Modelling the evolution of common cuckoo host-races: speciation or genetic swamping?

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Abstract

Co-evolutionary arms races have provided clear evidence for evolutionary change, especially in host–parasite systems. The evolution of host-specific races in the common cuckoo (Cuculus canorus), however, is also an example where sexual conflict influences the outcome. Cuckoo females benefit from better adaptation to overcome host defences, whereas cuckoo males face a trade-off between the benefits of better adaptation to a host and the benefits of multiple mating with females from other host-races. The outcome of this trade-off might be genetic differentiation or prevention of it by genetic swamping. We use a simulation model to test which outcome is more likely with three sympatric cuckoo host-races. We assume a cost for cuckoo chicks that express a host adaptation allele not suited to their foster host species and that cuckoo males that switch to another host-race experience either a fitness benefit or cost. Over most of the parameter space, cuckoo male host-race fidelity increases significantly with time, and gene flow between host-races ceases within a few thousand to a hundred thousand generations. Our results hence support the idea that common cuckoo host-races might be in the incipient stages of speciation.

Introduction

Co-evolution is regarded as one of the most fundamental processes producing evolutionary change (Brooke & Davies, 1988; Rothstein, 1990; Sorenson et al., 2003; Payne, 2005; Thompson, 2005). The strong reciprocal selection pressures between predator and prey, or parasite and host, often lead to remarkable adaptations and counter-adaptations in co-evolving species (Davies, 2000, 2011; Krüger & Davies, 2002, 2004; Lahti, 2005; Tanaka & Ueda, 2005; Krüger et al., 2007; Boerner & Krüger, 2008; Davies & Welbergen, 2009; Welbergen & Davies, 2009; Spottiswoode & Stevens, 2010). With increasing fitness costs of parasitism, selection for host defences increases, which in turn may force parasites to specialize and evolve fine-tuned adaptations that overcome a particular host’s defences (Soler & Moller, 1990; Davies, 2000; Langmore et al., 2003; Tanaka & Ueda, 2005; but see Krüger, 2011). The evolution of distinct, sometimes local adaptations (Reinhold, 2004; van Doorn et al., 2009), or even host-specific parasite races is commonly observed in both vertebrate and invertebrate parasite–host systems under such intense co-evolution (Malaua et al., 2005; Thompson, 2005; Ragland et al., 2012; but see Reichard et al., 2011). The ongoing arms race may ultimately result in disruptive selection and speciation or extinction events (Coyne & Orr, 2004; van Doorn et al., 2009) and might lead to elevated rates of speciation and extinction in parasitic taxa (Malaua et al., 2005; Krüger et al., 2009).

Avian brood parasites such as the common cuckoo (Cuculus canorus) depend entirely on hosts to raise their offspring by laying their eggs into the nests of their hosts and hence often inflict severe fitness costs on them (Rothstein, 1990; Payne, 2005). Due to the high selection pressures involved, hosts have commonly evolved egg rejection of parasitic eggs and parasites have evolved egg mimicry. The common cuckoo uses over 100 host species, and at least 17 distinct cuckoo egg morphs have been described (Moksnes & Roskaft, 1995; Fossøy et al., 2011; Liang et al., 2012). In the
common cuckoo, these egg morphs are called gentes (singular: gen, Punnett, 1933). The maintenance of host-races in the common cuckoo is an evolutionary enigma and has been recognized as such for over a century (Pycraft, 1910; Wynne-Edwards, 1933; Jensen, 1966). The maintenance of host-specific mimicry eggs in the common cuckoo requires either assortative mating of cuckoo males and females from a specific host-race or that cuckoo egg coloration is under maternal control (Marchetti et al., 1998; Gibbs et al., 2000; Fossøy et al., 2011).

Assortative mating could eventually lead to speciation, but it might be counteracted by sexual conflict as cuckoo males might gain more from mating promiscuously with many females, also from other host-races (Krüger, 2007). Both Fossøy et al. (2011) and Marchetti et al. (1998) found indeed that common cuckoo males mate across host-races using genetic data, whereas Hauber & Dearborn (2003) emphasized the high degree of monogamy in cuckoos. Fuiß & de Kort (2007) showed that cuckoo males have habitat specific, hence host-race-specific calls which could facilitate assortative mating. In a very influential paper, Gibbs et al. (2000) proposed a solution to this evolutionary conundrum: they found genetic differentiation between mitochondrial DNA from different cuckoo host-races, but not in nuclear DNA, which implies that females are faithful to their host species, whereas males might not be. Knowing that female birds are heterogametic (Stefos & Arrighi, 1971), the genetic basis for egg coloration was proposed to reside, as either a gene or a switch controlling other autosomal genes, on the female-specific W chromosome (Gibbs et al., 2000). An alternative would be epigenetic markers. Under these scenarios, female cuckoo imprint on the host by which they were raised and undergo local adaptation to lay mimic eggs for that host. Male cuckoos could mate across host-races without impact on host-specific egg coloration but maintaining the common cuckoo as one species.

Although this explanation may seem convincing at first, several recent discoveries have challenged it. Davies et al. (2006) showed that cuckoos of the ‘reed warbler’ host-race of both sexes have an innate response to their foster parents’ alarm calls. Hence, having the wrong alleles might carry a substantial fitness cost in cuckoo chicks. This innate response cannot be encoded for by a gene or switch on the W chromosome because it would be unclear how male cuckoo chicks could inherit it. In addition, the female-specific W chromosome seems to be rather uniform in birds with rather few genes (Berlin & Ellegren, 2004). This does not, however, preclude sex linkage of such genes or switches. Fossøy et al. (2011) recently reported genetic differentiation between cuckoo host-races also in nuclear DNA; hence, males might matter too in the evolution and maintenance of cuckoo host-races.

This evolutionary puzzle, however, is not only exciting within the realm of host-parasite co-evolution; it is also an exciting case of sexual conflict, which has been recognized as an important driver of speciation (Parker & Partridge, 1998; Gavrilets, 2000; Krüger, 2008). It is clear that both cuckoo females and males benefit from more fine-tuned adaptations to overcome a host’s lines of defence. Davies et al. (2006) found an innate response of cuckoo chicks to alarm calls of a host species, and there are profound differences in the growth rates of common cuckoo chicks raised by different host species (Kleven et al., 1999). Hence, they would benefit from strict assortative mating, and the long-term consequence of this can be speciation (Gavrilets, 2004). Although male cuckoos also benefit from better host adaptation of the eggs they fertilize, there are three other benefits to consider for them. First, it is well known that male fitness in many taxa, including birds, greatly depends on the number of matings males achieve (Bateman, 1948; Davies et al., 2012). Female cuckoos cannot benefit from this as they need to spend much more time finding and monitoring host nests (Davies, 2000). Second, males from another host-race might be particularly attractive, because strangers in general can be attractive due to optimal outbreeding (Bateson, 1978; Buss & Schmitt, 1993). Third, mating across host-races might lead to increased heterozygosity of offspring, which is often positively correlated with fitness (Amos et al., 2001).

Although there is yet no clear empirical evidence for any of the three benefits in the common cuckoo, it is well conceivable that cuckoo males face a trade-off between the benefits of multiple mating and the benefits of better adaptation to overcome a specific host’s lines of defence. The result of this might be either speciation or alternatively genetic swamping, where a genetic polymorphism is lost due to fixation of alleles that provide the highest mean fitness across all populations (Lenormand, 2002). Using a simulation model where cuckoo male host-race fidelity evolves, we tested which of the two outcomes, speciation or genetic swamping, is more likely in the common cuckoo.

Materials and methods

Description of the simulation model

Our model is based on three common cuckoo hosts: reed warbler (Acrocephalus scirpaceus), meadow pipit (Anthus pratensis) and dunnock (Prunella modularis). Host populations are treated as constant, that is, they are not modelled explicitly, and we ran simulations with a cuckoo carrying capacity of 12 000, 1200 and 120 cuckoo individuals for each host-race. Cuckoo populations were initially set to the respective carrying capacities in a 1:1 sex ratio, and they generally fluctuated closely around these carrying capacities. Each cuckoo host-race

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produces an egg type specific to its host. We assume that this egg type is maternally controlled as postulated by Gibbs et al. (2000) and that females are 100% faithful to their native host-race. Females lay a mean of ten eggs per season with a standard deviation of three eggs and a maximum of 20 eggs.

The biological basis of the model is as follows (Fig. 1): offspring survival is normalized such that two offspring per female will survive on average. It is then modified with a fitness function incorporating negative density dependence of the form $f_1 = x^{1-N/K}$ where $x$ is a host-specific factor, $N$ is population size and $K$ is the carrying capacity. As values for $x$, we chose 2.8 for ‘reed warbler’ cuckoos, 2.3 for ‘meadow pipit’ cuckoos and 2.0 for ‘dunnock’ cuckoos. This reflects different strengths of egg rejection in response to cuckoo density (Davies, 2000) and translates into highest survival for ‘reed warbler’ cuckoos below carrying capacity and highest survival for ‘dunnock’ cuckoos above carrying capacity. We also checked whether simulation results remain qualitatively unchanged if we assume equal functions for negative density dependence of offspring survival ($x = 2.0$) for the three hosts, and they do.

Survival of cuckoo chicks is further modified by one locus called ‘host-specific adaptation’. We assume a diploid locus. Each cuckoo host-race has a specific allele, and if a host-specific adaptation allele is expressed that fits to the host, survival remains unchanged. If a host-specific adaptation allele is expressed that does not fit to the host, the survival probability is multiplied by $z$.
1−c, where c is the cost of lacking adaptation. We varied c between 0 and 0.9 in our simulations and assumed a mutation rate of $10^{-6}$ per allele and generation. For comparison, we also performed the simulations assuming host-specific adaptation to be linked to the sex chromosomes; in this case, respective alleles are present either on both W and Z chromosomes or only on the Z chromosome.

As a third offspring survival modifier, we also introduced a heterozygote advantage (heterosis) in some of our simulations to reflect the potential fitness benefit of mating outside the natal host-race to maximize heterozygosity. The average heterozygosity was calculated from ten neutral loci (see below), and then, an increase in survival rate of the offspring relative to its average heterozygosity (up to a specified maximum) was applied.

To model cuckoo male host-race fidelity, we assume that male cuckoos visit their natal host-race with a probability $z$ and one of the three remaining host-races with a probability of $1−z$. $z$ is the key locus that evolves in our simulations. When the male does switch host-races, we simulated host-race choice to be made according to the ideal free distribution where males switch to the host-race with the highest cuckoo female to cuckoo male ratio. This may also be the natal host-race (see below). The benefit for males switching to another host-race with more females is that they increase their probability of mating. In a separate simulation, we assumed random host-race choice of cuckoo males switching host-races. Male host-race fidelity is governed by a diploid autosomal locus and mutates with a probability of $10^{-6}$. This cuckoo male host-race fidelity then evolves over time. To simulate potential genetic differentiation between the three cuckoo host-races, we also included ten neutral markers with 20 alleles at each marker. These ten neutral markers were subsequently used to calculate $F_{ST}$-values, following Hudson et al. (1992). To simplify the model, we assume discrete, nonoverlapping generations. We used different parameter settings varying from a host-race switching benefit of 0.1 to a host-race switching cost of 0.1 and between 0 and 0.9 cost of a mismatch in host-specific adaptation. Although there is no empirical evidence for this parameter space, we chose it to reflect potentially very high costs of lacking host-specific adaptation alleles but smaller costs and benefits of host-race switching.

For each generation, the following steps are then simulated (Fig. 1). For each female, the number of eggs this female will lay is determined. Eggs are fertilized by random males from her habitat. Each offspring inherits the mother's egg type, one host-specific adaptation allele from the father's two alleles at that locus, one host-specific adaptation allele from the father's two alleles at that locus, one male host-race fidelity allele from the mother's two alleles at that locus, one male host-race fidelity allele from the father's two alleles at the male host-race fidelity locus, one male host-race fidelity allele from the father's two alleles at the male host-race fidelity locus, one of the mother's two neutral marker alleles and one of the father's two neutral marker alleles for each of the ten neutral marker loci. Each of the alleles at the male host-race fidelity locus mutates with a probability of $10^{-6}$ from the old value to ± 1% point (i.e. with half the given probability to the old value +1 and half the given probability to the old value −1% point), always within the constraints of 0% and 100% male host-race fidelity. Hence, mutations are only possible to neighbouring values, so male host-race fidelity is effectively modelled as a quantitative trait. Each of the alleles at each of the neutral marker loci mutates with a probability of $10^{-6}$ to a random allele at that locus.

Each offspring then survives with the probabilities given in the above-described fitness functions. These take negative frequency-dependent selection due to cuckoo egg rejection by hosts, the costs of expressing a wrong host-specific adaptation allele, and potential heterosis benefits into account.

For each male offspring, the model determines whether or not it switches to another host species or stays with its natal host-race. The probability of switching host-races is given as 1 minus the average of the two male host-race fidelity allele values. If male offspring do not switch host-races, they stay with their natal host-race. If they switch host-races, they are placed in a pool of host-race switchers.

After the adults have died, the three host-race populations now contain all surviving female offspring and all surviving male offspring that did not switch host-races. For each male from the pool of host-race switchers, the new host-race is chosen either according to the ideal free distribution (i.e. the one is chosen where the expected female-to-male ratio is greatest, not considering potentially following male host-race switchers) or at random. This may also be the natal host-race, so the true host-race switching rate will usually be lower than 1 minus the average male host-race fidelity of all males. For those males that initially leave their natal host-race, the host-race benefit or cost parameter can be used to inflict either a benefit or a cost of switching to a different host-race. The benefit of host-race switching could be higher attractiveness of unfamiliar cuckoo males to cuckoo females (Krüger, 2007). The cost of host-race switching could reflect higher predation in an

**Description of the simulation flow**

The initial distribution of alleles at the host-specific adaptation locus is random. With regard to the cuckoo male host-race fidelity locus, alleles are set to random percentage values within the boundaries 0% and 100% natal host-race fidelity; hence, the starting mean male host-race fidelity is 50%. Allele frequencies at the ten neutral marker loci are set randomly.
unfamiliar habitat or while searching for a different habitat, or it might reflect the recent finding of Fuisz & de Kort (2007) showing that cuckoo males have habitat specific, hence host-race-specific calls which could facilitate assortative mating. Finally, all offspring become adults and form the next generation.

Simulation output and analyses

The simulation computes average male host-race fidelity, as well as an estimate of average genetic differentiation ($F_{ST}$-value) between the three host-races based on the ten neutral markers. As the results are most conservative with regard to cuckoo host-race fidelity with a cuckoo carrying capacity of 12 000 for each host-race, we mostly report those. We also performed a sensitivity analysis for the number of eggs and varied the mean number between 5 and 20, but results changed very little and only quantitatively.

We initially ran simulations for different parameter combinations for only 100 generations simply to test whether cuckoo male host-race fidelity departed from randomness. Five simulations were run for each parameter combination. To test for significant differences from randomness or from other simulations, $t$-tests were used.

In a second step, we determined how many generations were needed until $< 1$ cuckoo male switches host per host-race and generation (number of migrants per generation or $Nm < 1$) and how many generations were needed to reach $F_{ST}$-values of 0.15, which is considered to indicate significant genetic differentiation (Wright, 1951). The simulation program was written in Delphi® (Object Pascal, Delphi, Borland, Austin, TX, USA).

Results

Cuckoo host-race fidelity after 100 generations

Under most parameter combinations, we found a significantly elevated cuckoo male host-race fidelity after 100 generations (red areas of Fig. 2), regardless of whether host-specific adaptation alleles were under autosomal control (Fig. 2a) or sex-linked. Simulations with host-specific adaptation alleles being sex-linked (both W and Z chromosomes) showed a slightly higher mean cuckoo male host-race fidelity with, on average, 1% point higher host-race fidelity after 100 generations than when simulated under autosomal-only control. If we assume that the host-specific adaptation alleles are only located on the Z chromosome, we find even more elevated cuckoo male host-race fidelity (Fig. 2b). On average, cuckoo male host-race fidelity was 4.8% points higher than when simulated under autosomal-only control and differences were particularly marked at higher host-specific adaptation allele costs (Fig. 2b).

With host-race switching benefits, substantial fitness costs (at least 20%) of expressing a wrong host-specific adaptation allele are required (Fig. 2a) to lead to significantly elevated cuckoo male host-race fidelity (all $P < 0.05$). Under no or small (< 20%) fitness costs of wrong host-specific adaptation alleles, any host-race switching benefit leads to significantly reduced cuckoo male host-race fidelity (green areas of Fig. 2, all $P < 0.05$).

When cuckoo males switch between host-races according to the ideal free distribution and with no cost of switching between cuckoo generations, a 10% fitness cost of expressing a wrong host-specific adaptation allele is required to lead to a significantly higher cuckoo male host-race fidelity than expected by chance ($t_4 = 2.345$, $P < 0.05$). Regardless of this cost of expressing a wrong host-specific adaptation allele, any cost of host-race switching between cuckoo generations leads to significantly elevated cuckoo male host-race fidelity (all $t$-tests, $P < 0.01$). With no cost of host-race switching between generations and between 0% and 5% fitness costs of expressing a wrong host-specific adaptation allele, simulations do not lead to significantly elevated cuckoo male host-race fidelities (all $P > 0.1$). Introducing a heterozygote advantage did not change the conclusions qualitatively, even with a heterozygote advantage of 10% per locus, as allele diversity is sufficiently high even in the absence of host-race switching cuckoo males (Fig. 3). This is due to the large population size assumed for each cuckoo host-race.

When cuckoo males switch between host-races at random, the results are relatively similar. Similar to host-race switching under the ideal free distribution, regardless of the fitness costs of expressing a wrong host-specific adaptation allele, any cost of host-race switching between cuckoo generations leads to significantly elevated cuckoo male host-race fidelity that departs from randomness (all $t$-tests, $P < 0.01$). The increase in cuckoo male host-race fidelity with increasing fitness costs of expressing a wrong host-specific adaptation allele is much steeper compared with the ideal free distribution, and overall, cuckoo male host-race fidelity is 2.3% points higher after 100 generations. In the next section, we detail how these results differ when the population size is small.

Population size effects and cuckoo male host-race fidelity over time

With decreasing cuckoo population size, mean cuckoo male host-race fidelity after 100 generations increases, but since smaller populations are more severely affected by random events, variation in the simulation outcome and thus in male host-race fidelity strongly increases as well (Fig. 3). Thus, with a population size of 12 000 for each cuckoo host-race, there is a significantly elevated cuckoo host-race fidelity (51.7%; $t_4 = 5.152$, $P < 0.001$),
but although mean cuckoo male host-race fidelity increases to 54.1% for a population size of 1200 and to 61.7% for a population size of 120 for each cuckoo host-race (Fig. 3 black bars), simulation results revealed only statistical trends for an elevated cuckoo male host-race fidelity for a population size of 1200 cuckoos per host-race \((t_4 = 2.140, P < 0.1)\) and 120 cuckoos per host-race \((t_4 = 2.329, P < 0.1)\). Modelling a heterozygote advantage of 10% per locus does not change the conclusion for a population size of 12 000 or 1200 cuckoos per host-race (Fig. 3 grey bars). There is still a significantly elevated cuckoo male host-race fidelity (51.7%; \(t_4 = 5.188, P < 0.001\)) and a trend for 1200 cuckoos per host-race (52.7%; \(t_4 = 2.584, P < 0.08\)), respectively. For
a population size of 120 cuckoos per host-race, however, there was no evidence for an elevated cuckoo male host-race fidelity with a maximum of 10% heterozygote advantage (51.2%; \( t_4 = 0.271, P > 0.5 \)). Hence, a large heterozygote advantage could prevent the evolution of elevated cuckoo male host-race fidelity across small populations.

The road to speciation?

We simulated how many cuckoo generations were needed until < 1 cuckoo male switches host per host-race and generation (\( Nm < 1 \)), that is, until insufficient gene flow between host-races exists to genetically homogenize the populations (Wright, 1951). As can be seen from Fig. 4, the number of required cuckoo generations decreases sharply with increasing costs (red and yellow areas). The minimum parameter settings to reach this criterion under ideal free distribution of host-race switching within a season were no cost of host-race switching accompanied by at least a 10% fitness cost of expressing a wrong host-specific adaptation allele, where it took a mean of 39 848 cuckoo generations until \( Nm < 1 \) between cuckoo host-races. With 1% host-race switching costs and 2% fitness costs of expressing a wrong host-specific adaptation allele, it took a mean of 114 945 cuckoo generations until \( Nm < 1 \) between cuckoo host-races. With 2% host-race switching costs and no fitness costs of expressing a wrong host-specific adaptation allele, it took a mean of 59 376 cuckoo generations until \( Nm < 1 \) between cuckoo host-races, 27 452 generations with 5% host-race switching costs and 15 777 generations with 10% host-race switching costs.

The fastest parameter combination was a host-race switching cost of 10% and a 90% fitness cost of expressing a wrong host-specific adaptation allele where \( Nm < 1 \) after 2244 generations. Assuming host-race switching benefits, substantial fitness costs of expressing a wrong host-specific adaptation allele (at least 20%) are required until \( Nm < 1 \) between host-races. With lower fitness costs of expressing a wrong host-specific adaptation allele, gene flow continues to take place between cuckoo host-races (green areas of Fig. 4). Results were different if the host-specific adaptation alleles are sex-linked. If they are located on both W and
Z chromosomes, it takes on average 12.4% fewer generations until $Nm < 1$ and even 45.6% fewer generations if only the Z chromosome carries the host-specific adaptation alleles. Hence, if host-specific adaptation alleles are located on sex chromosomes rather than autosomes, gene flow between host-races ceases more quickly.

If cuckoo movements within a generation are simulated at random, fewer cuckoo generations are required until gene flow between host-races ceases. As for cuckoo host-race switching according to the ideal free distribution, minimum parameter settings until cessation of gene flow between host-races under random host-race switching within a season were at least a 10% fitness cost of expressing a wrong host-specific adaptation allele. Under random host-race switching of cuckoo males within a generation, gene flow between host-races ceases after, on average, 14.6% fewer cuckoo generations compared with host-race switching under the ideal free distribution, which was a significant difference (sign test, $P = 0.003$).

Most parameter combinations hence eventually lead to very high cuckoo male host-race fidelity and hence very little or no gene flow between cuckoo host-races, supporting the speciation hypothesis rather than the genetic swamping hypothesis.

**Genetic differentiation between cuckoo host-races**

The simulations show that $F_{ST}$-values increase exponentially with increasing costs of expressing a wrong host-specific adaptation allele. The absolute values after 100 generations are tiny, ranging from 0.0001 to 0.001. But they increase steadily and reach a $F_{ST}$-value of 0.15 after 2.1–3.3 times as many generations as are needed until the number of switching males ($Nm$) is < 1 per host-race. The fastest parameter combination to reach an $F_{ST}$-value of 0.15 was a host-race switching cost of 10% and a 90% fitness cost of expressing a wrong host-specific adaptation allele where $F_{ST} = 0.15$ was reached after 7487 generations. Note that Wright’s (1951) equation, $F_{ST} = 1/(4Nm + 1)$, to establish the relation between $F_{ST}$ and the number of switching males (migrants) cannot be applied here: the populations in our case are not at equilibrium, thus violating a central assumption of Wright’s equation (Wright, 1969; Hutchison & Templeton, 1999). On the contrary, in our case, the switching phenotype is under (negative) selection, and for gradually decreasing numbers of host switchers, the (increasing) $F_{ST}$-values will necessarily lag behind the values expected from Wright’s equation due to the populations’ recent history with higher numbers of switching individuals.

**Discussion**

Our simulations indicate that the most likely long-term evolutionary scenario for the host-races of the common cuckoo is a high degree of cuckoo male host-race fidelity. Under most parameter settings and more importantly, with modest fitness costs in terms of expressing a wrong host-specific adaptation allele and host-race switching, cuckoo male host-race fidelity increases significantly. In our simulations, cuckoo male host-race fidelity evolves in a nonlinear fashion over time along a curve of diminishing returns. Of course, the number of cuckoo generations required until gene flow between host-races ceases of course greatly depends on parameter settings, but a minimum of 10% fitness costs of expressing host-specific adaptation alleles and about 40 000 cuckoo generations are required or a 2% cost of host-race switching and about 60 000 cuckoo generations. In models with host-race switching benefits, substantial fitness costs of expressing a wrong host-specific adaptation allele are required (> 20%), otherwise genetic swamping is the long-term outcome.

One might argue that a 10% fitness cost of expressing a wrong host-specific adaptation allele is very high, and it might be said that any host-race switching cost is purely speculative. We would like to point out that Davies et al. (2006) found an innate response of cuckoo chicks to alarm calls of a host species. A failure to respond to alarm calls of the host species might well be fatal for cuckoo chicks. With regard to host-race switching, Fuisz & de Kort (2007) found that cuckoo males produce habitat-specific and hence host-race specific calls, thereby potentially facilitating assortative mating. Under such a scenario, female cuckoos could exert female choice for cuckoo males of the same host-race, with severe fitness consequences for cuckoo males trying to mate outside their natal host-race. Unfortunately, not much is known about how cuckoos select their mate (Fossøy et al., 2011), but several plausible mechanisms have been proposed, such as host preference, habitat imprinting or natal philopatry (Moksnes & Røskaft, 1995).

Our simulations indicate that cuckoo host-races could become genetically isolated from each other relatively quickly, in just 2000–100 000 generations. Co-evolutionary interactions between parasites and their hosts are well known to generate rapid evolutionary change (Coyne & Orr, 2004; Thompson, 2005). Indeed, a recent comparative study suggested elevated rates of speciation and extinction in parasitic cuckoo taxa compared with nonparasitic cuckoo taxa (Krüger et al., 2009). This study also found that cuckoo species that use more host species have more taxonomic subspecies described, but these taxonomic subspecies are not described based upon genetic data but morphological and distributional data. This raises the question of whether in these taxonomic subspecies we can already see a morphological footprint of future speciation events in parasitic cuckoos that parasitize many host species. There are profound differences in the growth rates of common cuckoo...
chicks raised by different host species (Kleven et al., 1999), and Fossøy et al. (2011) speculated about the possibility of assortative mating by size in common cuckoo host-races, but there is currently no empirical evidence for assortative mating by size. It is commonly observed that generalist parasites evolve host-specific races (Thompson, 2005), and our simulations indicate that the most likely outcome of this process in the common cuckoo will be speciation events.

A word of caution, however, is also necessary at this point. A cuckoo male host-race with even minute occasional gene flow between host-races might be sufficient for keeping the cuckoo as a single species, although speciation with gene flow is becoming more widely documented (Balakrishnan et al., 2009; Lawniczak et al., 2010). Recently, Spottiswoode et al. (2011) have documented host fidelity over millions of years in the greater honeyguide (Indicator indicator) using mitochondrial DNA but have found a complete lack of differentiation in nuclear DNA; hence, host-specific adaptation over long time scales does not necessarily result in speciation events.

Our model indicates that in line with the evolution of higher cuckoo male host-race fidelity, genetic differentiation will take place. The initial absolute values are very small, but it needs to be borne in mind that our model assumed a population size of 12,000 cuckoos for each host-race. Significant genetic differentiation ($F_{ST} = 0.15$) does occur within 10,000–300,000 generations. Any effects of heterozygote advantage only become pronounced with a population size of 120 cuckoos per host-race. Under this scenario, heterozygote advantage would massively slow down genetic differentiation. Cuckoo populations are often patchy and can be small (Lindholm, 1999). Our simulations show that this aspect of cuckoo biology could change the conclusion that genetic differentiation is the most likely outcome if cuckoo populations are small and heterozygote advantage is marked. More likely, it would slow down the differentiation process considerably.

Our model also shows that complete host-race fidelity will take a very long time to evolve. This means that a small percentage of males will most likely always father a few offspring with cuckoo females from a different host-race. This result fits to the empirical result obtained by Fossøy et al. (2011) who found that 9% of male descendants were fostered outside their fathers’ putative host species. They also reported, however, that 43% of cuckoo males in their study sired offspring in more than one host species. Marchetti et al. (1998) found a similar value of 37%. This indicates that although many cuckoo males regularly mate with a female from another host-race, they sire only a small proportion of their total number of offspring with females from another host-race. Reasons for this difference are currently unknown. In addition, Hauber & Dearborn (2003) reported a high rate of monogamy across several parentage analyses in cuckoos, indicating a high level of mate fidelity in both sexes. This might be explained by observations in several cuckoo species that male cuckoos cooperate with female cuckoos during egg laying to distract the hosts (Davies, 2000; Krüger, 2007).

In conclusion, our simulation results indicate that the most likely outcome of the co-evolutionary arms race coupled with the sexual conflict in common cuckoos is genetic differentiation between cuckoo host-races, rather than genetic swamping. This supports recent empirical evidence suggesting that assortative mating takes place in common cuckoos (Fuisz & de Kort, 2007; Fossøy et al., 2011). Only with minimal costs of expressing a wrong host-specific adaptation allele or in small, patchy populations coupled with strong heterozygote advantage does host-race fidelity lead to genetic swamping.

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