Habitat-dependent call divergence in the common cuckoo: is it a potential signal for assortative mating?

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The common cuckoo (*Cuculus canorus*) is an obligate brood parasite that mimics the eggs of its hosts. The host-specific egg pattern is thought to be inherited matrilineally, creating female-only host-specific races. Males are thought not to be adapted to their host and they maintain the species by mating arbitrarily with respect to host specialization of females. However, recent results suggest that male cuckoos may also show host-specific adaptations and these may require assortative mating with respect to host. The calls males produce on the breeding grounds could provide a potential mechanism for assortative mating. We tested whether male cuckoo calls differ more between nearby populations that parasitize different hosts than between distant populations that parasitize the same host. We recorded the calls of geographically distant pairs of populations in Hungary, with each pair consisting of a forest population and a nearby reed bed population. Each habitat is characterized by one main host species for the common cuckoo. Our results show that calls of distant cuckoo populations from the same habitat type are more similar to each other than they are to those of nearby populations from a different habitat. These results suggest that cuckoo calls differ sufficiently to allow recognition of habitat-specific individuals.

Keywords: brood parasitism; cuckoo; vocalizations; mate recognition; host specific

1. INTRODUCTION

The common cuckoo (*Cuculus canorus*) is an obligate brood parasite with more than 100 host species over its range, which extends from England to Japan (Cramp 1985; Moksnes & Roskaft 1995). It is divided into host races that are characterized by distinct egg morphs that mimic the eggs of their host. The formation of these host races is best explained by an evolutionary arms race (Dawkins & Krebs 1979) between the cuckoo and its host. Adaptations in the host such as improved egg recognition, stronger cuckoo egg rejection and reduced intra-clutch variability, lead to increased egg mimicry in the cuckoo (Oien *et al.* 1995; Stokke *et al.* 1999). However, how the cuckoo remained a single species despite these host-specific adaptations is one of the enduring enigmas in evolutionary biology (Davies 2000).

The best-supported hypothesis for the lack of speciation in host-specific cuckoo races, also called gentes, proposes that they are female specific. According to the gentes hypothesis, the genes for egg colour and pattern are stored on the female-specific W sex chromosome (Punnett 1933; Jensen 1966; Gibbs *et al.* 2000) with females being the heterogametic sex in birds. The accuracy of egg mimicry is therefore not jeopardized through mating with males that do not show adaptations to a specific host. As males do not belong to a host-specific race, they mate non-assortatively and prevent the races from accruing sufficient

genetic differentiation to cause speciation. Three lines of evidence support the gentes hypothesis. First, radio-tracking studies (Nakamura & Miyazawa 1997; Honza *et al.* 2002) and second, parentage analyses (Marchetti *et al.* 1998; Skjelseth *et al.* 2004) suggested that males mated with multiple females that were specialized on different host species. In addition, genetic analyses showed differences among host-specific cuckoos in maternally inherited mitochondrial DNA, but failed to find such differences in nuclear DNA (Gibbs *et al.* 2000).

However, the view that only female cuckoos specialize on their host is challenged by several observations. Gibbs *et al.* (2000) suggested that egg colour and therefore egg mimicry in cuckoos are inherited matrilineally. However, egg background colour inheritance is a polygenic trait in domestic fowl (Hutt 1949) and village weavers (*Ploceus cucullatus*, Collias 1993), suggesting that autosomes are involved in the egg colour phenotype. In great tits (*Parus major*), on the other hand, some egg pattern characteristics are inherited matrilineally (Gosler *et al.* 2000). It is unclear what egg colour and egg pattern inheritance system cuckoos have. However, since a good mimetic egg matches not only the background colour but also the egg pattern of the hosts' eggs, it is plausible that the egg inheritance patterns reside on both the female-specific W sex chromosome and the autosomes.

Moreover, another host-specific adaptation than egg mimicry suggests that not only female but also male cuckoos specialize on their hosts. Cuckoo chicks raised by reed warblers (*Acrocephalus scirpaceus*) are predisposed to

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Figure 1. Hungary, with the locations of the recording sites. Cuckoos were recorded in Kiskunság (north reed bed, N: 47° 09' 10" E: 19° 04' 15", N=20), River Dráva at Barcs (south reed bed, N: 45° 56' 40" E: 19° 04' 15" N=14) and Balmazújváros (east reed bed, N: 47° 36' 40" E: 21° 22' 42", N=20), in Pilis Mountains (north forest, N: 47° 37' 40" E: 18° 59' 25", N=18), north of Barcs (south forest, N: 46° 02' 07" E: 17° 35' 10", N=28) and north of Debrecen (east forest, N: 47° 34' 35" E: 17° 35' 10", N=29).

respond only to reed warbler alarm calls and not to alarm calls of other known cuckoo hosts (Davies *et al.* 2006). Since in birds females are the heterogametic sex and both male and female chicks show the above adaptation, it is impossible that the predisposition to respond to host-specific alarm calls only resides on the female-specific W sex chromosome. Finally, both sexes show habitat imprinting, and therefore the likelihood of becoming specialized on a certain set of possible hosts (Teuschl *et al.* 1998). In line with these observations, several authors have expressed hesitation about the validity of the gentes hypothesis, which states that only females specialize on their host (Jensen 1966; Teuschl *et al.* 1998; Davies *et al.* 2006). An alternative hypothesis suggests that the common cuckoo is in fact an amalgam of cryptic species (Davies & Brooke 1998).

The cryptic species hypothesis requires assortative mating with respect to host race. Cuckoos are raised individually and do not meet other cuckoos until after they fledge, which precludes imprinting on their own species. The recognition of conspecifics is thought to rely on the calls of males and these calls and their perception by females are thought to be unlearned in the common cuckoo. One mechanism that would allow assortative mating leading to cryptic species requires that males produce host race-specific calls. The aim of this study is to assess whether the calls of males differ between host-specific populations and, consequently, may facilitate host-specific assortative mating.

2. MATERIAL AND METHODS

Cuckoo calls were recorded in a pair of distinct adjacent (less than 50 km apart) habitat types, namely deciduous forest and reed beds, in three geographically distant (more than 200 km apart) locations in Hungary (figure 1). The most common host of the cuckoo in these forested habitats is the robin (*Erithacus rubecula*), while the most common host in reed beds has been the great reed warbler (*Acrocephalus arundinaceus*) since the beginning of the last century (Molnár 1944; Honza & Moskát 2005).

Recordings were made from 1998 to 2003 using a Sennheiser MK 66 Microphone and a DAT recorder (Sony TCD-8). Each recording location was visited only during one season to minimize the chance of recording the same individual in different years. Calling cuckoos were approached to approximately 20–30 m and the location determined with global positioning system (GPS). After an individual was recorded, a simultaneously calling male was approached. Subsequent individuals were approached and recorded while the previous one was still calling, thereby minimizing the chance of recording the same individual twice. Recordings were resampled (soundcard: sound blaster Audio PCI 128) using a sampling frequency of 8000 Hz. Analysis was done with AVISOFT-SASLAB PRO v. 4.23c. For measurements in the frequency domain, an FFT-size of 512 Hz with a bandwidth of 23 Hz and a time resolution of 43 ms was used. For measurements in the time domain, we used an FFT-size of 64 Hz with a bandwidth of 187 Hz and a time resolution of 5 ms. We measured nine acoustic parameters (figure 2) and added a further four derived parameters (table 1). We analysed the central call or one close to the centre in a bout of calls. If more than one recorded bout was available for one individual we took the average from a maximum of five calls from different bouts.

We used a principal component analysis (PCA) to create 3 independent parameters from the 13 acoustic parameters. We then used a multivariate general linear model (GLM) procedure to test whether the six populations show differences in their calls. The factor scores for the three PCs were used as dependent variables, and habitat (forest and reed bed) and geographical location (north, south and east) as fixed factors. All statistical analyses were done with SPSS v. 13.0.

3. RESULTS

We obtained recordings from a total of 142 individuals. The sample sizes for each location are presented in the legend for figure 1. The character loadings on the components for each variable after varimax rotation are presented in table 1. The PCA explains 72.3% of the variation in the data. The first component explains 28.3%

Figure 2. (a) Waveform and (b) spectrogram of a cuckoo call. Frequency measurements were taken from the spectrogram and temporal measurements were taken from the waveform with visual confirmation using the spectrogram. $T1$, duration of syllable 1; pause, duration of the interval between the syllables; $T2$, duration of syllable 2; $F1_L$, lowest frequency of syllable 1; $F1_H$, highest frequency of syllable 1; $F2_L$, lowest frequency of syllable 2; $F2_H$, highest frequency in syllable 2. In addition, the peak frequencies of both syllables were measured using the automated peak frequency measurement tool in AVISOFT.

of the variation in the data, while the second and third components explain 26 and 18%, respectively.

The multivariate analysis shows that both habitat ($F_{1,141}=23.51$, $p<0.001$) and geographical location ($F_{1,141}=12.4$, $p<0.001$) are significant factors in separating the populations. Partial eta-squared analysis (PES) provides a relative measure of the contribution of each factor to overall variation, with a higher value representing a stronger contribution. The factor habitat (PES=0.34) contributes more to the variation between populations than the factor geographical location (PES=0.21).

Of the three independent variables, PC1 contributes most to the factor habitat (PC1: PES=0.258, PC2: PES=0.064, PC3: PES=0.002, figure 3). The acoustic parameters with the highest character loading on PC1 are frequency parameters of the second syllable (table 1). PC2 and PC3 contribute most to the factor geographical location (PC1: PES=0.007, PC2: PES=0.239, PC3: PES=0.159, figure 3) and the variation in these components is best explained by temporal and frequency range parameters, and the difference in the peak frequency between the two syllables and frequency parameters of the first syllable, respectively (table 1).

4. DISCUSSION

Common cuckoo calls are more similar between locations more than 200 km apart but within the same habitat type, than between different habitat types less than 50 km apart. The habitat-specific difference is consistent for three independent pairs of sites and it is most pronounced in the frequency components of the second syllable. Cuckoo calls also show geographical variation, albeit to a lesser extent than the habitat-specific variation. The parameters that differ most between geographical locations are temporal measurements such as the duration of the call

Table 1. Character loadings of cuckoo call parameters for three extracted components. ($F1_L$, $F1_H$, $F2_L$, $F2_H$ and $T1$, $T2$ and pause are the same as in figure 2. $\Delta F1$ and $\Delta F2$ denote the difference between the highest and the lowest frequencies in syllables 1 and 2, respectively. ΔPF denotes the difference between the peak frequencies of syllables 1 and 2. Duration is the total duration of the call. The highest loading for each parameter with a component is indicated in bold.)

	components		
	1	2	3
$F1_L$	0.490	-0.726	0.193
$F1_H$	0.611	0.163	0.707
$F2_L$	0.822	-0.367	0.186
$F2_H$	0.956	0.224	-0.020
$\Delta F1$	0.153	0.698	0.492
$\Delta F2$	0.139	0.734	-0.250
$PF1$	0.584	0.003	0.782
$PF2$	0.984	0.104	0.007
ΔPF	-0.214	-0.094	0.947
$T1$	0.083	0.794	0.006
$T2$	-0.095	0.684	0.057
pause	-0.094	-0.213	-0.042
duration	-0.093	0.667	0.015

and frequency parameters of the first syllable. The geographical differences in cuckoo calls, like those described in other non-oscine birds species (e.g. tawny owl, *Strix aluco*, Galeotti *et al.* 1996; corncrake, *Crex crex*, Peake & McGregor 1999), may be due to drift.

There are two explanations for the habitat-specific differentiation in cuckoo calls. The first suggests that cuckoos develop different calls in their native habitats, while the second suggests that males, like females, show host-specific adaptations. Cuckoos, like most non-oscines,

Figure 3. Means (± 2 s.e.m.) of the three PCA scores (after varimax rotation) based on 13 acoustic parameters of cuckoo call recorded in forest habitats (filled squares) and reed bed habitats (open circles) for three locations in Hungary.

are thought not to learn their vocalizations. There is, however, some evidence that other non-oscines learn aspects of their call (the tree-wattled bellbird, *Procnias tricarunculata*; Kroodsmma 2004) or adjust spectral components of their call to behavioural contexts (scops owl, *Otus scops*; Hardouin *et al.* 2007). In addition, cuckoo chicks develop host-specific begging calls while in the nest in order to induce their foster parents to increase feeding rates (Payne & Payne 1998; Madden & Davies 2006). The difference in the production of the host-specific begging calls may be retained into adulthood, resulting in habitat-specific calls as adults.

Cuckoos may also learn to adjust the structure of their calls to habitat-specific transmission requirements. The main difference in the calls between the habitats is the lower peak frequency of the second syllable for forest cuckoos compared with reedbed cuckoos. Forest birds often use lower frequencies than their counterparts from open habitats (Catchpole & Slater 1995), probably because lower frequencies are less affected by scattering and frequency-specific attenuation through foliage and tree trunks than high frequencies (see Slabbekoorn (2004) for a recent review). A counter argument against local transmission requirements causing the difference in frequency use by cuckoos from different habitats is that the effect of scattering only affects sounds at frequencies above 1000 Hz (Wiley & Richards 1982), and the cuckoo call is substantially below this frequency.

The second explanation suggests that male cuckoos show host-specific adaptations in their calls. If this holds true then the difference in male calls constitutes a second adaptation to their hosts. The first one, reported by Davies *et al.* (2006), showed that chicks are predisposed to the alarm calls of their host and that this is not due to learning. These adaptations in males could result from absorption by the chicks of maternal hormones present in the yolk while still in the egg (Müller *et al.* 2007). Alternatively, both sexes may be involved in the parasite–host race, which would require that cuckoos mate assortatively with respect to their host.

If females were to choose mates based on their call characteristics, then they need to be able to discriminate between the calls of forest and reedbed cuckoos. One of the main differences between the calls from forest and reedbed cuckoos is the peak frequency of the second syllable, which ranges from 518 to 530 Hz for forest cuckoos and from 551 to 561 Hz for reed bed cuckoos. On average, birds perceive

differences of less than 1% in the frequency of a pure tone (Dooling *et al.* 2000), which is about 5 Hz in the case of the cuckoo calls. The difference between cuckoo calls from the two habitats exceeds the 1% difference (a 21 Hz difference equals approx. 4%) and female cuckoos are therefore likely to be able to discriminate between cuckoo calls from the forest and from the reed beds. The 1% difference threshold, however, is based on experiments in the laboratory where birds were exposed to two sequentially presented sounds (Dooling *et al.* 2000). The discrimination was thus based on relative pitch perception, which is easier than absolute pitch perception, at least in humans (Cuddy 1967). Birds, however, are thought to be particularly accurate with absolute pitch discriminations (Lee *et al.* 2006).

This study showed that male cuckoos produce habitat-specific calls. Irrespective of the underlying causes of the divergence in calls between cuckoos from different habitats, the variation is likely to be sufficient for females to choose their partners assortatively with respect to habitat. We do not know whether females choose their mates on the basis of habitat-specific calls, which is imperative if the differences are to be biologically meaningful. Furthermore, females prefer their native habitat when they are in the egg-laying stage and it was suggested that habitat imprinting may be part of a stepwise process that increases the likelihood of a cuckoo laying her eggs in a suitable host nest (Vogl *et al.* 2002). Both male and female cuckoos are philopatric and imprint on the habitat of their host (Teuschl *et al.* 1998), but there is no evidence for cuckoos imprinting on their host (Brooke & Davies 1991). Since cuckoos tend to parasitize predominantly one host species in a given habitat it is plausible that the species consists of habitat-specific, instead of host-specific races. Since male cuckoos also show some habitat and host-specific adaptations, the habitat-specific races may prove not to be exclusively female.

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