Host specialization and latitude among cuckoos

Yoram Yom-Tov and Eli Geffen


We tested the prediction that at higher latitudes there will be an increase in the number hosts per cuckoo species. This prediction is confirmed, and the number of hosts exploited per cuckoo species increases with increasing latitude. Although this result is strongly influenced by a single species (the common cuckoo Cuculus canorus) in high latitudes, it is significant and holds even at lower latitudes where this species is absent. This trend may be explained as a case of competitive release and niche expansion by the few cuckoo species that have expanded their ranges north, despite the shortage of hairy caterpillar prey species at high latitudes.

Y. Yom-Tov (correspondence) and E. Geffen, Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel. E-mail: yomtov@post.tau.ac.il

Although cuckoos may lay their eggs in nests of a large number of potential hosts, most species specialize on one or few hosts (Friedmann 1948, 1968, Payne 1977, Rothstein and Robinson 1998). Species that parasitize several host species often have gentes, each gense specializing in other species of host or a group of hosts that has similar eggs. For example, the common cuckoo Cuculus canorus has at least 15 different egg morphs in Europe (Mosknes and Roskaft 1995) and the African dideric cuckoo Chrysococcyx caprius has at least 5 gentes (Davies 2000). In areas where there are several species of related parasites, they tend to parasitize different hosts, a phenomenon described by Friedmann (1967) as alloxenia. Lack (1971) hypothesized that host segregation evolved by interspecific competition, and Higuchi (1998) has shown that in Japan the main host species are segregated among different species of cuckoos.

The decline in diversity towards higher latitudes is a common phenomenon among animals, including birds, and occurs in most orders apart from the marine ones (Gill 1994). The family Cuculidae includes 47 species of parasitic cuckoos, most of which live at low latitudes in Africa, Asia and Australia, although a few species breed at high latitudes in the Palearctic region. On the other hand, the order Passeriformes, while most diverse in the tropics, is represented by several hundred breeding species in the Palearctic region of which only about a hundred are affected by cuckoo parasitism. Thus, as latitude increase there may be an increase in the number of host species available to and used by to each high-latitude cuckoo species. The aim here is to provide a test of this hypothesis.

Methods

Using ornithological handbooks we calculated the number of breeding cuckoo species and passerines in several regions in the Old World (there are only 3 species of obligate parasitic cuckoos in the New World). We did not use other groups of obligate parasites either because they are less numerous (e.g. cowbirds), or have a more restricted geographical distribution (e.g. whydahs, hon-
had to be unsuitable hosts, mainly because they do not feed their young on a diet that is suitable for cuckoos, and were therefore never seen to successfully raise a cuckoo chick. Ultimately, a researcher’s decision as to which species are the principal hosts of a particular parasitic species is often based upon the frequency of parasitic eggs found in nests of potential hosts (note that various authors use the terms “main”, “biological” or “authenticated” host interchangeably).

In this study we used data on cuckoos’ brood parasitism from seven large regions in the Old World: (1) Europe (Cramp 1985, Priklonskiy 1993, Mosknes and Røskaft 1995, Davies 2000), (2) Southern Africa (Rowan 1983), (3) Western, Eastern and Northern Australia (Brooker and Brooker 1989), (4) Central Asia (Numerev 2003) and (5) North-West and Central India (Baker 1942, Johnsgard 1997). These regions were selected largely due to the fact that the number of host species for each cuckoo is known, and they represent a wide latitudinal range. Using the same sources, for each cuckoo species in each area we also determined the mean latitude of its distribution. Finally, we calculated the mean number of hosts for each of the above seven regions. Four categorizations of hosts were used: 1. Total number of hosts reported, without considering the number of cases listed for a particular species of host, 2. The number of hosts (category 1 above) excluding cases based on a single report, 3. The number of hosts (category 1 above) excluding cases based on only one or two reports, and 4. The number of host species, in declining order, accounting for approximately 70% of the reported cases of parasitism.

The sources of data used here differ from one another in the way that they represent the number of cases of brood parasitism. For Southern Africa we used data for nests where nestlings or fledglings were found, as this eliminates most cases of unsuitable hosts. For the rest of the regions we used data on the number of nests where cuckoo eggs or chicks were found. However, some of Baker’s (1942) data are apparently questionable. For example, Becking (1981) considered that only the brown (but not blue) eggs described by Baker (1942) as large-hawk cuckoo Cuculus sparverioides eggs actually belonged to this species, whilst the blue ones were probably common cuckoo eggs. Following this we considered only the brown eggs as those of the large-hawk cuckoo.


To accommodate for nonlinear relationships in the data, the number of cuckoo species and variables describing the number of hosts were log-transformed prior to analysis. To determine whether distribution of cuckoo species is associated with phylogeny, we defined three latitudinal zones (0–20°, 21–40° and >40°), and plotted the distribution zone of each species on the phylogeny tree of cuckoos. We used 546 bp of the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene to reconstruct the phylogeny for 47 cuckoo species that included both Old and New world species. Sequence data was obtained from Genebank and Sorenson and Payne (2002; M. Sorenson pers. comm.). Parsimony (PAUP 4.0, Swofford, 2002) and maximum-likelihood (FastDNAML, Olsen et al. 1994) were used as the reconstruction algorithms. We traced ancestry of species distribution (expressed as latitudinal zones) on the tree of cuckoos using the parsimony approach implemented in MacClade (version 3.08, Maddison and Maddison 1996).

Results

There is a positive, but strongly curvilinear relationship between the number of passerines and the number of cuckoo species breeding in a region ($r^2 = 0.664, F_{4,10} = 32.8, P < 0.0001$; Fig. 1). The best curve fitting was obtained by using the logistic equation presented in Fig. 1. This relationship is clearly driven by the fact that whilst there are 9 to 13 cuckoo species in most regions of low and mid-latitudes (up to about 35 degrees), at higher latitudes this number falls sharply to 4 species or less.

There is a significant positive linear relationship between the mean latitude of each parasite and the number of hosts calculated either as: total number of hosts reported ($r^2 = 0.143, F_{1,43} = 7.02, P < 0.011; y = 1.568x – 1.364$), the number of hosts involved in approximately 70% of the reported cases of parasitism ($r^2 = 0.165, F_{1,42} = 8.08, P < 0.007; y = 1.144x – 1.203$), the number of hosts excluding cases based on a single report ($r^2 = 0.202, F_{1,42} = 10.36, P < 0.002; y = 1.649x – 1.591$), and the number of hosts excluding cases based on only one or two reports ($r^2 = 0.225, F_{1,43} = 12.21$,
The number of cuckoo species as a function of number of passerines in 14 geographical regions (Central/North Europe (EuC), West Mediterranean (MeW), Northwest and Central India (InC), Central Asia (AsC), East Siberia (SiE), Central China (ChC), Southeast and South China (ChS), Philippines (Ph), Thailand (Th), West Africa (AfW), Kenya and Tanzania (AfE), South Africa (AfS), West Australia (AuW) and East Australia (AuE)). Stars, open squares and filled circles designate regions at 0°–20°, 21°–35°, and 36°–60° latitude ranges, respectively. The logistic curve ($r^2 = 0.664$, $P < 0.001$) was fitted using the equation:

$$y = \frac{11.45(1 - e^{-0.012(x - 122.41)})}{1 - 0.242e^{-0.012(x - 122.41)}}$$

$P < 0.001$; $y = 1.662x - 1.693$). However, latitude here is explaining only about 20% of the variance in number of hosts per cuckoo species.

A much higher proportion of this variation (about 85%) is accounted for when using the mean number of hosts across all cuckoo species per region (Fig. 2). Specifically, mean regional latitude (seven geographical regions: Europe, Central Asia, Northwest and Central India, Southern Africa, North Australia, Southeast Australia and Southwest Australia) had a very significant effect on: the total number of hosts reported ($r^2 = 0.805$, $F_{1,6} = 20.66$, $P < 0.006$), the number of hosts involved in approximately 70% of the reported cases of parasitism ($r^2 = 0.830$, $F_{1,6} = 24.39$, $P < 0.004$), the number of hosts excluding cases based on a single report ($r^2 = 0.825$, $F_{1,6} = 23.53$, $P < 0.005$), and the number of hosts excluding cases based on only one or two reports ($r^2 = 0.945$, $F_{1,6} = 85.32$, $P < 0.0002$). These relationships, outlined in Fig. 2, are all strongly influenced by the large number of hosts exploited by the common cuckoo in Europe and Central Asia, where there are almost no other cuckoo species competing for available passerine hosts (i.e., the great spotted cuckoo *Clamator glandarius* breeds only in parts of southern Europe). However, removal of these two regions containing the common cuckoo does not eliminate the observed result of a positive effect of latitude on the number of hosts per cuckoo species ($r^2 = 0.872$, $F_{1,4} = 20.49$, $P < 0.020$ for the number of hosts excluding cases based on only one or two reports).

Of the 546 bp used for phylogenetic reconstruction, 317 were parsimony-informative. A single parsimony tree was generated (tree length = 2265, CI = 0.2715, RI = 0.530) using the heuristic search option. Transition/transversion ratio of 2.7 and the global rearrangement option were the initial settings for the maximum likelihood (ML) algorithm. The ln likelihood for the best tree found was $-10903.87$. We used two pigeon species (*Treron sieboldii* and *Columba leucocephala*) and one parrot (*Neophema elegans*) as outgroup species in both reconstructions. These taxa were among the species selected as outgroup in the analysis by Sorenson and Payne (2002). Three major clades are defined by the ML tree (Fig. 3). The most parsimonious tree showed similar division but the genus *Centropus* formed a separate clade that was placed as the most basal among the cuckoos. Both trees corresponded to chief topologies in the published cuckoo phylogenies (Aragon et al. 1999,
Most of the parasitic species were assigned to a single clade (i.e., *Cuculus* clade). However, the genera *Clamator* and the sister taxa *Tapera* and *Dromococcyx* are of two distinct radiations that are not related to the *Cuculus* clade. This pattern was observed in both the parsimony and the ML trees.

The trace of the latitudinal zones (0°–20°, 21°–40° and >40°) on the cuckoo phylogeny revealed that none of the clades was zone-specific, thus no evidence for association between latitude and ancestry (Fig. 3). The lack of association between latitude and ancestry was notable even after the two clades of the American species (i.e., the genera *Coccyzus*, *Crotophaga*, *Dromococcyx*, *Geococcyx*, *Guira*, *Neomorphus*, *Piaya*, *Saundera* and *Tapera*) were excluded from the analysis. The capability of the parasitic species to range over the >40° zone was observed for all three radiations (i.e., *Clamator coromandus*, *Tapera naevia*, and some of the species in the genera *Chrysococcyx*, *Cacomantis*, and *Cuculus* (Fig. 3).

Further, branch lengths of the parasitic species, which correspond to the age of these species, were neither correlated with species most distant latitude from the equator ($r_{15} = 0.31$, $P = 0.224$; branch lengths were log-transformed), nor with the species most proximate latitude to the equator ($r_{15} = 0.23$, $P = 0.383$; branch lengths were log-transformed). In other words, age of species was independent of latitude.

**Discussion**

The main result of the present analysis is that the number of hosts exploited by each cuckoo species increases with increasing latitude. Although this result is strongly influenced by a single species (the common cuckoo) in high latitudes, it is significant and holds even at lower latitudes where this species is absent.
It is well known that the number of bird species declines from low to high latitude, and both cuckoos and passerines are no exception to this general trend. Up to 14 cuckoo species breed in any single region at low and mid-latitudes, but their number falls sharply at high latitudes to 1–4 (Fig. 1). However, the number of cuckoo species is necessarily less than that of hosts, and the slope of decline in number of cuckoo species is steeper than that of passerines, resulting in more passerine hosts per cuckoo species in higher latitudes. In other words, due to the scarcity of cuckoo species, the number of potential host species available per cuckoo species is proportionally greater in higher latitudes than in lower latitudes. This situation is at its extreme in the Western Palearctic region, where only two cuckoo species occur (and one of them, the great spotted cuckoo, occurs only in the southern part of the Palearctic), in comparison with about ten or more cuckoo species in Australia, India and Southern Africa. It seems that in the other regions the presence of several cuckoo species forces them to divide the available hosts among them, and each cuckoo species specializes in only a few hosts (alloxenia). Such a situation was reported in Japan, and was interpreted as character displacement (Higuchi 1998). However, lack of competitors probably enabled competitive release in the case of the common cuckoo, and it was able to widen its niche by exploiting many hosts. Being a semi-generalist in its host selection (Mosknes and Roskaft 1995), this species has exploited this opportunity and is now parasitizing a large number of hosts in Europe and Central Asia. It is no coincidence that such a large cuckoo invaded Europe, because as Brooker and Brooker (1989) pointed out, larger species of cuckoos are more successful than smaller ones through being able to exploit a greater number of hosts.

An alternative explanation for the large number of hosts exploited by high-latitude cuckoos is that time is a major factor in determining co-evolutionary interaction, as suggested by Rothstein et al. (2002) for parasitic cowbirds. It is possible that cuckoos have recently invaded higher latitudes and had less time for cuckoo speciation, and given time, gentes of existing species will evolve to new ones. This hypothesis is feasible, but since we are not aware of data on time of invasion of cuckoos to high latitude, we cannot test it.

It is not clear why so few cuckoos breed at high latitudes. We discuss two possible explanations: 1. Phylogeny or time-cuckoo species that breed at high latitudes must be adapted to the lower ambient temperatures and less stable weather, frequent in these areas, relative to the tropics. The phylogenetic information presented in Fig. 3 clearly indicates that cuckoo species breeding in high latitudes originate from several radiations, and suggests no association between ancestry and latitude. Apparently these invaders did not have enough time since the last warming during the Pleistocene to diverge into more species than exist today. 2. Diet-all cuckoos feed on invertebrates, especially larvae of butterflies and moths, and they are known for their ability to consume without harm spiny and hairy caterpillars (i.e., Arctiidae, Lasiocampidae, Limacodidae, Lymantriidae, Megalopygidae, Noctuidae, Notodontidae, Nymphalidae, Saturniidae, Zygaenidae). Diet could be a strong selective force upon cuckoo distributions provided that such food is more abundant in the tropics, and that cuckoos are highly dependent on it. One may assume that a larger number of species also means greater food abundance (in number of individual prey items and biomass) in more equatorial areas and we searched for data to support or refute this hypothesis. Although the data on the distribution and abundance of these moth species are lacking, there are more data on some relevant butterfly families. These data show great species diversity at low latitudes, with about 700–600 species of unpalatable butterfly species in the tropics (latitude 10°S–10°N, respectively), but only 10–25 species at high latitudes (40–50°S and 40–50°N, respectively; Sime and Bower 1998). Using data on the number of unpalatable butterfly species in 10 degree bands across the globe (from Fig. 1 in Sime and Bower (1998) and on cuckoos (from maps in Payne 1997), we found that the number of unpalatable species of butterflies explains about 88% of the variation in the number of cuckoos across latitudes (Fig. 4). The diet of cuckoos is unlikely to be restricted to hairy caterpillar larvae, and so it is unlikely that the availability of this food type is directly responsible for whole of the observed trend. However, this brief analysis suggests that a shortage of hairy caterpillar species may contribute to the lack of cuckoo...
species at high latitudes independently of the availability of passerine host species. It would have been interesting to compare the cuckoos’ host specialization in relation to latitude to the situation in other avian brood parasites. Recent studies based on molecular systematics suggest that obligate brood parasitism has evolved independently in seven avian lineages (Sorenson and Payne 2002). However, of these seven lineages only the old-world cuckoos fulfill the conditions that enable testing the above relationships, namely the occupation of a large latitudinal range with a large number of species. The five species of parasitic cowbirds do occupy a wide latitudinal range, but they have much shorter history of parasitism than do cuckoos, and have fewer adaptations to parasitism (Rothstein et al. 2002). Due to these restrictions we confined our analysis to old-world cuckoos.

In conclusion, our prediction that at higher latitudes there will be an increase in the number hosts per cuckoo species was confirmed. This trend may be explained as a case of competitive release and niche expansion by the few cuckoo species that have expanded their ranges north, despite the shortage of hairy caterpillar prey species at high latitudes.

Acknowledgements – Michael D. Sorenson kindly provided the sequence data for the published cuckoo phylogeny in Sorenson and Payne (2002). We thank Nick Davies, Alex Kazelnik, Arnon Lotem, Arne Mosknes, and Claire Spottiswoode for fruitful discussions, Mike Brooke, Jon Wright and two anonymous referees for useful comments on the manuscript, and Linda Birch and Mike Wilson for assistance in obtaining data. We thank Roland Sandberg and the Scientific Editor for careful editing. Special thanks are due to Nick Davies for his hospitality to YYT during a sabbatical at Cambridge.

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(Received 21 January 2005, revised 24 July 2005, accepted 1 August 2005.)