*) are indicated in parentheses. Overall parasitism frequency is the value recorded in the entire Italian peninsula.

Cuckoo host species		Regional parasitism frequency (n)	Overall parasitism frequency (*n*)
NORTH			
Motacilla alba	White Wagtail	1.00 (1)	0.03 (110)
Sylvia curruca	Lesser Whitethroat	1.00 (1)	0.03 (34)
Anthus campestris	Tawny Pipit	1.00 (1)	0.02 (51)
Galerida cristata	Crested Lark	1.00 (1)	0.05 (64)
Acrocephalus schoenobaenus	Sedge Warbler	1.00 (2)	0.05 (37)
Phylloscopus sibilatrix	Wood Warbler	1.00 (1)	0.25 (4)
Turdus merula	Blackbird	1.00 (4)	< 0.01 (1,083)
Tichodroma muraria	Wall Creeper	1.00 (1)	0.04 (28)
Anthus spinoletta	Water Pipit	1.00 (2)	0.06 (35)
Saxicola rubetra	Whinchat	1.00 (2)	0.09 (22)
Hirundo rustica	Swallow	0.75 (4)	0.01 (416)
Cisticola juncidis	Fan-tailed Warbler	0.40 (5)	0.07 (70)
Erithacus rubecula	Robin	0.38 (65)	0.23 (150)
Acrocephalus arundinaceus	Great Reed Warbler	0.31 (1,133)	0.27 (1,416)
Phoenicurus phoenicurus	Redstart	0.29 (163)	0.16 (331)
Acrocephalus scirpaceus	Reed Warbler	0.27 (30)	0.08 (820)
Prunella modularis	Dunnock	0.21 (28)	0.20 (35)
Sylvia nisoria	Barred Warbler	0.21 (29)	0.16 (38)
Acrocephalus palustris	Marsh Warbler	0.20 (122)	0.19 (131)
Sylvia hortensis	Orphean Warbler	0.15 (33)	0.13 (38)
Phoenicurus ochruros	Black Redstart	0.13 (32)	0.05 (123)
Sylvia borin	Garden Warbler	0.11 (47)	0.09 (53)
Lullula arborea	Woodlark	0.10 (10)	0.16 (32)
Saxicola torquata	Stonechat	0.09 (87)	0.05 (186)
Troglodytes troglodytes	Wren	0.06 (68)	0.02 (191)
Sylvia communis	Whitethroat	0.06 (109)	0.05 (159)
Muscicapa striata	Spotted Flycatcher	0.05 (84)	0.02 (226)
Lanius collurio	Red-backed Shrike	0.04 (23)	< 0.01 (323)
Sylvia cantillans	Subalpine Warbler	0.04 (47)	0.03 (101)
Emberiza cirlus	Cirl Bunting	0.04 (124)	0.02 (204)
Motacilla flava	Yellow Wagtail	0.03 (31)	0.03 (69)
Hippolais polyglotta	Melodious Warbler	0.03 (95)	0.02 (128)
Sylvia atricapilla	Blackcap	0.03 (232)	0.01 (701)
Phylloscopus bonelli	Bonelli's Warbler	0.03 (36)	0.02 (45)
Oenanthe oenanthe	Wheatear	0.02 (41)	0.04 (77)
Carduelis carduelis	Goldfinch	0.02 (89)	0.01 (293)
Serinus serinus	Serin	0.01 (135)	0.01 (229)
Miliaria calandra	Corn bunting	0.01 (141)	0.01 (208)
Luscinia megarhynchos	Nightingale	0.06 (107)	0.03 (219)
CENTRE			
Lanius senator	Woodchat Shrike	1.00 (1)	0.01 (73)
Turdus viscivorus	Mistle Thrush	1.00 (3)	0.08 (38)
Acrocephalus arundinaceus	Great Reed Warbler	0.14 (152)	0.27 (1416)

continued

Cuckoo host species		Regional parasitism frequency (*n*)	Overall parasitism frequency (*n*)
Acrocephalus scirpaceus	Reed Warbler	0.09 (449)	0.08 (820)
Acrocephalus melanopogon	Moustached Warbler	0.01 (125)	0.01 (151)
SOUTH			
Sylvia atricapilla	Blackcap	0.02 (45)	0.01 (751)
Cisticola juncidis	Fan-tailed Warbler	0.05 (20)	0.07 (70)
Sylvia communis	Whitethroat	0.06 (18)	0.05 (159)
Oenanthe oenanthe	Wheatear	0.08 (12)	0.04 (77)
Muscicapa striata	Spotted Flycatcher	0.09 (11)	0.02 (226)
Saxicola torquata	Stonechat	0.09 (11)	0.05 (186)
Sylvia sarda	Marmora's Warbler	0.10 (10)	0.11 (27)
Sylvia cantillans	Subalpine Warbler	0.10 (10)	0.03 (101)
Galerida cristata	Crested Lark	0.11 (19)	0.05 (64)
Lullula arborea	Woodlark	0.11 (9)	0.16 (32)
Motacilla alba	White Wagtail	0.18 (11)	0.03 (110)
Acrocephalus scirpaceus	Reed Warbler	0.19 (48)	0.08 (820)
Phoenicurus ochruros	Black Redstart	0.20 (10)	0.05 (123)
Erithacus rubecula	Robin	0.20 (35)	0.23 (150)
Turdus merula	Blackbird	1.00 (1)	< 0.01 (1,083)
Sylvia melanocephala	Sardinian Warbler	1.00 (1)	0.02 (124)
SARDINIA			
Sylvia melanocephala	Sardinian Warbler	1.00 (1)	0.02 (124)
Sylvia sarda	Marmora's Warbler	1.00 (2)	0.11 (27)
SICILY			
No records		-	-

geographic area contributes little to our knowledge of avian brood parasitism across the Italian peninsula. Only a quarter of the total records reported precise nest location and among those there was clearly an imbalance with reported numbers that decreased steeply from North to South, and no records for either Sicily and Sardinia. Systematic studies such as that conducted by Quaglierini (2006), are needed because the added information facilitates addressing questions of the interaction between parasitism and other behavioural/ecological aspects that may reveal the population trend of this biodiversity indicator. Investigating habitat-related demography (Di Maggio et al. 2016), the role of size in breeding assemblages (Di Maggio et al. 2015), or the potential advantage of information transfer (Campobello and Hare 2007), may reveal how Cuckoos choose their breeding site, parasitize solitary versus social species, or refine nest searching, respectively. Further investigations are warranted to reveal the causes related to the Cuckoo's decline (Hewson et al. 2016).

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