



## Essay

# Evolutionary change: facultative virulence by brood parasites and tolerance and plastic resistance by hosts



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Coevolutionary theory predicts that parasitism selects for defensive traits in the hosts that counteract the negative effects of parasites. Such antagonistic interactions may continuously coevolve within cycles without end, or result in host specialization and speciation of parasites. Here, we argue that particularities of brood parasite–host systems explain whether the coevolutionary relationships result in parasite specialization and speciation. Highlighted particularities of the system are (1) virulence of the parasites, (2) the ability of parasites to alter host behaviour, (3) the relative importance of defensive tolerance and defensive resistance of hosts, and (4) phenotypic plasticity of parasite virulence and host resistance. Fixed virulence of parasites selects for fixed resistance of hosts and both enhance the process of specialization and speciation of parasites. In contrast, phenotypic plasticity in virulence of the parasites would select for tolerance and facultative resistance in their hosts. These host characteristics imply limited escalation in resistance defences and therefore would facilitate continuous coevolutionary cycles preventing parasite specialization. Thus, when studying the diversification of brood parasites within the avian phylogeny, considering these three factors would help us understand what drives their evolution. To illustrate the importance of virulence, phenotypic plasticity and defensive tolerance for the evolution of parasites, we compare evolutionary radiation experienced by the genus *Clamator* and the Tribe Cuculini, which includes the genus *Cuculus*, and speculate whether particularities of brood parasitism by the great spotted cuckoo, *Clamator glandarius*, and the common cuckoo, *Cuculus canorus*, explain differences in evolutionary radiation experienced by these two groups of brood parasites.

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Parasites obtain benefits from other individuals (hosts), thereby decreasing the hosts' fitness. Coevolutionary theory predicts that parasitism selects for defensive traits in the hosts that counteract the negative effects of this antagonistic relationship (Thompson, 1994). Such antagonistic interactions may continuously coevolve within cycles without end, or result in host specialization and speciation of parasites. Hosts evolve to resist and/or to tolerate parasite attacks, which would imply different evolutionary outcomes and affect the speed of evolutionary change (Svensson & Råberg, 2010). While defensive resistance refers to characteristics that prevent or release hosts from parasitism, defensive tolerance applies to host characteristics that reduce the negative fitness effects of parasitism without affecting parasite fitness. Immune responses are examples of resistance defences because they eliminate

parasites from hosts, while red blood cell disorders that reduce the incidence of malarial parasites without affecting parasite loads is considered defensive tolerance (Råberg, Graham, & Read, 2009). The relative importance of both defensive strategies and, therefore, characteristics of the evolutionary process depends on parasite virulence and other particularities of the host–parasite system (Medzhitov, Schneider, & Soares, 2012; Moore, 2002; Svensson & Råberg, 2010).

Virulence, defined as the strength of negative effects of parasitism, selects for strong defensive resistance in the parasites' hosts, which reduces parasite fitness and, among other counter-defences, may select for increased virulence in parasites (Schmid-Hempel, 2011). Thus, reciprocal evolutionary change in both the parasite and the host species triggering successive defences and counter-defences, which is known as a coevolutionary arms race (Dawkins & Krebs, 1979), will be driven by the level of virulence of the parasite and the intensity of the evolved host defences via resistance. In contrast, reciprocal evolutionary changes would be expected to occur slowly, if at all, in host–parasite systems in which

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hosts mainly show defensive tolerance (Best, White, & Boots, 2014; Miller, White, & Boots, 2006).

In addition, phenotypic plasticity in host defences and parasite counter-defences may be of selective advantage depending on the level of parasite virulence and host defences and, therefore, may influence coevolutionary relationships between the host and parasite (Garland & Kelly, 2006; Mougí, Kishida, & Iwasa, 2011). Co-occurrence of inducible offenses and defences (i.e. reciprocal phenotypic plasticity) is well documented in antagonistic coevolutionary systems, and has been suggested as enhancing the evolutionary potential of species (Agrawal, 2001). For instance, plants induce defences that are dependent on the density of herbivores, and herbivores induce counter-defences that are dependent on the concentration of defences in consumed plants (Agrawal & Karban, 2000). These antagonistic interactions may affect the probability of changes occurring in the host and, thus, of host and parasite diversification (Agrawal, 2001). Thus, parasite virulence, the relative importance of defensive tolerance of hosts and phenotypic plasticity of parasites and hosts may be related to each other and affect the evolution of hosts and parasites.

A particular type of parasitism is that in which individuals exploit the parental care of nonrelatives, thereby reducing the costs of parenting (parental-care parasitism; Roldán & Soler, 2011). Obligate avian brood parasitism is an extreme form of parental-care parasitism, and an appropriate study system to test predictions related to a variety of coevolutionary scenarios and outcomes (Medina & Langmore, 2016b), including the influence of coevolution in promoting species richness (Krüger, Sorenson, & Davies, 2009) or the evolutionary rate of change of morphological traits of brood parasites (Medina & Langmore, 2015). Here we suggest that virulence of the parasite and defensive strategies of the hosts, together with phenotypic plasticity in host defences and parasite counter-defences, would affect rates of specialization and speciation by brood parasites (see Fig. 1). We argue that less virulent brood-parasitic species (i.e. those that do not evict host eggs or nestlings) would differentially facilitate the evolution of defensive tolerance in their hosts, resulting in reduced rates of evolutionary change (i.e. specializations and speciation processes). Phenotypic plasticity of virulence of the parasites and of host defences would play a central role in this scenario since it affects specialization and speciation processes and its evolution would depend on particularities of host–parasite systems (see above). To exemplify these

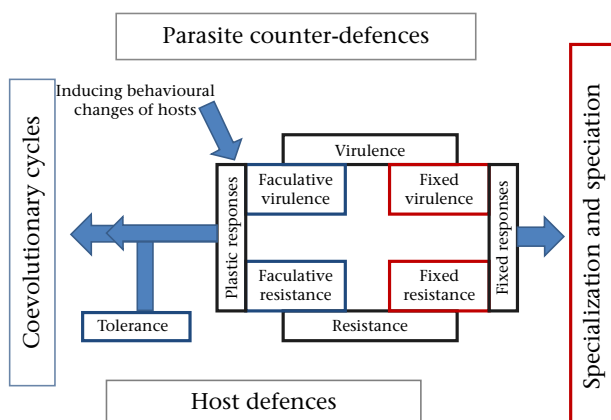
points, we use particularities of evolutionary radiations and associated characteristics of brood parasites, mainly within the Family Cuculidae.

## PARASITE VIRULENCE AND THE EVOLUTIONARY RADIATION OF CUCKOOS

Brood parasitism had a polyphyletic origin within the Family Cuculidae (Aragón, Møller, Soler, & Soler, 1999; Sorenson & Payne, 2002, 2005; but see ; Hughes, 2000). The Family includes 59 species of obligate brood parasites and 82 species with parental care distributed across all continents except Antarctica (Payne, 2005). The Cuculinae is the largest subfamily and includes two Tribes: the Cuculinii and the Phaenicophaeni. The former Tribe includes 11 genera and 51 species, all obligate brood parasites. Most of the species in the Phaenicophaeni are nesting cuckoos, but there are also four species of the brood-parasitic genus *Clamator* (Sorenson & Payne, 2005). Interestingly, all species within the Cuculinii evict host chicks or kill them, while brood parasites of the genus *Clamator* are less virulent and sometimes allow some host chicks to survive together with the cuckoo chicks (Krüger et al., 2009). Thus, it is likely that, together with other particularities, differences in virulence of brood parasites explain the differential diversification experienced within each lineage. Notably, more than 50 years ago Friedmann (1964, page 95) wrote: ‘The fact that *Clamator*, during its very long existence, has produced only 4 species, as against 12 in the younger *Cuculus*, or 12 in *Chrysococcyx*, coupled with the evolutionarily inert nature of its polymorphic trends, suggests that the genus is one that has been relatively less affected by evolutionary change’. *Cuculus* and *Chrysococcyx*, within the Cuculinii, both include more species than the genus *Clamator*. Our point is that differences in virulence would select for different kinds of defences in hosts, and both affect the evolutionary process within different clades.

The great spotted cuckoo, *Clamator glandarius*, and the common cuckoo, *Cuculus canorus*, are the best known species of these two brood parasitic lineages, and may serve to exemplify differences between the lineages potentially responsible for the diversification of each group. The common cuckoo lays eggs that frequently mimic those of their hosts and, soon after hatching, their chicks evict the host eggs or nestlings (Davies, 2000). In contrast, the great spotted cuckoo lacks these adaptations (Soler & Soler, 2000; Soler, Avilés, Soler, & Møller, 2003). Killing host offspring is the most virulent behaviour of brood parasites. The common cuckoo nestlings evict all host eggs (or nestlings) in the nests soon after hatching (Honza, Voslajerova, & Moskat, 2007), while those of the great spotted cuckoo outcompete host nestlings, although some sometimes survive. In addition, great spotted cuckoos are facultatively virulent since they are able to depredate host nests as a response to defensive resistance (egg ejection) of their hosts (Soler, Soler, Martínez, & Møller, 1995). Thus, although both common cuckoos and great spotted cuckoos are able to kill all host offspring, the latter do so facultatively and the former obligately. The key point is that the reproductive success of hosts of nonevicting brood parasites is not fixed, and on average is higher than zero. These and some other differences between great spotted cuckoos and common cuckoos are useful for explaining the relatively higher radiation rate experienced by the Cuculinii along their evolutionary history.

A long-standing hypothesis in ecology is that specialization can lead to the generation of new species (Futuyma & Moreno, 1988). Positive associations between specialization and speciation have been suggested for brood parasites (Davies, 2000; Krüger et al., 2009; but see ; Lanyon, 1992; Medina & Langmore, 2016b) and, thus, factors affecting the former are central for explaining the



**Figure 1.** Relationships between characteristics of host defences and parasite counter-defences explaining parasite specialization and speciation on the one hand and coevolutionary cycles on the other. Special attention is paid to virulence of parasites and resistance and tolerance of hosts, which may be fixed or plastic responses to the parasite. Characteristics of hosts and parasites within the same colour frame indicate positive associations, while those of different colour frames are negatively related.

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