

PARASITISM AND NEST PREDATION IN PARASITIC CUCKOOS

Brood parasites such as cuckoos often considerably depress the reproductive potential of their host (Jensen and Vernon 1970). Cuckoo nestlings are usually markedly different from the nestlings of their hosts, and the eggs sometimes do not mimic at all the eggs of the host (Jensen and Jensen 1969). In spite of this, many host species do not discriminate against cuckoos. I try to suggest why some hosts do not evolve discriminating mechanisms against their cuckoos in spite of high selective pressure. It is suggested that the habits of cuckoos as nest predators select against the evolution of discriminating mechanisms in certain host species.

Discrimination is costly. The cost of discrimination against a brood parasite may involve mistakes which the host is likely to make when, instead of eliminating the parasite, it eliminates its own offspring or abandons its nest on false alarm. Assume a mixed host population of discriminators and nondiscriminators. In the nonparasitized section of the population there is a disadvantage to the discriminators, since in their attempts to destroy a potential parasite they may kill or abandon their own young by mistake. Nondiscriminators in the nonparasitized section of the population do not suffer from such mistakes. Discrimination could therefore only evolve in the parasitized section of the population. This may be prevented if the breeding success of that section is reduced considerably. The model suggests that cuckoos revisit the parasitized nests after they hatch and prey upon the host nestlings. Under such circumstances there will be no advantage to a discriminating host over a nondiscriminating host (in the parasitized section of the host population), since both eventually do not fledge their young. The only way the host could avoid the cuckoo is to abandon the parasitized nest. This is in fact a very common mechanism of discrimination (Rothstein 1975). However, this is a very costly mechanism since it involves the acquisition of a new nesting site, the building of a nest, and the laying of another clutch. Therefore, only a species which may build a new nest and escape parasitism by the cuckoo is likely to evolve into a discriminating host. Perhaps nondiscriminating species are composed of populations in which the individual is unable to leave the breeding area to exploit the possibility of breeding away from the cuckoos, either in place or in time (e.g., because the whole habitat is saturated with breeding hosts or it is too late for an additional brood).

There is as yet little direct evidence in support of the above model. There have been various observations on cuckoo predation on nests (Ingle 1911; Witherby et al. 1949; Wyllie 1975). Wyllie observed a European cuckoo preying upon nestlings in a nest from which a cuckoo egg had earlier been removed. Mendelssohn and Golani (personal communication) observed a cuckoo *Clamator glandarius* which had laid in captivity. Later they put a nestling of the cuckoo host (the hooded crow *Corvus corone*) into the nest. The nestling, which was alone in the nest, was killed by the cuckoo. A nestling cuckoo was later put into the nest. That nest was closely observed by the cuckoo but was not touched.

The nestlings of the green cuckoo which parasitize the ploceid finches call so loudly from the nest that the human observer can easily distinguish a nest with a cuckoo nestling from one without a cuckoo (Kemp, personal communication). This

peculiar adaptation may make sense if it helps the cuckoo nestling to avoid being killed by its own parents when they revisit the nest.

The model suggested may be useful for understanding the interactions between other parasites and their hosts. Cowbirds, unlike cuckoos, do not mimic the eggs of their hosts. Cowbirds do not prey upon young but do take the eggs of their hosts. I suggest that egg predation by cowbirds, like nestling predation by cuckoos, helps to maintain a high rate of parasitism. If cowbirds did mimic the eggs of their host they would not be able to prey upon them.

The success of parasites which are also predators may explain the success of many parasites which castrate their hosts (Obrebski 1975). Parasitic trematodes feed first on gonads of their snail hosts (Kuris 1974). Parasitic ants castrate their hosts, which continue to produce worker ants but no sexual forms (Wilson 1975). Castration decreases the likelihood that the host will evolve adaptations against the parasite because even if an individual host eventually rids itself of its parasite, its adaptations cannot be transmitted to the following generation.

The model suggests that adaptations of parasites as predators or as agents of castration may improve their ability to exploit their host population as parasites. It does not suggest that parasites may evolve predatory habits to improve their adaptations as parasites. The two characteristics should evolve independently of one another, each selected by its own merits. The advantage gained by the parasite is a consequence of the coincidence of parasitism and predation.

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LITERATURE CITED

- Ingle, A. P. 1911. Cuckoos as nest robbers. *Emu* 11:254-255.
- Jensen, R. A. C., and M. K. Jensen. 1969. On breeding biology of southern African cuckoos. *Ostrich* 40:163-181.
- Jensen, R. A. C., and C. Vernon. 1970. On the biology of the didric cuckoo in Southern Africa. *Ostrich* 41:237-246.
- Kuris, A. M. 1974. Trophic interaction: similarity of parasitic castrators to parasitoids. *Q. Rev. Biol.* 49:129-148.
- Liversidge, R. 1971. The biology of the Jacobin cuckoo *Clamator jacobinus*. *Ostrich Suppl.* 8:117-137.
- Nicolai, J. 1964. Der Brutparasitismus der Viduinae als ethologisches Problem. *Pragungsphanomene als Faktoren der Rassen und Artbildung. Z. Tierpsychol.* 21:129-204.
- Obrebski, S. 1975. Parasite reproductive strategy and evolution of castration of hosts by parasites. *Science* 188:1314-1316.

- Rothstein, S. T. 1975. Evolutionary rates and host defenses against avian brood parasitism. *Am. Nat.* 109:161-176.
- Wilson, E. O. 1975. *Sociobiology, the new synthesis*. Cambridge, Mass.
- Witherby, H. F., F. C. R. Jourdain, N. F. Ticehurst, and B. W. Tucker. 1949. *The handbook of British birds*. Witherby, London.
- Wyllie, I. 1975. Study of cuckoos and reed warblers. *Br. Birds* 68:369-378.

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