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Kateřina Tvardíková (hereafter KT) submitted in August 2013 to the University of South Bohemia in České Budějovice a Ph.D. Thesis entitled: **Trophic relationships between insectivorous birds and insect in Papua New Guinea.** Below follows my evaluation of this thesis.

The thesis, of 184 pages, comprises an Introduction (concise review) and six chapters in the shape of manuscripts intended for publication in research journals, one of which is already published (in Journal of Tropical Ecology) and four in review. In addition there is a Summary and Appendices. Co-authorship declarations emphasizes that KT was the principal researcher and leader of the comprehensive fieldwork program in New Guinea.

The Introduction offers a description of the tropical environment of New Guinea and reviews how tropical avian communities are assumed to respond to environmental change. The question of how the diversity of tropical forest birds varies in relation to environmental conditions (elevation, habitat disturbance etc.) has been in focus for as long as conservation of tropical rainforests has been on the conservation agenda. Yet, because of the bulk of new data, the constant effort across study sites, and the use of a broad range of techniques to document the environmental variable, the work of KT represents a significant step forwards. Of particular value in this respect is the quantitative documentation of the supply of arthropod foods and the food selection by a large number of bird species. The quantitative assessment is one of the most comprehensive to date for testing predictions about what factors that best explain the variation in avian diversity in tropical rain forest.

<u>Chapter I: Species richness of birds along a complete rainforest altitudinal gradient in the tropics.</u> This builds on a constant-effort data collecting over two years, at 10 study sites, 8 of these regularly spaced along an altitudinal gradient from 200 to 3700 m at Mt Wilhelm on New Guinea. The data are analyzed in relation to environmental data, including climate and numerous parameters that describe vegetation structure. Results obtained in the subsequent chapters are taken into account in the interpretation, and Chapter I therefore represents the last stage in the research project, although apparently placed in the front to emphasize what is the most significant outcome of the work.

The diversity of insectivorous birds was generally high up to 1700 m elevation, but then declined sharply, while herbivores (mostly frugivores) declined more gradually, although most rapidly near the tree-line. Specific predictions from the existing theoretical framework were tested in order to explain this variation. Available area and mid-domain effect were rejected as causes and the best predictor appears to be habitat complexity, although climate explains well the decline in herbivore diversity with altitude. Nevertheless, I was missing an analysis of niche packing (with morphological diversity of species as proxy), species turnover along the gradient, consideration of the specific role of vegetation structure in the condensation zone (leaf-types and epiphyte cover).

<u>Chapter II: New avian records and range shifts of birds along altitudinal gradient of Mt. Wilhelm, Papua New Guinea (MS in review)</u> presents the full list of bird species recorded, and specifies new

records for the area and extension of the known altitudinal distributions of species. KT does not in this chapter speculate over the possible causes of altitudinal expansion.

Chapter III. Diet of land birds along an altitudinal gradient in Papua New Guinea (MS in review). This is based on identification of >3500 identified food items in regurgitated stomach contents of 999 mist-netted birds representing 99 species. Little was previously known about the diets of these species. With quantitative data for what tropical forest birds had in their stomachs it was possible to demonstrate that many presumed insectivores are in fact more opportunistic than assumed, feeding also on fruit or nectar. In spite of this opportunism, diet samples from conspecific birds generally clustered together, which probably reflects preference for specific micro-habitats or use of specific search tactics to find concealed prey, rather than preferences for particular prey types. A general trend was documented for reduced dietary diversity at high altitudes, with a predominance of small birds feeding on tiny insects, and supplementing with fruit.

Chapter IV. Herbivore damage increases avian and ant predation of caterpillars along altitudinal forest gradient in Papua New Guinea (MS in review). In a well-designed experiment with artificial caterpillars placed exposed on the vegetation or semi-concealed in rolled leaves it was demonstrated that predation by ants (especially in the lower part of the altitudinal transect) and birds increased after artificial damaging of leaves, simulating herbivory. Thus, predators can detect odors and colour changes by plants signaling herbivory, and birds appear to be important predators of herbivorous insects at mid-altitude. Regrettably, little was done to explain the minimal increase in predation on caterpillars after simulated herbivory above 2500 m (Fig. 3).

Chapter V. Disappearance of birds from forest fragments in Papua New Guinea (MS in review). This study compared composition of bird communities in fragmented lowland rainforest with a range of environmental variables, including food supply. The study suggests, in accordance with the trend found in Chapter I, that reduced diversity of insectivorous bird species is caused by loss of certain microhabitats (notably closed canopy and open understory) in fragmented and disturbed forests, rather than by limited amounts of arthropod foods. The Chapter is supplemented with a matrix of ecological requirements for all species, many of which have never been assessed previously.

Chapter VI. Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea (J. Tropical Ecology 2012: 11 pp. This paper examines the incidence of attacks by wasps, ants and birds on artificial caterpillars (see under Chapter IV). The discussion warns that such results should be interpreted with caution, but yet emphasizes that predation on exposed larvae by birds and ants is significant, and notably so in fragmented and secondary forest. Apparently, no attempts were made to use bite marks on artificial caterpillars to identify the responsible bird species.

The chapters are followed by a quite detailed Summary of the main findings, and Appendices.

Evaluation of fieldwork and analysis

The studies outlined above are all based on data gathered during a comprehensive fieldwork program, with four periods of data collecting and altogether 265 days of fieldwork. A total of 34.000 individual birds and 260 species were recorded during standardized counts, and environmental parameters and abundance of arthropods plus leaf weight and area on several tree saplings was recorded at every point-count site. Obtaining such data in natural forest habitat in tropical montane areas with high rainfall is indeed a difficult task, and represents hard work. KT is to be congratulated with her management of the field work as well as with the well planned project design.

In addition to considering specific questions about the relationship between birds and their prey (Chapters II-VI), KT designed her data collecting protocol with the aim to test a more general macroecological question, namely what governs the variation in species diversity along the altitudinal gradient. She presented a good test of specific predictions from the rapidly growing literature concerning causalities that may explain the variation on species diversity on this gradient. Empirical climate data, obtained over one year at each site, gives an advantage in detecting possible topography-driven local anomalies that would not emerge from lapse-rate based statistical climate models that build on interpolation between widely scattered weather stations (as used in many other macroecological studies). Over all, KT is to be applauded for the good planning and great pioneering work to collect standardized empirical data, instead of relying on models or general (and poorly founded) published data. KT emphasizes the great flexibility of diets of most tropical forest birds, as her detailed studies contradict the traditional (and probably rather naïve) classifications of broad trophic guilds ('frugivores', 'insectivores', 'nectarivores'). It is instead suggested that most species are rather opportunistic in terms of what they eat, but that many species instead have distinct preferences for feeding habitat and for where and how they find and catch cryptic or evasive prey. This links the avian diversity with the complexity of their habitat. Of great interest, although not a new discovery, is also the experimental work to document how insectivorous birds can detect signs of damage on the vegetation in their search for aggregates of arthropod foods.

In her data analysis, KT employs a range of statistical tools, including canonical correlations. I did not detect incorrect or inappropriate use of statistics

The results, and interpretations of observations, make sense in relation to my own experiences from many other (similar) tropical environments.

Originality and contribution to existing knowledge

The thesis presents a multifaceted approach to understanding factors that govern the variation in avian diversity in mature tropical forest, with powerful tests of specific predictions. The analysis also provides a better explanation of why insectivorous rainforest birds are so sensitive to habitat disturbance (compared with birds with other feeding specializations). The decline of insectivorous birds in degraded rainforest habitats is a widespread but poorly explained phenomenon, but KT presents strong evidence linking the pattern to loss of microhabitats (used by species with specialized feeding habits), as opposed to declining amounts of food. The loss of specialized insectivores may cause dramatic changes in the trophic interactions in the ecosystem, and may have significant implications for conservation work in tropical forest.

The study provides detailed new information on habitat selection and food preferences of a large number of birds inhabiting the entire altitudinal forest gradient. Such data (in the Supplementary Material to Chapter V) will be useful for others working on ecology and conservation in the region

Presentation of data

The entire thesis is well structured and nicely produced. The papers are well written, concise and clear, with attention to grammatically correct English. Very few typos were detected (some of these being errors in scientific names that may well be caused by the automatic spell-check).

Literature citation

KT covers the literature well with respect to studies of variation in species diversity of forest bird communities in relation to habitat variables and food supply, especially in the tropics, as well as prevailing theory concerning the variation along environmental gradients. Gaps in the coverage are mainly studies published in obscure journals and reports (grey literature) relating to management of tropical forest. Chapter I provides a general review of the literature dealing with how species richness varies along the altitudinal gradient, but does not outline the root of controversies or attempt to relate the different models to latitudes or climates.

Concluding evaluation

KT has covered a diverse range of topics in her thesis. It is clear, throughout the work, that KT is a very competent observer in the field, and also able to thoroughly analyze her data in a macroecological framework. I am satisfied that the candidate has attained the required standard for a doctorate. Thus I recommend, without hesitation, that the degree of Doctor of Philosophy is awarded.

Copenhagen, 1st October 2013

Jon Fjeldså
Professor

PhD thesis review report

"Trophic relationships between insectivorous birds and insect in Papua New Guinea" by Kateřina Tvardíková

On 184 pages of text (including appendices), a submitted PhD thesis strives for bringing out something new about avian species richness and bird-insect feeding interactions along changing tropical environments. I was really interested in reading this work as avian ecological specializations within equatorial areas are poorly known and as an advocate of classical ecological views, I believe that they significantly contribute to observed patterns of tropical species diversity. The current lack of knowledge about tropical systems is caused mostly by inadequate research efforts in the region and Katka's thesis seems to be a nice example how such knowledge might be deepen by concentrated field work. Apparently, she invested an extraordinary huge amount of time to data collection and its elaboration during her studies which resulted in six completed manuscripts tied together in her dissertation (one of them is already published in *Journal of Tropical Ecology*) and couple of other "science friendly" outputs. From a formal point of view, the only thing which was slightly incomprehensible to me is different order of manuscripts in an opening list if compared with the thesis itself. It is argued that the order in the list is chronological but once dating in not available for unpublished contributions, the reader must just believe. Anyway, I have to say that the submitted thesis has a typical structure, is written in a polished style and contains minimum of typing errors (if any). Thus, the formal aspect requires no more attention here.

If I look at the papers included, I see sort of two groups. In the first one, the author endeavours to describe avian diversity in terms of species richness and diet composition among different environments (mostly elevations but one contribution focuses on forest fragments of different sizes). The second group in simple terms investigates predation rate of artificial caterpillars by birds and ants while elevation plays an important role again. Generally, the two groups differ in perspective as the first one tries to understand the birds' situation whereas the second one primary describes rather a caterpillars' point of view. Katka, however, fairly well "turned the coin" in favour of birds already in the Introduction by emphasizing the ways by which they search for food. Thereby, she fitted her entire work convincingly into the field of avian ecology, still exploring the focal interaction from both sides.

Comments on particular contributions:

In the first paper (let's follow the real order), the authors aimed to describe changes in avian species richness along an elevational gradient on Mt. Wilhelm and explain them by several variables representing diverse hypotheses suggested earlier. I really appreciate the robustness of support for elevational decline in richness similarly as attempt to differentiate among feeding guilds of birds. However, I have doubts about capability of employed statistical models to distinguish clearly among mechanisms generating the pattern. Except for mid-domain effect, all the hypotheses predict an observed decline is number of species and the explanatory variables are strongly correlated with altitude and therefore between each other. Thus, it is very difficult for me to agree with the statement that area represents rather source of error because the fits of models were relatively poor (0.76-0.91). It makes sense that one should conclude something but in this case only mid-domain effect seems to be convincingly sent off the game while area, habitat, species pool and climate further interact. One cannot expect that the effect of area is similarly fine if compared to habitat structure (which is by the way strongly determined by climate), however, this does not necessarily mean that for instance area related population sizes do not support species richness within an elevational band. Authors further suggest that richness of insectivorous species more likely reflects habitat complexity whilst the climate governs the diversity pattern in herbivores. This is interesting and I also like the explanations provided in the Discussion. Nevertheless, it seems to me that overall proportional decline in number of species is quite similar for both groups and the difference is created by elevations 2200 and 2700 m a.s.l., where insectivorous species drop "quickly" down. This corresponds to the change in tree diversity as well as density of stems and makes the trend in richness of insectivores less smooth if compared to herbivores. The difference in trend smoothness is in my opinion responsible for differences in relationship to climate and habitat complexity measure, respectively. However, does this necessarily mean the stronger bond to climate for herbivores? Isn't it possible that some part environment (such as a forest stratum) important for maintaining diversity of insectivores is missing or changed at these elevations? Why the two elevations differ markedly in canopy openness from neighbouring sites? Besides, differences in space use might be responsible for the contrast between these two feeding groups. I mean, frugivorous birds are relatively mobile animals opportunistically exploiting resources which might lead to larger home ranges, wider elevational ranges and finally to lower estimates of habitat specialization (smoother changes between elevations). Is that true, have you compared average elevational extends or habitat specialization estimates for abovementioned feeding guilds? Finally, I am little bit confused by usage of predictions I and II. Are they independent among hypotheses tested, or there is something in common for e.g. prediction I in all the hypotheses?

The second chapter focuses on elevational ranges and is mostly descriptive, adding new points to the current knowledge. This is certainly important but I would be cautious in stating that novel distributional information reflects real shifts rather than more exact estimates. As far as I understand, range extension is reported especially for larger species, non-passerines and frugivores. These groups comprise rather mobile species with larger home ranges and lower densities. Therefore, interaction between lower probability of detection and variable spatial distribution might be definitely responsible. The fact that observed shifts were mostly upward ones might in turn indicate better knowledge of lower elevations. Was the previous research distributed evenly across all the elevations?

Chapter III provides an extremely interesting data about diet of birds. These data is possible to use in couple of other attractive ecological studies in future. What a pity that information about elevational variation in food supply is not reported along the diet composition (sorry, for being too ambitious). It is not surprising to me that nectarivorous birds take always some insects, more interesting is common mixing of insects and fruits. The issue of seasonal variation in food composition is not discussed. Do you expect some variation in proportion of fruits/insects in the course of the year within a species/individual? Would it be theoretically dependent on elevation? Figure 4 which reports on elevational changes in proportion of plant material and arthropods is based on all birds captured. How it would look like if only fruit-insectivorous (mixed diet guild) birds are included? Abundances of Coleoptera and Diptera show hump-shaped pattern along elevation. Does this reflect the species richness patterns similarly as suggested for ants? Is it possible, that an abundance pattern of spiders, fitting into Coleoptera and Diptera patterns, indicates replacement of beetles by spiders in the diet of birds along altitude? Might it be connected to differences in type of birds caught at particular sites? Provided that spiders might be more frequently in the diet of birds searching for food at places with more bare ground/less shrubs (cf. Chapter I). Formal note, B part of figure 3 is very difficult to read.

Chapters IV and VI investigate experimentally some aspects of predation rates of leaf-eating caterpillars and one of them evidently received already some attention of reviewers. I believe that methodological approach tells us relevant stories about real processes in nature and I find the outputs convincing. It looks like predation pressure is a result of changes in total abundances of predators. It is remarkable that number of caterpillars attracted by birds fits better to overall abundances of birds if experimental herbivory is presented (figure 3, page 113). This supports the idea that important part of insect feeding birds switches the food preferences to specific search for caterpillars when damaged leafs are available. It is somehow strange to me why experimental herbivory enhances probability of predation while leaf fold decreases it. Basically, I understand that a caterpillar is less visible when it is concealed, but are leaf folds without caterpillars common in the forest? Why do avian predators use leaf cutting as a clue and not leaf folds? Isn't this an indirect support for "olfaction hypothesis"?

Chapter V deals with the effects of forest fragmentation on avian diversity and feeding habits. I do not want to question here the main conclusions about mechanisms behind lower species richness in forest fragments, they seems to be meaningful. I have a point to spatial distribution of study sites. Forest fragments were situated close to the coast, i.e. at the border of lowland forest environment, while continuous plot is more inland. Can this influence the results? In other words, can large scale context support higher diversity at Wanang forest independently of size of the fragment itself or its habitat structure? *Arses insularis* was the only species having lower intake of arthropods in smaller fragments and the result is quite robust. Why exactly this species? As number of arthropod individuals per leaf area appears to not vary among study sites, the change in *Arses insularis* diet is rather a product of different feeding strategy, isn't it? Finally, acceptable state of avian species richness in fragmented landscapes led me in the past to claiming that smaller patches are better than nothing and maybe even form a perfect environment for some of the forest species. Now, I am careful about saying officially anything positive about forest fragments in tropical regions as true forest birds are really confined to true forests which are disappearing extremely rapidly. Unfortunately, practical actions to protect them are truly inaccessible.

To conclude I must say that although sometimes it is a long way from perfect field data to complete understanding of the natural processes, Katka Tvardíková with a support of her supervisor did an excellent job and her work undoubtedly provides a relevant contribution to the field avian ecology in tropics. The thesis meets all the demands placed on it by the academic environment and I am really happy to recommend her for awarding a PhD degree.

Prague, 27th September 2013

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