

## **Evaluation of Tomas Grim's thesis for requirements of a lectureship**

### ***Overview***

Thomas Grim has submitted an excellent thesis as a partial fulfillment for the requirements of a lectureship at the Faculty of Sciences, Palacky University, Czech Republic. The main focus of this body of work concerns the evolutionary ecology of avian brood parasites, species of birds that lay their eggs in the nests of other species and depend entirely on those 'hosts' to raise their chicks. The reciprocally antagonistic relationship between brood parasites and their hosts has made them a model system for the study of antagonistic co-evolution and it is in this area that Dr. Grim has made a number of general and significant contributions. Dr. Grim's publication rate is very good (I received tenure the University of California with a similar publication rate) and, based on the large number of submitted publications, even appears to be accelerating. In addition, many of the papers are of broad interest and published in very high quality international journals (Proceedings of the Royal Society, Behavioral Ecology and Sociobiology, Evolutionary Ecology Research). As a side note, I also found the papers to be exceptionally well written and it is clear that Dr. Grim invests a great deal of time crafting his high quality papers! Dr. Grim's papers are being well-cited, and a tally from the Web of Science reveals a total of over 50 citations to date for all papers combined. This is a very respectable citation rate and confirms that Dr. Grim's papers are having an impact in the field. Finally, I am very impressed with the number and diversity of popular science articles Dr. Grim has published. Too few scientists take the time and effort to make their work accessible to the public, and Tomas Grim's endeavors in this area are very noble. Overall, I find the body of work to be very impressive and, in my opinion, should easily meet the requirements for a lectureship.

### ***Specific Comments on the Research and Papers***

Here I briefly discuss some of the more important papers published by Dr. Grim, in particular their main findings, contributions and, where necessary, points of contention. I will focus on the work pertaining to the interactions between brood parasites and their hosts (papers 1-10) since this is my own area of expertise. These papers concern host discrimination, the evolution (or lack

thereof) of chick mimicry in cuckoo chicks and factors that affect the growth and performance of cuckoo chicks. The papers span the range from reviews (paper 1 and 2), a thought piece (paper 3), a critical reevaluation of the research and conclusions of others (papers 6, 8, 10) and observational and experimental studies (papers 4, 5, 7, 9). As Grim points out in one of his papers (3), far more research on brood parasites is focused on the egg stage than the chick stage — a contribution of this thesis is to provide more data on the chick stage and the two reviews in particular help to separate what we know from what we think we know. For example, Paper 1 makes a very useful contribution by reviewing the current evidence for chick mimicry (i.e. parasitic chicks whose appearance or traits have evolved by natural selection to resemble those of the hosts). His review of other factors that could lead to apparent mimicry, and the experimental or phylogenetic data that will be required to distinguish among these various hypotheses, will help to add rigor to this area of research. Paper 2 makes the valuable contribution of focusing attention on parental discrimination — the mechanism that would lead to any evolution of chick mimicry — as opposed to a more narrow focus on the outright rejection of parasitic chicks. The paper then provides a critical review of the hypotheses that have been proposed to account for the lack of chick rejection. In my opinion, of all of the papers in this thesis, the two review papers will have the biggest impact on the field.

Two empirical studies (4,5) are also noteworthy by showing that chick discrimination can occur without recognition — essentially the parental care tactics of the host are insufficient to fully meet the needs of the cuckoo chicks. This is an interesting finding that has important implications for the field in general. A slight quibble with these two papers is a semantic one, but I raise it because semantic issues seem to crop up in a couple of the other papers as well, and it is one area where this otherwise very promising scientist could show a small amount of improvement. In this specific case, Grim uses the term 'discrimination' to describe the fact that natural levels of parental care in the host are not sufficient for the needs of the parasite, and that the hosts are not "willing to increase their parental effort above the level designed by selection for the needs of their own nestlings". In other words, a term normally used to describe a phenomenon based on some sort of active response (discrimination) is used to describe no change in action or behavior whatsoever. I think this has the potential to add confusion. Moreover, there are hints throughout the paper that the observed chick desertion behavior is an

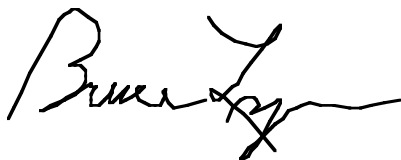
adaptive host defense: technically, however, if there has been no evolution, it does not make sense to refer to adaptation. Without further evidence, the simplest interpretation of these patterns is that, in some cases, the parental behaviors of this host make it a suboptimal host, but not due to any evolutionary response on the part of the host. Grim makes a very interesting comment in the discussion of paper 4 that I believe is the crux of any adaptive interpretation of the failure of hosts to fully raise cuckoo chicks. The issue is whether the window of parental care in host populations sympatric with the cuckoos is shorter than those in allopatry. In other words, has adaptive evolution in fact occurred to shorten the length of parental care in populations that suffer brood parasitism? This is a fascinating question and I would encourage further comparative work to answer the question. Another interesting question that is raised by these studies, and worthy of future studies is: why is there variation among hosts in propensity to desert (Why did only 10% of the birds desert rather than 100% in the observational study?) Are there factors that predict which individuals in the population will desert? Paper 5, the experimental investigation of the proximate cues parents use when deserting offspring, is an excellent paper and a very elegant study overall. The discovery that some birds have a built-in timer that shuts down parental care is really fascinating and this whole area is worthy of additional research. Since the paper has been submitted, but is not yet accepted, I suggest that it might be worth referencing such time effects found in other contexts. For example, I recall reading of a similar timing effect that shuts off infanticide in male mice, a mechanism that apparently functions to prevent males from killing their own offspring. Referring to timing effects in a broader context would make the paper of broader interest than just the brood parasitism researchers.

The final studies I will comment on concern cuckoo chick signals and their effect on parental provision (papers 6 and 8). There has been much current interest in determining how cuckoo chicks are able to obtain feedings from their hosts and, in particular, whether the cuckoos simply tap into existing parental feeding rules to obtain the same amount of food for a given signal as a host chick or host brood, or whether cuckoos have somehow evolved signals that allow them to extract a disproportionate amount of food from parents (the so called 'superstimulus' hypothesis). Dr. Grim has investigated these issues and his results are contrasted with a series of earlier similar studies, aimed at answering the same questions, by Kilner, Davies

and other colleagues (the cuckoo research group at Cambridge England). Grim presents results that he suggests differ from those of the earlier studies, including the conclusion as to whether some of the begging signals should be interpreted as superstimuli. In some cases, the differences boil down to how one measures or defines the term and I think there is less controversy here than is being suggested. For example, Grim points out that a cuckoo chick received far more food than a single host chick, a result he claims differs from the findings of Kilner et al's Nature paper. However, he also made a completely different comparison: Kilner et al. compared feeding rates of cuckoo chicks versus entire broods (4 chicks) of host chicks. While it might be legitimate to debate which measure is more meaningful (but even here this might just be semantics as opposed to biology) it is not reasonable to claim that the results of a study lead to a different conclusion from a previous study when completely different measures are compared. Finally, after reading all of Dr. Grim's combined papers, I was left with the slight impression that the cuckoo group in Cambridge, and Dr. Kilner in particular, has been singled out as adversaries (i.e. the tone of some parts of Dr. Grim's papers appear a bit more adversarial than the differences between the studies merit). Obviously, the process of science is based on additional tests of the findings of others, which at times involves criticism, but the style and approach in such studies can make a huge difference: overstating a controversy to get work published or being unnecessarily adversarial can reflect badly on a scientist, especially if it becomes a pattern.

To sum up, Tomas Grim has submitted a high caliber thesis as a partial fulfillment for the requirements of a lectureship. He has been prolific, published papers of very broad interest in top international journals, and has helped focus attention on some areas of the field that were not getting the attention they deserve. I give him my very strong support for his application to become a lecturer.

Bruce Lyon

A handwritten signature in black ink, appearing to read 'Bruce Lyon', with a stylized flourish at the end.

Associate Professor  
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