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Report on Habilitation thesis submitted by Dr. Tomáš Grim

Scope

The thesis comprises 25 original scientific papers in English (17 published and 8 manuscripts) and 10 popular scientific articles in Czech. Many of the published papers are in the top international journals of biology (Proceedings of the Royal Society, Biological Journal of the Linnean Society), ecology and behaviour (Evolutionary Ecology Research, Behavioural Ecology and Sociobiology) or ornithology (Ornithological Science, Auk, Journal of Avian Biology), and 15 of the 17 are in IF journals. Most of the papers are concerned with brood parasitism, particularly the interactions between the cuckoo *Cuculus canorus* and its hosts, and I shall concentrate my remarks on these before giving an overview of the thesis.

Cuckoo-host studies

During the last twenty years, cuckoo-host interactions have attracted much interest from researchers because they provide an example of co-evolution amenable to study by experiment. This work has revealed some exquisite examples of parasite adaptations that have evolved in conjunction with host counteradaptations (eg. host egg mimicry evolving in response to host egg rejection). However, there are also striking examples of apparent lack of adaptation (eg. some hosts accepting parasitic eggs or chicks very unlike their own). This has given rise to vigorous debate concerning whether these cases reflect evolutionary lag (hosts need more time to evolve defences) or an equilibrium set by the costs and benefits of defences (if defences are too costly, they may never evolve). Dr. Grim's papers make an important contribution to this topic in several novel way.

First, he has produced critical reviews which will help to clarify arguments in this debate. In paper 1 (2005, *Biol. J. Linn, Soc.*) he draws together studies from a wide literature (including classic work on Mullerian and Batesian mimicry in insects) to show that similarity can come about through a variety of processes in nature, including: common ancestry, chance, common environments, selection for crypsis against predators, as well as through selection imposed by co-evolving signal receivers (eg. cuckoos and hosts). The review makes two useful general points: first, the term mimicry is best reserved for similarity evolving by this last process, and second, experiments are usually needed to identify the processes leading to similarity.

Papers 2 (2006, *Evol. Ecol. Research*) and 3 (manuscript) provide critical reviews of the evidence for host rejection of parasite chicks, and of the various hypotheses for why this is much rarer than host rejection of parasite eggs. Building on an idea proposed by Planque et al. (2002), Grim suggests that because hosts often reject parasite eggs, they will encounter parasite chicks less frequently than parasite eggs. Thus there will be less strong selection for chick rejection than egg rejection. The key prediction from Grim's hypothesis is that chick discrimination should evolve especially in cases where the parasite has defeated the host at the egg stage. Clarification of this process, coined the "rarer enemy effect", should stimulate

more studies of chick discrimination by brood parasites. I fully endorse Grim's plea for more studies of host responses to parasitism at the nestling stage.

Second, Grim provides the first convincing evidence for rejection of cuckoo chicks by reed warbler hosts from a careful field study (paper 4; 2003, *Proc. R. Soc.*). He documents desertion of healthy cuckoo nestlings at 16% of reed warbler nests. These desertions occurred when the cuckoo chicks were about 11-14 days old, around the time that their nestling period began to exceed that expected for a brood of reed warbler young. In paper 5 (submitted manuscript), some elegant experiments involving cross-fostering of single and 4-chick broods of reed warblers, to force parents to care for artificially prolonged nestling periods, confirmed that desertion occurred when the length of the nestling period exceeded that of a normal healthy brood of their own young. These are fascinating results and something that has been completely missed by other workers. We are left with the puzzle of why only 16% of reed warbler pairs use this apparently fool-proof cue to parasitism, with the majority (84%) continuing to provide nestling care to the cuckoo for 16-21 days in the nest. I hope that Grim will continue with this novel study to tackle this question.

Third, Grim has made a valuable contribution to knowledge on how hosts provision cuckoo chicks. Two papers (1997, *Folia Zool*. and 2001 *Behav. Ecol. Sociobiol*) show that the diet brought by reed warblers to a cuckoo nestling is similar to that brought to a brood of their own young. However, a cuckoo nestling is given food at a greater rate than to a single reed warbler of the same mass, suggesting it is a "supernormal stimulus" compared to a host chick. Furthermore, larger cuckoo nestlings were fed smaller prey, perhaps because hosts become less selective when trying to meet their excessive demands. I agree with Grim's conclusions here, but I also wonder whether demands differ between cuckoo and reed warbler chicks of the same mass because they differ in the ages (masses) when their most rapid growth occurs.

Two papers (8 and 9) address the begging stimuli which influence host provisioning. Grim argues that two cues identified by previous authors, namely gape area and begging call rate, are insufficient to explain the increasingly high provisioning rates to older cuckoo nestlings (two – three weeks old). He proposed that "wing shaking" provides an additional stimulus. This is certainly a likely candidate. Experiments are now needed to test both whether wing shaking indeed signals hunger levels, and whether it influences host provisioning. In another critique of previous literature (paper 10, 2006, *Orn. Science*), Grim argues that in some species, parasitic chicks may end up sharing the nest with host young, not because it pays to tolerate them (to increase host parent provisioning to the nest) but because they are too costly to evict (too large). I agree with this, but believe both arguments may hold, and apply to different cases.

A question that has long puzzled cuckoo researchers is why the cuckoo does not parasitise several common species that seem eminently suitable as hosts. These include song thrushes and blackbirds. Three papers address the puzzle of why these are not regular cuckoo hosts (paper 7, 2006 in press *Behav. Ecol. Sociobiol*; paper 17, 2001 *Biologia* and paper 24 manuscript). By transferring cuckoo chicks from reed warbler nests to nests of song thrush and blackbird, Grim tested directly their suitability as hosts. He showed that cuckoos cross-fostered to song thrush nests grew well (in fact better than in reed warbler nests) but those in blackbird nests fared badly (none survived to fledge). These are fascinating results. They show that cuckoos can flourish on a diet of molluscs and earthworms, very different from their normal insectivorous diet. But the marked difference between song thrush and blackbird is surprising. Grim suggests an intriguing hypothesis. Blackbirds are well known to vary their reproductive output by brood reduction. If they favoured larger nestlings (to enhance brood reduction), the cuckoo chick (smaller than a blackbird chick at hatching) may be disfavoured. Song thrushes, by contrast, may vary their reproductive output by adjusting their clutch size and so may more carefully tend smaller nestlings to ensure the whole brood survives. If so, cuckoo chicks may fare much better in a thrush nest. This is an ingenious suggestion. I hope Grim follows this up. It may help to explain host choice by cuckoos.

Fourth, and finally, Grim has added to our knowledge of how hosts react to adult cuckoos as an enemy. In well designed experiments, involving excellent statistical analysis, he shows the importance of careful choice of control stimuli with which to compare responses to the cuckoo (paper 16, 2005 *Auk*), and reports mobbing responses of reed warblers (paper 18, *Bird Study*) and blackcaps (paper 19, manuscript). These studies show how hosts may attack the adult cuckoo as a first line of defence against parasitism.

Other studies

The other papers in the thesis include a record of an endangered nightjar in tropical South America, detailed studies of nestling diets in various birds, and experiments to test whether egg colour signals female quality, and could, therefore, be a sexually selected signal to increase male parental care. These attest to Grim's broad interests in ecology and evolutionary biology. The ten papers in Czech cover a wide range of issues, including cultural evolution, carnivory in plants, and conservation strategies. I applaud this effort put into explaining scientific issues to the general reader.

Recommendation

I congratulate Dr. Grim on an outstanding thesis. I am impressed, in particular, with his novel contributions to studies of co-evolution through: his careful critiques of the recent literature; through field work and elegant experiments, which have revealed new discoveries concerning how hosts react to parasitic chicks, and how the parasitic chicks, in turn, manipulate their hosts; and through new theories concerning why chick rejection is rare in hosts, and why some hosts might be more suitable than others because of differences in their chick rearing strategies. He has identified some excellent topics for future research. I am also impressed with the clarity of his writing, his detailed knowledge of a wider literature, and with his commitment to explaining current research to a general audience.

I warmly recommend that this thesis is accepted and that Dr. Grim is qualified for an assistant professorship.