“cu-coo”: Can You Recognize My Stepparents? – A Study of Host-Specific Male Call Divergence in the Common Cuckoo

Won-Ju Jung, Jin-Won Lee*, Jeong-Chil Yoo
Korea Institute of Ornithology & Department of Biology, Kyung Hee University, Seoul, Republic of Korea

Abstract
The presence of multiple host-specific races in the common cuckoo *Cuculus canorus* has long been recognized as an evolutionary enigma but how this genetic divergence could be maintained is still equivocal. Some recent studies supported biparental genetic contribution in maintaining the host-races, implying the necessity that they should recognize and mate assortatively with those who belong to the same host-race. One potential mechanism to accomplish this is that males may produce distinctive calls according to host-specific lineages. In order to test this hypothesis, we carried out a comparative study for male cuckoo calls recorded from three distant populations, where two populations share a same host species while the other parasitizes a different host species. Populations with similar habitat structures, maintaining comparable distance interval (ca. 150 km) between neighboring ones, were selected so as to minimize any other causes of vocal differentiation except the pattern of host use. By comparing the vocal characteristics of male cuckoos at the population level according to individual as well as population, we found that individual males indeed produced different calls in terms of spectral and temporal features. However, these differences disappeared when we compared the calls at the population level according to host species and geographic location. In conclusion, it seems unlikely for the cuckoos to identify the stepparent of male cuckoos based solely on the vocal characteristics, although they may be able to use this cue for individual recognition. Future studies including detailed morphological and genetic comparisons will be worthwhile to further elucidate this issue.

Citation: Jung W-J, Lee J-W, Yoo J-C (2014) “cu-coo”: Can You Recognize My Stepparents? – A Study of Host-Specific Male Call Divergence in the Common Cuckoo. PLoS ONE 9(3): e90468. doi:10.1371/journal.pone.0090468

Editor: Pawel Michalak, Virginia Tech Virginia, United States of America

Received October 25, 2013; Accepted February 4, 2014; Published March 6, 2014

Copyright: © 2014 Jung et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This research was supported by Basic Science Research Program through the National Research Foundation of Korea (NRF; www.nrf.re.kr) funded by the Ministry of Education, Science and Technology (NRF-2012R1A6A3A04040003). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: jwlee99@khu.ac.kr

Introduction

As a model system for the study of reciprocal natural selection, brood parasitism by the common cuckoo *Cuculus canorus* has attracted a lot of research interests over a long period (e.g., [1–7]). It is now said that cuckoos parasitize over 100 different host species across their range but at the same time they specialize on a particular host species at a local level [6,8–11]. Due to cuckoo parasitism inflicting acute fitness costs to hosts, this specific interaction involving high selection pressures cause an evolutionary arms race between the parasites and hosts; the hosts develop a defense strategy against cuckoo parasitism and the parasites counter-adapt to overcome this host defense [6]. As a key fitness component, genetically determined phenotypic adaptation such as egg color mimicry is at the core of this race [12,13]. Hosts recognize and reject conspicuous parasitic eggs, which provoke cuckoos to mimic egg colors and spotting patterns of host species. Furthermore, not only phenotypic adaptation but innate behavioral adaptation was also reported in this race. For example, Davies et al. [14] demonstrated that cuckoo chicks possess an innate pre-tuning alarm call response so that they react specifically to the alarm call of stepparents on which their biological mothers specialize. All these host-specific traits are genetically determined, which may indicate that the cuckoos might be composed of multiple host-specific races with distinct genetic profiles [1,9].

As an evolutionary puzzle, an intriguing question that naturally arises is how multiple host-specific races coexist within a species. In other words, how genetic divergence among the cuckoo host-races maintains without speciation in the cuckoos? A conventional answer that was first supported by some field and genetic studies is that each female lineage may specialize on a particular host species over an evolutionary time scale (‘the gentes hypothesis’) [15–17]. More specifically, if the genes for host-specific traits are located on the female specific W chromosome (in birds, females are heterogametic in sex chromosome), then female-oriented host-specific races can be maintained without disturbance by the genetic contribution of males [16,17]. Furthermore, if male cuckoos choose a mate irrespective of her host-specificity, then gene flow between the cuckoo host-races could occur and thus the cuckoos could remain as one species. However, increasing recent evidence has challenged this traditional view. First of all, it seems almost unlikely that all the genes controlling host-specific traits such as egg colors and nesting behavior are located on W chromosome or other sex-linked loci. This is because the W chromosome turned out to be so small that it contains few functional genes [18], and it is also difficult to explain the fact that innate behavioral adaptations such as host-specific alarm call
response are observed in both sexes of cuckoo chicks [14]. Therefore, considering the sophisticated host-specific adaptation shown by both sexes of the cuckoo, the gentes hypothesis sounds plausible at first but now it seems to need further evidence to be confirmed concretely.

Recent empirical and theoretical studies have supported the alternative view that not only females but males also may belong to a host-specific race and thus the cuckoo may be a complex of cryptic species (‘the cryptic species hypothesis’, [19]). Fossay et al. [20] showed that biparentally inherited microsatellite DNA as well as maternally inherited mitochondria DNA diverged significantly among the cuckoo host-races at a local scale (ca. 10 km²). This implies that male and female cuckoos mate assortatively according to preferable host species, being a potential support for this alternative view. With the simulation modelling approach, Kruger & Kolss [21] also showed theoretically that a coevolutionary arms race between the parasites and hosts may result in male cuckoos having host fidelity, which in turn causes genetic divergence among the cuckoo host-races. Furthermore, as mentioned above, the genes for innate behavioral adaptation should be inherited biparentally because it occurs in both sexes [14], confirming again the necessity of paternal contribution in the inheritance of host-specific traits.

Under the scenario of the cryptic species hypothesis, they should mate selectively with partners who belong to the same host-races so that they can avoid the collapse of this finely-tuned host-specific adaptation and thus keep genetic host-specific races. As a potential mechanism to this, vocalizations may be one of the first cues to be proposed in birds. In line with this hypothesis, Fuisz and de Kort [22] showed that call structures differed significantly among male cuckoos occupying different types of habitats, with which they proposed the possibility of assortative mating according to habitat types. Because both sexes of the cuckoo are known to be imprint on where they grew up, and they appear to parasitize one predominant host in each habitat they occupy [23], habitat-specific male call divergence may play a potential role in maintaining genetic host-specific adaptation.

However, the evidence suggest that female cuckoos seem to selectively exploit one host species even though they could potentially use multiple species within a certain habitat [24], indicating that cuckoos seem to have a fidelity to not only a specific habitat type but also a specific host species within a habitat. This situation may imply the need of a more direct prediction; that is, the characteristics of male calls should diverge according to host races rather than habitat types in order to maintain host-specific genetic adaptation. So far, however, experimental studies testing this prediction are still lacking, despite its importance in the evolutionary study of avian brood parasitism. This may be partly due to practical difficulties in catching and housing the sufficient number of cuckoos in the field. A comparative approach would be an alternative to test the prediction while escaping such difficulties. In this study, the vocal characteristics of male cuckoos that exploit different host species were examined. We first investigated if male cuckoos indeed produce different calls at the individual level and then analyzed how these differences are associated with host specificity of male cuckoos at the population level.

**Methods**

**Ethics statement**

Field studies were carried out in accordance with relevant national and international guidelines and did not involve endangered or protected species. Male cuckoo calls were recorded at three geographically distant sites which are located in Chungcheongnam-do (36°27’N, 127°07’E), Jeollanam-do (34°48’N, 126°22’E) and Jeju-do (33°31’N, 126°32’E), respectively and no specific permissions were required for these locations and activities.

**Study system**

Fieldwork was conducted at three geographically distant sites located in Chungcheongnam-do, Jeollanam-do, and Jeju-do (hereafter, “CN”, “JN”, “JJ”), respectively; Fig. 1; each site covers about 500 km². CN and JN are located along the mainland of Korea and JJ is the largest island (1,848 km²) of Korea located at the south of the Korean peninsula. Each of the neighboring populations are about 150 km away from each other, which let us control the effect of geographic distance on call divergence. The habitat structures of three study sites were more or less similar in that they were open fields surrounded with mountains and forests, although vegetation types might be dissimilar due to latitudinal difference. Interestingly, cuckoos in JJ are clearly different in that they exploit a different host species from the other two populations. In the mainland of Korea, the primary host parasitized by the cuckoos is the vinous-throated parrotbill, Paradoxornis webbianus [25]. As secondary host species, the daurian redstart Phoenicurus ochruros and the stone chat Saxicola torquatus are also parasitized by the cuckoos, albeit with low frequency. The eggs of all of these host species have blue lines of background color and the cuckoos parasitizing these species in mainland Korea mimic their eggs very well. However, these species do not inhabit JJ or at least do not breed in JJ at all [26]; instead, anecdotal observations suggest that the meadow bunting Emberiza cioides which lays grayish white eggs with black lines may be a potential primary host in JJ [26]. The meadow bunting is known as a strong rejecter [27], which thus imply that the cuckoo host-race using this species should mimic their eggs well in order to overcome host defence. Therefore, it is highly unlikely that the cuckoo-race laying blue eggs in mainland Korea successfully parasitize the meadow bunting’s nests which contain grayish white eggs in JJ. This circumstance evidently indicates that whichever species cuckoos in JJ parasitize, they form a distinct host-specific race from those in CN and JN of the mainland of Korea. Therefore, these situations may provide a unique chance to elucidate male call divergence with respect to host use while controlling geographic cline in call variation.

**Call records and analyses**

Using a Zoom H1 recorder (ZOOM) with a directional microphone, ordinary male cuckoo calls were recorded at three locations (CN, JN, JJ) between May and June in 2012. In order to avoid duplicated recording of the same individual, we regularly changes the study site by driving to new locations, never again visiting a place where we conducted recordings. Once we spotted a calling male, we tried to approach him as closely as possible in order to record his calls clearly. Occasionally, we used playback to check for the presence of cuckoos where no cuckoo calls were heard, stopping playback as soon as a male was located to prevent playback calls affecting its behavior. Recordings were digitized with FairStars Audio Converter (v 1.97), at 16 bits at a sample rate of 44.1 kHz to a PC. To remove background noise, the digitized sound files were filtered with band-pass filters in Sound Analysis Pro (SAP, [28]). A range of calls which were at a similar level of amplitude were extracted from each individual to minimize measurement errors caused by variable amplitude. Then, because ordinary male calls are individually highly repeatable (see below and results), we randomly chose one call per individual from this range of individual calls for further analysis. Referring Fuisz and
is known to be a potential primary host on JJ. Emberiza cioides Korea while this species does not inhabit JJ at all. The meadow bunting doi:10.1371/journal.pone.0090468.g001
d E. webbianus doi (JJ; 33 Jeollanam-do (JN; 34

u taken by one observer to avoid interobserver bias. window = 10 ms, advance window = 1 ms). All parameters were
dF duration time (pause), highest

F2L) of 1st syllable and 2nd syllable, peak frequencies (PF1, PF2), the
dF differences between maximum and minimum frequency (AF1, AF2) and the gap of peak frequency between 1st and 2nd syllable (APF). The frequency parameters were averaged across a

dF succession of narrow and overlapping time windows (FFT data window = 10 ms, advance window = 1 ms). All parameters were
dF taken by one observer to avoid interobserver bias.

Statistical analyses
The consistency of male cuckoo calls was measured by calculating the repeatability (r) of each parameter of the calls

dF based on repeated measure of individual calls and an analysis of variance [29], for which we selected 3 males per site and 5
dF different calls per individual; in total 9 individuals with 45 different
calls were used.

dF To account for correlations among call parameters and avoid multiple testing, call features extracted by SAP were examined with a Principal Component Analysis (PCA). We retained
dF principal components with eigenvalues greater than 1 after varimax rotation by the Kaiser criterion. Then we conducted an

ANOVA to determine geographical differences of principal component scores among the three populations. In addition, we
tried to combine the data according to the pattern of host utilization (JJ vs. CN+JN) and then compared their component
score using Welch’s t-test [30]. All statistical analyses were done with R version 2.14.1 [31].

Results
Individual call variation and consistency
In total, the ordinary calls of 24, 22 and 22 different males were recorded in CN, JN and JJ, respectively. Calling male cuckoos typically produced clearly distinct two-syllable calls, in which the
first syllable was louder and higher pitched with the maximum frequency below 1 kHz (Fig. 2). Overall, there was a broad range of variation in each call parameter (Table 1), which may suggest that individual calls differ from one another. The repeatability test using 45 calls from 9 individuals revealed that most call parameters indeed varied and these differences resulted from between-individual variation rather than within-individual, indicating that each male produced a highly consistent call (Table 1, Fig. 3).

Male call variation at the population level
In the PCA for the call parameters from 68 different individual calls, 4 principle components (PCs) with eigenvalues larger than
one explained 78.3% of the variation in the data (Table 2). Each

principal component explained 26.3%, 21.9%, 16.5% and 13.8% of the variation in numerical order. Overall PC1 and PC2 included parameters most related to spectral features while most
temporal features were included in PC3 and PC4 (Table 2).

As inferred by the repeatability test, individual PC scores differed from one another (Fig. 4), showing again that individual
male cuckoos produced different calls at the local level. However, these differences did not lead to population-level differences (Fig. 4, Fig. 5). Scores of each PC were similar among three populations, indicating that spectral and temporal features of male calls did not differ across the geographic regions (PC1: F2,65 = 0.541, ns; PC2:
F2,65 = 0.504, ns; PC3: F2,65 = 0.127, ns; PC4: F2,65 = 2.098, ns, Fig. 5). Likewise, male calls did not appear to be differentiated according to the host species which they exploit; component scores of JJ and those pooled from CN and JN, where the cuckoos use the
same host species, did not differ significantly (PC1: t = 0.29, df = 34.999, ns; PC2: t = −0.76, df = 28.996, ns; PC3: t = −0.19, df = 30.819, ns; PC4: t = 1.76, df = 34.741, ns).

Discussion
Although male cuckoo calls varied significantly at the individual
level, there was no clear and consistent difference in call parameters between populations exploiting different host species. These results suggest that male calls may be able to play a function of individual recognition at a local level; that is, individuals may discriminate their partners, neighbors, or intruders based on this
individul call variation. It seems ambiguous, however, if calls
Cuckoos may benefit from recognizing other individuals in the vicinity during the breeding season. For example, male cuckoos are highly territorial and thus expend a lot of time and energy dealing with territorial disputes with neighbors. However, once territorial borders are well-established, neighboring males may save time and energy by reducing defensive aggression toward one another ('dear enemy' effect, [41]). Individual recognition should be an essential prerequisite for this to happen, although the presence of this effect has not been demonstrated objectively in this species. In addition, recognizing breeding partners might be very important if coordinated behavior between breeding pairs increases the chance of brood parasitism and thus enhances the

Convey the identity of the stepparents of the caller so that it may facilitate host-specific assortative mating in the cuckoos.

Figure 3. Spectrograms of male cuckoo calls illustrating between-individual variation and within-individual consistency. Ordinary calls of male cuckoos differ individually, showing consistent differences in time duration (A) and frequency range (B) of their calls. Colors of spectrograms in each panel represent different individuals.

doi:10.1371/journal.pone.0090468.g003

Table 1. The range of 9 call parameters and its consistency measured by calculating repeatability (r).

| Parameters | Mean ± s.d.* | Range (Min–Max) | \( r^b \) | \( p^b \) |
|------------|--------------|-----------------|------------|----------|
| \( T_1 \) | 85 ± 12.8 ms | 62–118 ms | 0.72 | \( r_{ks} = 14.29, p < 0.001 \) |
| pause | 236 ± 29.3 ms | 175–310 ms | 0.85 | \( r_{ks} = 29.90, p < 0.001 \) |
| \( T_2 \) | 148 ± 20.1 ms | 107–219 ms | 0.58 | \( r_{ks} = 8.12, p < 0.001 \) |
| \( F_{PF1} \) | 792 ± 32.6 Hz | 715–883 Hz | 0.58 | \( r_{ks} = 8.15, p < 0.001 \) |
| \( F_{PF2} \) | 642 ± 26.4 Hz | 595–708 Hz | 0.94 | \( r_{ks} = 81.3, p < 0.001 \) |
| \( F_{F1H} \) | 852 ± 44.1 Hz | 749–987 Hz | 0.85 | \( r_{ks} = 30.06, p < 0.001 \) |
| \( F_{F2H} \) | 667 ± 34.8 Hz | 611–764 Hz | 0.32 | \( r_{ks} = 3.45, p < 0.001 \) |
| \( F_{F1L} \) | 690 ± 37.7 Hz | 592–781 Hz | 0.10 | \( r_{ks} = 1.55, p = 0.172 \) |
| \( F_{F2L} \) | 601 ± 25.0 Hz | 549–669 Hz | 0.25 | \( r_{ks} = 2.69, p = 0.019 \) |

*aThe mean and range of parameters were obtained from 68 calls of 68 different male cuckoos.

*bRepeatability calculation and following tests were conducted using 45 calls from 9 individuals (5 calls per individual).

Table 2. Variable loadings of male cuckoo calls for four principal components.

| Component | PC1 (26.3%) | PC2 (21.9%) | PC3 (16.5%) | PC4 (13.8%) |
|-----------|-------------|-------------|-------------|-------------|
| \( T_1 \) | 0.192 | −0.169 | 0.396 | 0.239 |
| pause | −0.133 | −0.130 | −0.035 | −0.165 |
| \( T_2 \) | 0.287 | −0.091 | 0.308 | 0.387 |
| \( F_{PF1} \) | −0.454 | 0.214 | 0.172 | 0.015 |
| \( F_{PF2} \) | −0.310 | −0.373 | 0.107 | 0.303 |
| \( F_{F1H} \) | −0.202 | 0.018 | 0.529 | −0.352 |
| \( F_{F2H} \) | −0.173 | −0.541 | 0.012 | −0.260 |
| \( F_{F1L} \) | −0.478 | −0.025 | −0.156 | 0.024 |
| \( F_{F2L} \) | −0.397 | −0.204 | 0.215 | 0.286 |
| \( \Delta F_1 \) | 0.182 | 0.034 | 0.566 | −0.318 |
| \( \Delta F_2 \) | 0.122 | −0.415 | −0.153 | −0.501 |
| \( \Delta PF \) | −0.232 | 0.500 | 0.095 | −0.214 |

The percentages of variation explained by each principal component are given in parenthesis and the component that was loaded most highly for each parameter is in bold.

*T1 = duration of syllable 1; pause = temporal gap between syllables 1 and 2; T2 = duration of syllable 2; PF1 = peak frequency of syllable 1; PF2 = peak frequency of syllable 2; F1H = highest frequency of syllable 1; F2H = highest frequency of syllable 2; F1L = lowest frequency of syllable 1; F2L = lowest frequency of syllable 2; \( \Delta F_1 \) = the difference between the highest and the lowest frequencies of syllable 1; \( \Delta F_2 \) = the difference between the highest and the lowest frequencies of syllable 2; \( \Delta PF \) = the difference between the peak frequencies of syllables 1 and 2.

doi:10.1371/journal.pone.0090468.t001

doi:10.1371/journal.pone.0090468.t002
Fuisz and de Kort [22] showed that call structures differed significantly among male cuckoos occupying different types of habitats. In this study, we intentionally chose three sites with similar habitat structures so as to avoid any effects of habitat type itself on male call variation. Nonetheless, there may be some potential difference in environmental resonance capacity among study sites due to the latitudinal difference of vegetation types but our results indicate that these subtle environmental differences seem not to be mirrored into the characteristics of male calls. They also reported a geographical difference in male cuckoo calls and proposed genetic drift as a potential cause. However, this phenomenon was not observed in this study. One possible reason is that the geographic range of our study site may not be large enough to generate genetic drift which may randomly alter anatomical structures involved in vocal production and thus underlie the geographic variation of the vocalization [42–44], even though the common cuckoos are known to have strong site fidelity [45]. Unfortunately, however, it is not yet clearly demonstrated if male calls reflect the characteristics of genetic profiles in a population of cuckoos. We are currently carrying out a population genetic study with these populations to test the assumption that vocal variation may parallel genetic divergence among populations in cuckoos.

In this study, we hypothesized host-specific call variance as a feasible way for cuckoos to mate non-randomly according to host species, and predicted male call divergence between host-specific races. However, no such difference was found between two cuckoo host-races. From a non-selective point of view, this result suggests that these two host-races may not have been genetically differentiated enough to generate call divergence by means of genetic drift. Alternatively, it can be assumed that selection pressure causing call divergence may not be strong enough because host species distribute allopatrically in our study system. Based on the result that male calls diverged according to habitat types, Fuiz & de Kort [22] proposed the possible presence of habitat-specific races including both sexes of the cuckoo as an alternative way of maintaining cuckoo host-races. This view might be easily over-interpreted as if cuckoos really mate assortatively and thus form genetically distinct races. However, habitat-specific male call divergence itself may not be concrete support for the presence of assortative mating which enables cuckoos to maintain genetic adaptation in the arms race against host defense. A relatively small area often consists of a mosaic of different types of

Figure 4. Scatter plot of the principal component analysis for male cuckoo calls in three populations. The first two principal components were plotted and each symbol represents a different population. doi:10.1371/journal.pone.0090468.g004
habitats, and some different cuckoo host-races coexist in a small area while cuckoos keep distinct host-specific adaptation [20,24,46]. Furthermore, some host species like the vinous-throated parrotbill Paradoxornis webbianus breed in a range of diverse habitats from reedbed through grassland to mountains [47]. Therefore, although it could be said that male cuckoo calls diverge according to habitat types, this may not necessarily mean that male and female cuckoos mate assortatively via the diverged call and thus not only female but also male cuckoos belong to habitat-specific races. Instead, all these observation may indicate that the presence of habitat-specific races in cuckoos may not sufficiently guarantee the genetically-distinct host-specific adaptation which we currently observe in the cuckoo-host interaction. Therefore, until it has been proved concretely, we should be cautious about mentioning male cuckoo calls divergence as evidence of assortative mating and males belonging to the gentes.

Comparing host-specific male calls in a population with multiple cuckoo gentes may be one way to clarify all of the above issues, although it is extremely difficult to discriminate host-specificity of calling male cuckoos in the field. Alternatively, experimental approaches such as measuring male response and/or female preference for various male calls with different host-specificity will definitely be needed to objectively test the function of male calls for the assortative mating. However, as already perceived [48], the role of males in maintaining host specific adaptation in the cuckoos needs first to reach a consensus. After such a consensus, attempts to reveal how the cuckoos mate assortatively will ultimately become meaningful.

Acknowledgments
We would like to thank Sei-Woong Choi, Kyung-Gyu Lee, Jeong-Yeon Lee, Yong-il Lee and Ju-Yeol Shin for their valuable help in the field and laboratory. We are also grateful to two anonymous reviewers for their helpful comments that have improved the manuscript. Kirk Hart kindly provided his valuable time to proofread an earlier version of the manuscript.

Author Contributions
Conceived and designed the experiments: JWL. Performed the experiments: JWL. Analyzed the data: WJJ JWL. Wrote the paper: WJJ JWL JCY.
References

1. Chance EP (1940) The truth about the cuckoo. London: Country life.
2. Wylie I (1981) The Cuckoo. London: Batford.
3. Davies NB, Brooke MdL (1989a) An experimental study of co-evolution between the cuckoo Cuculus canorus and its hosts. I Host egg discrimination. J Anim Ecol 58: 207–224.
4. Davies NB, Brooke MdL (1989b) An experimental study of co-evolution between the cuckoo Cuculus canorus and its hosts. I Host egg discrimination. J Anim Ecol 58: 224–236.
5. Rothstein SI (1990) A model system for coevolution: Avian brood parasitism. Annu Rev Ecol Syst 21: 461–508.
6. Davies NB (2000) Cuckoos, cowbirds and other cheats. London: T & AD Poyser.
7. Payne RB (2005) The Cuckoos. New York: Oxford University Press.
8. Berlin S, Ellegren H (2004) Chicken W: a genetically uniform chromosome in a highly variable genome. P Natl Acad Sci USA 101: 15967–15969.
9. Brookes MdL, Davies NB (1988) Egg mimicry by cuckoos Cuculus canorus in relation to discrimination by hosts. Nature 335: 630–632.
10. Honza M, Taborsky B, Taborsky M, Teuschl Y, Vogl W, et al. (2002) Behaviour of female common cuckoos, Cuculus canorus, in the vicinity of host nests before and during egg laying: a radio-telemetry study. Anim Behav 64: 861–868.
11. Moksnes A, Roskaft E, Rudolfsen G, Skjelseth S, Stokke BG, et al. (2008) Genetic evidence for female host-specific races of the common cuckoo. Nature 456: 1167–1176.
12. Taborsky B, Taborsky M, Teuschl Y, Honza M, Vogl W, et al. (2002) Behaviour of female common cuckoos, Cuculus canorus, as shown by ringing. Ibis 119: 309–322.
13. Robson C (2007) Family PARADOXORNITHIDAE (PARROTBILLS). In: del Hoyo J, Elliott A, Christie DA, editors. Handbook of the Birds of the World, Volume 12. Barcelona: Lynx Edicions. pp. 292–320.
14. Kru¨ger O, Kolss M (2013) Modelling the evolution of common cuckoo host-races: speciation or genetic swamping? J Evol Biol 26: 2447–2457.
15. Kroodsma DE, Konishi M (1991) A suboxic bird (eastern phoebe, Sayornis phoebe) develops normal song without auditory feedback. Anim Behav 42: 477–487.
16. Malard H, Aubin T, White, JF, Harper DH, Danchin E (2009) Voice variation may signify ongoing divergence among black-legged kittiwake populations. Bird Biol Linn Soc 97: 269–297.
17. Seif DC (1957) Migration of the northwestern European population of the common cuckoo (Cuculus canorus), as shown by ringing. Ibis 119: 309–322.
18. Stoddard MC (2011) The past, present and future of ‘cuckoo versus weed warblers’ Anim Behav 83: 695–699.
19. Poyster.
20. Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB, editors. Acoustic communication in birds, volume 2. New York: Academic Press. pp. 237–278.
21. Punnett RC (1933) Inheritance of egg-colour in the parasitic cuckoos. Nature 132: 892.
22. Stoddard MC, Stevens M (2011) Avian vision and the evolution of egg color preference. Anim Behav 82: 271–278.
23. Stoddard MC, Kilner RM (2013) The past, present and future of ‘cuckoo versus weed warblers’. Annu Rev Ecol Evol 7: 178–179.
24. Stoddard MC, Lambrechts MM (1992) Individual voice recognition in birds. Trends Ecol Evol 7: 178–179.
25. Stoddard MC, Lambrechts MM, Dohout AA (1995) Individual voice discrimination in birds. In: Power DM, editor. Current ornithology, volume 12. New York: Plenum Press. pp. 113–139.
26. Dooling R, Lohr B, Dent M (2000) Hearing in Birds and Reptiles. In: Dooling R, Lohr B, Dent M, editors. Comparative Hearing, Birds and Reptiles. New York: Springer. pp. 308–359.
27. Dooling R, Lob R, Dent M (2000) Hearing in Birds and Reptiles. In: Dooling R, Lohr B, Dent M, editors. Comparative Hearing, Birds and Reptiles. New York: Springer. pp. 308–359.
28. Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB, editors. Evolution As a Process. London: Allen & Unwin. pp. 71–83.
29. Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB, editors. Evolution As a Process. London: Allen & Unwin. pp. 71–83.
30. Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB, editors. Evolution As a Process. London: Allen & Unwin. pp. 71–83.
31. Fisher J (1954) Evolution and bird sociality. In: Huxley J, Hardy AC, Ford EB, editors. Evolution As a Process. London: Allen & Unwin. pp. 71–83.