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A CRITIQUE OF NEOTROPICAL ORNITHOLOGY: IS RESEARCH ON NEOTROPICAL BIRDS SCIENTIFIC?

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Survage to Modigliani: “Why did you paint a portrait of me with only one eye?”

Modigliani: “Because you look at the world with one eye; with the other, you look into yourself.”

Resumen. – **Una crítica de la ornitología Neotropical: ¿Es científica la investigación sobre aves Neotropicales?** – En esta reseña, se presenta un análisis crítico de la manera de llevar a cabo investigaciones ornitológicas en la Región Neotropical. ¿Como consideramos el mundo ornitológico Neotropical cuando estudiamos aspectos de su biología? ¿Como resolvemos el problema operacional, de la definición del “método científico” aplicado a nuestra ciencia en nuestra región? ¿Como resolvemos el problema epistemológico de establecer si nuestros trabajos sobre las aves de esta región constituyen, o no, “ciencia”? ¿Tratamos de alcanzar a explicaciones generales (teorías) de los fenómenos que estamos investigando, o tratamos solamente de proponer explicaciones ad hoc? ¿Cuales son las metas de la ciencia? ¿Como planteamos programas de investigación? ¿Como desarrollamos nuestro pensamiento mientras llevamos a cabo nuestras investigaciones? ¿Utilizamos la inducción, o la deducción? ¿Como establecemos hipótesis que se pueden verificar o rechazar (o falsificar)? ¿Como integramos resultados de investigaciones empíricas con conceptos teóricos? Para dar algunas respuestas preliminares a tales preguntas y inquietudes, se discuten tres temas, la especiación (un fenómeno evolutivo con orígenes en el tiempo y el espacio), la disminución de las aves migratorias Neárticas-Neotropicales (otro fenómeno espacio-temporal), y el tamaño de la puesta (“clutch-size”; un fenómeno adaptativo y posiblemente muy plástico, bajo el doble control genético y ecológico).

Resumo. – **Uma crítica da ornitologia Neotropical: a pesquisa feita com aves Neotropicais é científica?** – Na presente revisão, eu analiso criticamente o modo pelo qual a pesquisa ornitológica é realizada na Região Neotropical. Como consideramos o mundo ornitológico no Neotrópico? Como resolvemos o problema operacional da definição do “método científico” aplicado à ciência no Neotrópico? Como resolvemos o problema epistemológico de estabelecer se nossos trabalhos sobre as aves dessa região constituem ou não “ciência”? Buscamos encontrar padrões gerais (teorias universais) dos fenômenos sendo investigados, ou somos propomos explicações ad hoc? Quais são as metas da ciência? Como planejamos os projetos de pesquisa? Como desenvolvemos nosso pensamento equanto a pesquisa está sendo realizada? Utilizamos indução o dedução? Como estabelecemos hipóteses que podem ser testadas

ou refutadas (ou falsificadas)? Como integramos resultados de pesquisas empíricas com conceitos teóricos? Com a objetivo de chegar a algumas respostas a essas perguntas e preocupações, três temas são discutidos, especiação (um fenômeno evolutivo com origem no tempo e no espaço), declínio das aves migratorias Neárticas-Neotropicais (outro fenômeno espaço-temporal), e tamanho da ninhada ("clutch size", um fenômeno adaptativo possivelmente muito variável e dependente de fatores genéticos e ambientais).

Abstract. – In this review, I critically examine the manner in which ornithological research is carried out in the Neotropical Region. How do we look at the ornithological world of the Neotropics? How do we resolve the problem of the definition of the scientific method applied to our science in our region? How do we deal with the epistemological problem of whether our work on the birds of that region constitutes, or not, "science"? Are we concerned whether our research results allow us to reach and formulate general explanations (universal theories), or only ad hoc hypotheses, of the phenomena that we study? What are the goals of science? How do we develop our thinking as we go about our research work? Do we use induction or deduction? How can we posit hypotheses that can be either verified or refuted (or falsified)? How can we integrate the results of empirical research with theoretical concepts? In order to give some preliminary answers to such questions and concerns, three topics are discussed as examples, speciation (an evolutionary phenomenon having origins in both time and space), the decline of Nearctic-Neotropical migrant birds (also a spatio-temporal phenomenon), and clutch-size (a possibly plastic adaptive phenomenon depending on genetic and environmental factors). *Accepted 29 April 2004.*

Key words: Neotropical Region, ornithology, Popper, scientific method, philosophy of science, theory, hypothesis testing, speciation, Nearctic-Neotropical migration, clutch size.

INTRODUCTION

A long-standing tradition for presidents of International Ornithological Congresses (IOCs), which, like Neotropical Ornithological Congresses (NOCs), are held every four years, is to present in their presidential address a critical review of recent advances in ornithology. Thus, Thomson (1955) discussed migration, territoriality, mating systems, speciation, and behavior; Berlioz (1960) emphasized the role of museums, museum collections, and systematics; Mayr (1963a) reviewed progress in much the same fields as had Thomson eight years earlier, but from a slightly different point of view (see also Mayr 1984, 1989); and Immelmann (1988) advocated the interdisciplinarity of ornithology. Instead of broadly ranging reviews, other IOC presidents preferred to evaluate empirical progress in a specific field of ornithology. Dorst (1976), for instance, analyzed the

biogeographical origins of the South American avifauna. Yet another approach selected by at least one IOC president, and this is a very difficult one, has been to articulate a new theory of a broad field within ornithology, as did Berthold (1999), who proposed a comprehensive theory for the origin and evolution of migration systems. By theory here, I mean an universal theory, according to rules of reasoning such as those described by Popper (1972a, 1972b, 1973; see Murray 2001), namely a theory that leads to predictions, the components of which can then be falsified.

For my own address to the VIIth NOC, I decided not to follow the approaches chosen by these former IOC presidents, however meritorious they were and still are. Unlike Thomson (1955), Berlioz (1960), Mayr (1962), or Immelmann (1988), therefore, I do not present in this essay an annotated checklist of topics in Neotropical ornithology. Given my

long-term interest in speciation in Neotropical birds, I could have prepared a synthesis of speciation patterns in that region, similar to Dorst's (1976) earlier analysis, but I decided against it. And finally, I simply do not have either the evidence or the imagination, or both, to propose a new theory of a field within Neotropical ornithology.

Alternatively, I could have chosen to describe whether, and how, Neotropical ornithologists have adopted recent advances in technology in their work. For example, papers presented at the 121st Stated Meeting of the American Ornithologists' Union in 2003 include a wide range of techniques: spectrophotometry (Hofmann *et al.* 2003), microsatellite analysis (Schmalz & Quinn 2003), satellite imagery (Kriese 2003), telemetry (Steiger *et al.* 2003), geographic information systems (GIS; Leumas *et al.* 2003; see also Isler 1997), high-performance liquid chromatography (McGraw *et al.* 2003), high-speed video recording (Bostwick 2003), DNA sequences of mitochondrial versus nuclear genes in phylogeny (Moyle 2003), and DNA fingerprinting (Eimes *et al.* 2003). I could also cite the use of night vision light intensifiers to observe nocturnal behavior (e.g., Robert *et al.* 1989) and of cranes to study rainforest canopy birds (e.g., Walther 2004).

Instead, I will focus on several questions that are as much philosophical as empirical and that, in my opinion, should underlie our work in Neotropical ornithology. Do we have well defined goals when we design our research on Neotropical birds? Do we pursue this research in a deliberate search for patterns? Do we attempt to explain observed or perceived patterns with hypotheses or theories? How do we design ways of testing these hypotheses or theories? What is a predictive theory? How do we integrate the empirical content of our research with theoretical concepts? Does our research qualify as science? In order to approach these questions, I will

discuss especially the views of one of the most influential philosophers of science, Karl Raimund Popper (1902–1994; for a fascinating and extremely readable look into both Popper's philosophical and his personal world views, as well as those of his rival Ludwig Wittgenstein, see Edmonds & Eidinow's 2001 book, but don't be deceived by its somewhat misleading title). Popper's ideas about induction versus deduction, testing versus falsifying hypotheses, empirical work versus theoretical work, and science versus non-science (or pseudo-science), have been widely used by biologists. I feel, however, that biologists have often either misunderstood or misapplied Popper's ideas. Whether or not one subscribes to Popper's reflections on research, science, evolutionary biology, and theory, they cannot be ignored because they can only sharpen one's attitude toward how one carries out research, views science, understands evolutionary biology, and constructs theories. The present essay is a prolongation of reflections that resulted in a plenary lecture at the XXIInd IOC (Vuilleumier 1999) and that stemmed from my analysis of the development of Neotropical ornithology (Vuilleumier 2003).

PREMISE FOR THIS REVIEW

I do not consider myself to be either a philosopher of science or a theoretician of biology. My research on the systematics, evolution, ecology, and biogeography of Neotropical birds has been empirical, in other words I have gained knowledge in these fields through observation and experience. Nevertheless, inasmuch as possible I have also attempted to (a) relate my empirical work to theory (for example insular biogeography, Vuilleumier 1970, 1996), (b) integrate my research into a theoretical framework (biodiversity, Vuilleumier 1998), (c) pursue research along theoretical (deductive) lines of reasoning (speciation,

Vuilleumier 1991, 1993; Cheviron *et al.* 2002, in prep.).

Although I have not carried out theoretical and philosophical work myself, interest in these aspects of intellectual enquiry as applied to biology and ornithology has led me to review and analyze the theoretical and philosophical backgrounds of research in several areas, especially the ontology of species (Vuilleumier 1976) and the ontology and epistemology of zoogeography (Vuilleumier 1978, 1993a, 1999a). Similarly, I have wondered what role, if any, theoretical and philosophical thinking has played during the tremendous progress made in Neotropical ornithology in recent decades (Vuilleumier 1995, 2003). I have been interested in Murray's reflections about whether theoretical ecology is a science and whether there are universal laws in evolution (Murray 1999, 2000, 2001), especially as ecological and evolutionary thinking permeates much work on Neotropical birds. After reading a wide range of papers on Neotropical birds, I have concluded that there is a general lack of interest in theory thinking and a lack of understanding of the philosophical issues that underlie theoretical thinking. Specifically, I have observed that many papers on Neotropical birds lack clear indications that their authors followed explicit theoretical guidelines, mentioned whether they embraced inductive or deductive reasoning, or designed their research to address a particular theory by attempting to falsify its predictions. To give a specific example, of 345 papers published in *Ornitología Neotropical* in the 14-year period from 1990 to 2003, only 16 (less than 5%) address theoretical issues. Of these 16, only 3 (less than 1% of total) propose theories (Table 1).

Assuming that this sample is representative of a general trend, does the general absence of an underlying theoretical background in research on Neotropical birds mean that Neotropical ornithology is not a

"science" (*sensu* Popper), but instead is what Mayr (1963), for example, called a *scientia amabilis*? To answer this question, which I believe to be important, I focus selectively on the analysis of three topics, speciation, decline of Nearctic-Neotropical migrants, and clutch-size, about which theorizing has been extensive, and also briefly mention mating systems and austral migration. Before exploring theory building and testing in these areas, I first review some of Popper's ideas and concepts, hoping thereby to minimize or avoid misunderstandings in my later discussion of these three areas of investigation.

SOME OF POPPER'S IDEAS

Science and its aim. Although many scientists, including biologists (and therefore also ornithologists), are concerned with describing nature in ever greater detail, in an endeavor that Kuhn (1962, 1970) has called "normal science," I agree with Popper (1972b: 191) that the ultimate "aim of science [is] to find *satisfactory explanations* [*italics his*], of whatever strikes us as being in need of explanation." In other words, we should strive to seek satisfactory explanations of what we observe. Bertram J. Murray (pers. com.) reminded me that even though Popper would argue that the ultimate aim of science is to find satisfactory explanations of phenomena, it is clear that the aim of individual scientists might be different. Therefore, describing patterns in nature can, and often does, lead to descriptive explanations of these patterns. MacArthur (1972: 1), for example, started his well-known book, "Geographical Ecology" (subtitled "Patterns in the Distribution of Species"), thus: "To do science is to search for repeated patterns, not simply to accumulate facts. ..."

The general aim of science, to explain what we observe, leaves wide latitude to individual scientists for selecting and then pursuing research projects. The important point is

TABLE 1. Number of articles, short communications, points of view, and commentaries with theoretical content published in *Ornitología Neotropical*, 1990–2003.

Vol. No./Year	Number of papers	Number of papers with theoretical content ¹	Number of papers proposing theory ²
1/1990	4	0	0
2/1991	14	2	1
3/1992	9	2	0
4/1993	13	1	0
5/1994	16	2	0
6/1995	14	1	0
7/1996	21	3	0
8/1997	29	1	1
9/1998	28	1	0
10/1999	27	0	0
11/2000	41	0	0
12/2001	30	0	0
13/2002	43	2	1
14/2003	56	1	0
Totals	345	16	3

¹The category “Papers with theoretical content” includes papers with an indication that one or more particular hypotheses (usually ad hoc) are discussed and/or being tested.

²The category “Papers proposing theory” includes papers in which the author’s or authors’ intent was to propose a theory explaining a particular field in Neotropical ornithology.

that these projects should be designed to answer questions about the observable world. Thus, as understood here, “science” should not be confused with “scholarship.” For example, Carl Eduard Hellmayr’s fundamental work on the systematics and distribution of Neotropical birds (reviewed in Vuilleumier 2003), or Raymond A. Paynter’s indispensable gazetteers of Neotropical birds (e.g., Paynter 1995 and earlier volumes) are remarkable pieces of scholarly work but are not works of science. I hasten to add that the work of a Hellmayr or of a Paynter is extremely significant. Their work has contributed and is still contributing to progress in Neotropical ornithology, even though they did not carry out

research designed to explain observable phenomena with a given method of science.

The method of science. Given a broadly defined aim for science as an intellectual endeavor, the method of science should be a rather straightforward, two-step process of acquiring knowledge and of explaining it. This process is one of trial and error, during which we “learn from our mistakes” (Popper 1973: vii). Two quotes from Popper are in order. In the Preface to his book “Conjectures and Refutations,” Popper (1973: vii) wrote: “The way in which knowledge progresses, and especially our scientific knowledge, is by unjustified (*and unjustifiable*, italics mine) anticipations, by

guesses, by tentative solutions to our problems, by *conjectures* (italics Popper's). These conjectures are controlled by criticism; that is, by attempted *refutations* (italics his), which include severely critical tests. ... Criticism of our conjectures is of decisive importance: by bringing out our mistakes it makes us understand the difficulties of the problem which we are trying to solve. This is how we become better acquainted with our problem, and able to propose more mature solutions: the very refutation of a theory – that is, of any serious tentative solution to our problem – is always a step forward that takes us nearer to the truth.”

Elsewhere, Popper (1972b: 70) makes an interesting and vivid comparison: “The difference between the amoeba and Einstein is that, although both make use of the method of trial and error elimination, the amoeba dislikes to err while Einstein is intrigued by it: he consciously searches for his errors in the hope of learning by their discovery and elimination. The method of science is the critical method.” Thus science is a flexible, not rigid, endeavor, one in which the method is made of conjectures (guesses) and refutations (severe criticisms, or tests). The scientist can therefore use his or her imagination in proposing theories, provided he or she systematically learns through a critical review of errors.

The role of theories. Theories are intellectual constructs that are elaborated to explain a body of empirical observations that may be applied to other similar bodies of observations and that may predict observations that have not yet been made. For example, Newton's laws were designed to explain celestial motions and were later used to explain the motions of molecules. Theories, because of their synthetic nature, are an essential step in what we call “doing science” and in applying what we call “the method of science.”

Ad hoc hypotheses vs universal theories. Ninety-nine per cent of our theories are ad hoc. That is, they are descriptive statements that claim to explain a phenomenon (say, migration) or part of a phenomenon (say, austral migration), but in fact actually describe how that phenomenon, or part thereof, occurs. For example, ad hoc hypotheses regarding the determination of clutch size in birds include the predation hypothesis of Skutch (1949), which was intended to explain the small clutches of tropical species, but not the larger clutches at higher latitudes, and the lipid limitation hypothesis of Ankney *et al.* (1991), which was intended to explain the clutch size in waterfowl, but not in other species. By contrast, universal theories are truly explanatory and attempt to “encompass a wide range of seemingly disparate phenomena, and they seemingly provide explanations for why the [world] is the way it is” (Murray 2001: 261). Murray was referring to such universal theories in physics as Newton's law of motion, the theory of general relativity, and the theory of quantum electrodynamics. Examples of biological theories to explain variation in clutch size that were intended to be general in their application include those of Lack (1947, 1948, 1954; clutch size is a consequence of the amount of available food), Cody (1966; food supply is partitioned into several resource components graphed according to a model called the fitness set by Levins 1962, 1968), and Murray (1979, 1985, 1991; using a mathematical and demographic argument involving parameters that describe the lifetime reproductive success of females of given genotypes).

The question is: Are there, or can there be, universal theories in biology? Specifically, do we, Neotropical ornithologists, have any universal theories? Of course, as Murray has pointed out (pers. com.), there cannot be universal theories that are applicable only to the Neotropics or only to Neotropical birds. Uni-

versal theories should be applicable anywhere. The question, therefore, becomes: Are there universal theories that Neotropical ornithologists could profitably use to guide their research? Can we construct universal theories about how tropical (including Neotropical) conditions affect the evolution of tropical biota, or about why the tropical (including Neotropical) world is so diverse, or else about what controls the evolution of clutch size in the tropics? Interesting as they are, ad hoc hypotheses will not help us answer such questions fully, although they can surely constitute stepping stones that lead toward universal theories. What is crucial is how these hypotheses and theories are designed so that they can be falsified.

Falsification of theories vs testability of ad hoc hypotheses. When we establish an ad hoc hypothesis, we usually attempt to test it, often invoking Popper's (1972a, 1972b, 1973) canons of scientific reasoning to justify our activity. Some of us instead attempt to falsify ad hoc hypotheses. This is where a trap has been sprung. An ad hoc hypothesis may be rejected only for the specific situation (or species) for which it was applied. Yet this very same ad hoc hypothesis is often, but mistakenly, thought to be applicable to another situation (or species). As Murray (pers. com.) has put it, even if it rejected, an ad hoc hypothesis is not killed. Indeed, "It is important to remember that Popper suggested that universal explanatory theories in science could not be tested by verificationist principles" (Murray 2001: 271). In other words, we often, perhaps even most of the time and also perhaps unconsciously, confuse ad hoc hypotheses with universal theories. A universal theory about a given phenomenon is an intellectual instrument that gives us the means to make testable predictions, which are then confronted with empirical facts. If the facts agree with the theory, it is provi-

sionally accepted; if they do not, the theory is rejected.

The role of imagination in science. In Popper's words: "The method of science is the method of bold conjectures and ingenious and severe attempts to refute them" (Popper 1972b: 81). In other words, even though we try to be rigorous in our research protocols, there is nothing preventing us from having a lot of imagination, and of using it in our attempts to understand the world. Of course, the caveat here is that our imagination is, or should be, constrained by facts of observation.

What are facts? A fact is a fact is not a fact. Many biologists, leery of theory and theoreticians (and of philosophers of science) claim that in the long run, the only important activity is to describe facts about nature. Sooner or later, the accumulation of facts will lead one to recognize patterns, patterns that will then beg for an explanation. Popper (1972b: 46) wrote: "A statement is true if and only if it corresponds to the facts." Elsewhere he states (Popper 1972b: 290): "...by fact finding I mean, of course, the discovery of statements or theories which correspond to facts." And further (Popper 1972b: 329): "...we may distinguish *real facts*, that is (alleged) facts that are real, from (*alleged*) *facts that are not real* (that is, from non-facts)" (italics his). Interestingly, Popper does not define what a "fact" is. Indeed, he seems to have little interest in definitions in general: "I am not in the least interested in definitions or in the linguistic analysis of words or concepts" (Popper 1972b: 78).

So, if facts and the activities of finding and describing facts are so important in the pursuit of research, and so crucial in one's ability to falsify theoretical statements, what, indeed, is a "fact"? Furthermore, is a "statement" a fact? For example, is the assertion: "members of the family Columbidae always lay two

eggs” a fact, an “empirical statement of science” (cf. Popper 1972a: 98), or a hypothesis? The American Heritage Desk Dictionary (1981: 355) defines fact thus: “Something that is objectively true and accurate,” and: “Something having real, demonstrable existence.” The above assertion about clutch size in Columbidae is based on a demonstrable observation (a fact), namely that at least some species of Columbidae always lay two eggs. The statement, “species of the family Columbidae lay two eggs” then becomes a hypothesis when the qualifier “always” is added. This hypothesis is verifiable empirically. Observation of Columbidae species laying 1 or 3 eggs (facts) will falsify the hypothesis. Popper used a similar example: “All swans are white.”

AD HOC HYPOTHESIS: SPECIATION IN *GEOSITTA*

A number of years ago, while engaged in a study of speciation in the genus *Geositta* (Furnariidae) as part of a research program on speciation in Andean and Patagonian birds, I first analyzed species-level status of the various taxa (species and subspecies) that had been described in *Geositta*. Next I tried to evaluate the interspecific relationships of these entities within the genus and, on this basis, to elaborate a hierarchic classification scheme including taxonomically isolated species, members of superspecies, and species groups. Finally I proposed scenarios for some patterns of species-level evolution in the genus (Vuilleumier 1967). One pattern, in particular, caught my attention and led me to further research (Vuilleumier 1991).

Two species overlap in extreme southern South America. One, *G. cunicularia*, has an extensive geographical range (high Andes from Peru to Chile and Argentina, coastal Peru and Chile, much of Patagonia) and a

broad set of ecological tolerances over that range. The other, *G. antarctica*, has a restricted geographical range (Tierra del Fuego and adjacent Patagonian mainland to the north), and apparently more uniform ecological preferences. These two species, as I judged from comparisons of museum specimens, appeared to be closely related (sister species). These observations were the foundation for an ad hoc hypothesis of speciation.

I reasoned as follows: (1) On the basis of my observations (facts) that (a) morphological differentiation between these two species is small, and (b) that geographical overlap is slight, then, (2) on the basis of the conventional wisdom of the allopatric speciation model of Mayr (1963b), I hypothesized: (i) that the two taxa had a common ancestor distributed along the Andean-Patagonian axis, (ii) that a vicariance event separated the ancestral species into two populations which later diverged in geographical isolation, (iii) that the divergence was geologically recent, (iv) that subsequent disappearance of the barrier allowed colonization and secondary overlap, and (v) that presence of reproductive isolating mechanisms indicates that speciation is complete.

The ad hoc hypothesis itself was that the barrier that allowed the initial vicariance within the ancestral species was caused by eco-geographical changes correlated with the last major episode of glaciation in South America's Late Pleistocene (the Llanquihue glaciation). Deglaciation, starting about 20,000 years ago and ending about 14,000 years ago, removed the glacial barrier and allowed secondary contact.

The main assumption of this scenario is that the two modern species, *cunicularia* and *antarctica*, are sister species. The falsification of this assumption would allow one to conclude that the hypothesis of allopatric speciation is incorrect. It would next remain to be seen how and where speciation took place,

and at what rate. In order to falsify the assumption, one needs genetical data that should show unequivocally whether the sister species status is correct or not. Museum data on external morphology are equivocal, as are field data on habitat, breeding behavior, and vocalizations. Biochemical data based on electrophoresis of proteins were equivocal, but DNA sequence data proved to be the decisive piece of information. The sequences of three mtDNA genes (cytb, ND2, and ND3) showed, not only that *cunicularia* and *antarctica* are not each other's closest relatives, but that they are members of two different clades within *Geositta* (Chevignon *et al.* 2002, in prep.).

Rejection of the assumption of close relationship therefore refutes ("falsifies") the ad hoc hypothesis that these two species were sister species. Speciation in these two distant species of *Geositta* did not take place between them. The series of steps taken from the start to the current finish of the research into speciation of *Geositta cunicularia* and *G. antarctica* correspond closely, I believe, to what Popper (1972: 32) described as the "Deductive Testing of Theories." ... "From a new idea, put up tentatively, and not yet justified in any way – an anticipation, a hypothesis, a theoretical system, or what you will [*Geositta cunicularia* and *G. antarctica* are related] – conclusions are drawn by means of logical deduction [they are sister species and speciation proceeded locally in southern South America via vicariance caused, in part, by the consequences of glacial events]." And further (Popper 1972: 33): "...if the decision [about the validity of the theory, made by comparing its statements with the results of observations] is negative, or in other words, if the conclusions have been *falsified* [italics Popper's], then their falsification also falsifies the theory from which they were logically deduced." Erring here means that, learning from this mistake, one can re-focus the research program in another direction,

through fresh hypotheses. I was reasoning along the lines of what Kuhn (1962, 1970) called "normal science," trying to give the best possible interpretation of the facts, so identified on the basis of knowledge available at the time. Incidentally, the biochemical/molecular test of this hypothesis does not constitute a test of Mayr's allopatric speciation theory. Similarly, my fieldwork on patterns of speciation (allopatry, parapatry, and sympatry) in steppe birds of Patagonia (Vuilleumier 1993b) is not designed to provide tests of Mayr's allopatric speciation theory.

GREATER RIGOR: DECLINE OF NEARCTIC AND NEOTROPICAL MIGRANTS

Many species of birds that breed at temperate latitudes in North America in the northern spring (May–June) subsequently leave their breeding range, fly in July–September over intermediate areas, and eventually spend the northern hemisphere winter (October–March or April) in tropical latitudes in Central America, northern South America, and the Caribbean Islands, before returning north to breed, assuming they have survived this migration and wintering ordeal. Much recent evidence points to significant declines in the numbers and/or density of these migratory birds on their breeding grounds. Less evidence has been adduced from the wintering grounds, but the overall trend is clear: there are fewer of these birds now than there used to be. In addition to documenting this decline, much ink has been devoted to understanding and explaining the causes of the decline, and this of course, with a view to take appropriate conservation measures.

Rappole & McDonald (1994) have proposed a theoretical construct designed to help focus future research toward analyzing and understanding this decline. They have proposed a scenario that is more formal than was

mine about speciation in *Geositta*. Their “chief aim is to move the debate on migratory-bird demographics and conservation from the realm of speculation based on inferences into one in which hypothetico-deductive principles can be applied.”

They started by stating: “...we do not evaluate the evidence for declines per se. Rather, we make several predictions regarding demographic aspects of migratory bird populations based on the assumption that these populations are declining as a result of breeding-ground factors.” I take it that their term “assumption” means “hypothesis,” or, in Feynman’s (1965: 156) words (as quoted by Murray 2001), “guess”: “In general we look for a new law [= hypothesis] by the following process. First we guess it. Then we compute [= predict] the consequences of the guess to see what would be implied if this law that we guessed is right.” For his part, Popper (1972a: 38) noted: “. . . I am inclined to think that scientific discovery is impossible without faith in ideas which are of a purely speculative kind, and sometimes even quite hazy. ...”

Rappole & McDonald’s “hypothesis ... is that populations of Nearctic avian migrants are declining as a result of breeding-ground events.” They list 14 predictions “based on this hypothesis.” As examples, I summarize four of the 14 predictions and the evidence for or against each.

Prediction 3: “Migratory bird declines should not be observed in breeding habitats that are undisturbed, and presumably optimal.” Evidence: “Contrary to this prediction, long-term studies have been performed in apparently undisturbed breeding habitats that have found declines in Nearctic migrants.”

Prediction 8: “There should be little or no evidence of floaters (wanderers) in wintering populations.” Evidence: “In contrast to this prediction, ... studies ... have documented

evidence of floaters. ...” [For a discussion of the concept of floaters, see Winker 1998.]

Prediction 10: “The numbers of territorial individuals in optimal winter habitat should show sharp annual fluctuations.” Evidence: “Where studied, wintering migratory-bird densities in optimal habitats have remained remarkably stable across years and latitude. ...”

Prediction 12: “Declines in Nearctic migrants should be paralleled by changes in temperate nonmigrant populations occupying the same breeding habitats.” Evidence: “Contrary to this prediction, most breeding-ground studies have found that, while migratory species declined on study sites, resident populations did not decline. ...”

Rappole & McDonald (1994) concluded: “Examinations of these [14] predictions based on the literature do not support the hypothesis.” Instead, they suggested that: “Alteration of wintering-ground habitat provides the most-parsimonious explanation for the observed demographic characteristics.” They also pointed out that some of their predictions can easily be tested, either by field experimentation (removal of floaters; food supplementation) or by construction of life tables. What remains to be done, then, is to carry out what Popper called “ingenious and severe attempts to refute” their conjectures. I believe, as does Murray (pers. com.) that there could be a universal theory of population decline, or growth, starting with laws of population dynamics, then stating initial conditions, and ending by deducing some conclusions.

UNIVERSAL THEORY: VARIATION IN CLUTCH-SIZE

For many decades, some of the most brilliant ornithological minds have tried to explain

patterns of variation in clutch size. Most of these explanations have been of an ad hoc nature, but a few have been called “general” and were attempts at “universal theories” *sensu* Popper. One of the most often cited patterns is the increase in clutch size with increasing latitude in the northern (Lack 1954, Cody 1966, Klomp 1970) and in the southern (Moreau 1944) hemispheres. This description of the latitudinal pattern is, of course, an oversimplification. When variation in clutch size is examined in greater detail, other more subtle patterns emerge. Thus, Marchant (1960) found that clutches in arid tropical southwestern Ecuador were larger than those in other tropical regions. When comparing clutch size in equatorial with temperate Africa, and in equatorial with temperate South America, Klomp (1970: 84) noted that: “On the southern hemisphere an increase of clutch-size away from the equator has been found in Africa and South America. Of 141 species common to equatorial and southern Africa, 38 per cent has a larger clutch and only 3 per cent a smaller one in south than in central Africa, though the average difference is only small, less than half an egg (Moreau 1944a [= Moreau 1944]). Similarly, of the 59 species occurring in the equatorial and southern states of South America, 63 per cent had a larger clutch, and only 14 per cent a smaller one in the southern states (Snethlage 1928).”

One important consideration to keep in mind is that the proper comparisons must be made within, not between or among, species (see Klomp’s sentences above). Thus, contrary to some authors (Rowley & Russell 1991, Yom-Tov 1987, Yom-Tov *et al.* 1994), there is a slight latitudinal increase in clutch size in the temperate parts of the southern hemisphere. Clearly, much more work needs to be done in this respect, and, most importantly, it needs to be done with universal theory in mind more than with ad hoc hypotheses.

Murray (2001) reported that at least 15 ad hoc hypotheses have been suggested in the literature to explain patterns in clutch size variation, including protein limitation, cost of reproduction, nest size, egg viability, and protection of young (list and references in Murray 2001: 260). But major attempts at formulation of a general (universal) theory of clutch size are few. They include notably those of Lack (1947, 1948, 1954; food limitation), Cody (1966; resource allocation), and Murray (1979, 1985, 1991; length of breeding season).

Murray’s (1979, 1985, 1991) universal theory of clutch size variation, based on probability arguments about the fecundity of females having different genotypes (for mean clutch size), uses demographic parameters to take into account lifetime reproductive success and the length of the breeding season. With regard to latitudinal variation in clutch size, Murray’s (2001: 279–280) theory predicts that because the mean number of broods reared per year by a given female of a given genotype “is greater where breeding seasons are longer, the clutch size should be smaller where breeding seasons are longer.” ... “[this] prediction is confirmed by clutch size being smaller at tropical latitudes than at higher latitudes ... and smaller in the southern hemisphere than in the northern ... because breeding seasons are longer in the tropics than at higher latitudes and at southern latitudes than at comparable northern latitudes ...”.

Carefully executed field studies that were designed, in part, to test Skutch’s predation hypothesis, were carried out by Martin *et al.* (2000; see also Martin 1988, 1992) in extensive comparisons between equivalent sets of species in both North and South America. They showed that there is no correlation between clutch size and the level of nest predation, and therefore concluded that Skutch’s theory was insufficient to account for

latitudinal patterns. Martin *et al.* (2000) thought that “The inability of the most widely invoked hypotheses [nest predation, food limitation, low seasonality in the southern hemisphere] to explain latitudinal patterns in clutch size illustrate that alternative hypotheses, such as adult mortality, deserve more attention, and that current theories of clutch size evolution need major revision.” Martin *et al.* (2000) did not, however, propose a new theory. They apparently confused ad hoc hypotheses with universal theories. Furthermore, they had seemingly not realized that Murray (1979, 1985, 1991) had already proposed such a universal theory of clutch size (see also Murray & Nolan 1989, Murray *et al.* 1989), which refuted the predation hypothesis.

DISCUSSION

Universal theories can be proposed. I hope to have shown that, in three fields of research in Neotropical ornithology (speciation, decline of migrant birds, clutch size variation), it is possible to use deductive reasoning in order to posit hypotheses, the consequences of which can then be tested (falsified, not verified; see the distinction between these two concepts in Popper 1972: 40–42, and Murray 2001). Whereas some of these hypothetical deductions are ad hoc, such as the one about the tempo and mode of speciation in southern South American species of *Geositta*, others are universal theories, like Murray’s theory of clutch size based on demographic parameters. We can falsify, and therefore reject, either (a) specific ad hoc hypotheses (speciation in two species of *Geositta* took place as a result and/or consequence of late Pleistocene glacial-interglacial events in Fuego-Patagonia) on the basis of empirical facts (data provided by DNA sequence analysis), or (b) more general (but still ad hoc) hypotheses (“populations of Nearctic avian migrants are declining as a

result of breeding-ground events”), again on the basis of empirical facts (census and demographic data obtained in both the Nearctic breeding areas and the Neotropical wintering areas of the migrant species). This is trial and error work with emphasis on learning from errors (Popper’s distinction between an amoeba and Einstein).

Therefore it is possible to propose bold guesses (*à la* Popper and Feynman), thus fully engaging our imagination, and to construct general theories using the deductive method. I find this very exciting. However, we must not be complacent. The painter Amedeo Modigliani was right: most of us look at the world with only one eye, the other being turned inwards. Thus our descriptions and our explanations of the world are often distorted, one-eyed portraits. We must attempt to use our vision more completely.

From single facts or statements to multiple facts and patterns. Until not very long ago most research on Neotropical birds was of a wholly descriptive nature (Vuilleumier 2003) and relied on isolated facts and singular statements of observations. The questions that were asked were of this nature: Is this a new species? What is the geographical distribution of this or that species? What habitats does this or that species occupy? What kind of nest does it build? How many eggs are there per clutch? How many species are found in a 10-ha plot of lowland rain forest?

Enormous progress has been made in this area of basic fact finding. One example will suffice. In 1968 I published the first description of the nest of the Andean furnariid *Lep-tasthenura yanacensis* in Bolivia (Vuilleumier 1969). Thirty-five years later, Cahill and her co-workers presented information at the VIIth Neotropical Ornithological Congress on the biology and ecology of this species based on a sample of 46 nests (Cahill *et al.*

2003a, 2003b). This trend of substantially increased fundamental knowledge about Neotropical birds indicates that we can now go from single events to multiple ones. We can thus truly start thinking as population biologists on the basis of biologically significant sample sizes. This is not to say that descriptive notes and papers on Neotropical birds are not useful. Indeed, *Ornitología Neotropical* is an appropriate conduit for such papers, because they clearly serve as stepping stones for further work. But authors of such notes and papers must couch their observations and data within the framework of hypotheses, and not be content to report single observations or make singular statements *in vacuo*. For instance, I published a critique of papers that list body masses of Neotropical birds without giving any biological background for them: "...what is now needed is information about body mass that is fully integrated into a biological [read also theoretical] framework" (Vuilleumier 1999b: 208).

Some promising areas for universal theories. I would like to emphasize that in the 21st Century, ornithologists working on Neotropical birds must make every effort to carry out their research in a deductive mode. The future of Neotropical ornithology as an integral part of science is bright, but its progress depends on clear thinking before starting new research programs or re-orienting older ones. I give two examples below.

Mating systems. At the VIIth Neotropical Ornithological Congress, Morton & Stutchbury (2003) called for more data on the mating systems of tropical birds before the evolution of such systems can be more completely understood. In spite of insufficient data they presented a "general model of the evolution of extrapair mating systems." Their hypothesis is based largely on an analysis of correlations between mating systems and climatic

regimes at high and low latitudes. Interesting as it is, it remains an ad hoc hypothesis. Murray (1984, 2001) proposed a general theory of mating systems based on demographic considerations instead. In his own words, his "theory seems consistent with the fragmentary evidence that is available." Morton and Stutchbury are right to call for more data. These data should now be collected within the framework of Murray's theory and with a view to testing (falsifying) the predictions of Murray's theory.

Austral migration system. Recently Joseph (2003) proposed a general hypothesis to explain the distribution of species that breed in southern South America and migrate north after the breeding season (austral migrants, see Chesser 1994; Joseph 1997). Joseph's goal was "to explore whether a climatic approach to describing distribution patterns might provide the basis for predicting seasonal changes in distributions of austral migrants generally, but especially those in fragmented environments." Given the fact that until recently we knew precious little about these birds' migration systems, Joseph's paper shows the kind of research trends that will focus attention on a more theoretical approach to a variety of phenomena. A clearly enunciated universal theory of austral migration would sharpen our views of the phenomenon. In particular, predictions derived from such a theory would be the guiding lines for future investigations. Thus, we would have gone from (a) a long period of collecting anecdotal data on a more or less random geographical and taxonomic basis (reviewed in Vuilleumier 1995: 100; see also Paynter 1995a), to (b) a critical review of these sparse data (Chesser 1994), leading to (c) a short period of preliminary theorizing (Joseph 2003). The way has clearly been paved for a universal theory. Also, broadly based comparisons between the Nearctic-Neotropical and the Palearctic-Afri-

can migration systems (e.g., Keast 1995 and references therein) reveal that there is enough information to start thinking of proposing a universal theory of continental migration systems.

CONCLUSIONS

The ideas discussed in this paper and the examples chosen to illustrate specific points about ad hoc hypotheses versus universal theories will, I hope, provide Neotropical ornithologists, especially of the younger generation, with food for thought as they sit down to start to design (or begin to refocus) their research programs. I also hope that, while not being truly theoretical or philosophical, this paper has presented some important theoretical and philosophical concepts simply enough yet in sufficient detail to spur Neotropical ornithologists to read some of the theoretical and philosophical literature that pertains to biology in general (e.g., Popper 1972a, 1972b) and to ornithology in particular (e.g., Murray 2001), and so also to Neotropical ornithology. To think carefully about the almost dialectical relationships between empirical efforts and theoretical ones can only sharpen one's attitude toward science.

I wish to make it clear again that there is nothing wrong with descriptive work or work that is designed to test ad hoc hypotheses. The point is that whatever sort of work one carries out, the ultimate goal of the research and the sort of method followed should be explicitly mentioned (and not simply the standard "materials and methods" sections where details are given about how many hours were spent in a tent observing the lek of a manakin, or how many milliliters of a given buffer were employed in the lab).

An analysis of papers in *Ornitología Neotropical* from 1990 to 2003 (Table 1) reveals how little of a theoretical nature has been

published in the journal of the Neotropical Ornithological Society. Of a total of 345 papers published in 14 years, only 16 (less than 5%) are either about a theoretical issue in Neotropical ornithology or have at least some theoretical implications (testing of ad hoc hypotheses, for example). Only 3 of these 16 papers (less than 1% of total) actually propose theories. In spite of this scarcity of theoretical papers, I am convinced that theory has a place in Neotropical ornithology, as seems to be clearly demonstrated by points of view like those of Estades (2002). What are needed are (a) deliberate attempts at framing one's work within existing hypotheses and theories, (b) serious attempts at clearly indicating what kinds of theoretical and philosophical guidelines are being followed (induction versus deduction; ad hoc hypotheses; predictions from initial conditions; severity of tests), and (c) a greater attempt at proposing bold universal theories.

SOME PRACTICAL SUGGESTIONS

In order to end this essay on a practical note, I list a few of the many questions of an evolutionary nature that spring to my mind, and that need further work along theoretical lines:

Specific questions. Does Berthold's (1999) theory of migration explain the origin of the Nearctic-Neotropical migration system, including austral migration? What theory can explain the origin of the "circum Amazonian" pattern of distribution (Ramsen *et al.* 1991)? What theory can explain the "leap-frog" (actually better called checkerboard) pattern of geographic variation and speciation in Andean birds (Ramsen 1984)? What theory can explain Mayr's (1963b: 523–524) "species border" phenomenon? (For a possible example, see Vuilleumier 1994). What theory can explain the evolution of fruit eating in tropical

birds (see Snow 1973, Morton 1973, Bosque *et al.* 1995)?

General question. What are the most important unresolved problems in Neotropical ornithology and what theories can be proposed to explain them?

GLOSSARY

I include in this glossary terms that are commonly used in philosophy and history of science. Many biologists use them in their publications, but often, however, not in the sense given to them by philosophers or historians of science. Hopefully, therefore, this glossary will help Neotropical ornithologists who wish to read this literature, and so may facilitate the dialogue between empirical workers and theoreticians. Terms in quotation marks (“...”) without any further reference are cited from Bynum *et al.* (1981).

Conjecture/refutation. “The genesis and exodus of a scientific hypothesis.” This is based on Popper’s work (Popper 1972a, 1972b, 1973). Popper (1973: 33) “... wished to distinguish between science and pseudo-science; knowing very well that science often errs, and that pseudo-science may happen to stumble on the truth.” Popper distinguished “... the empirical method, which is essentially *inductive*, proceeding from observation or experiment” (p. 33) from his method, in which one progresses by trial and error (by “*conjectures and refutations*”; Popper 1973: 46). A conjecture is a guess, a hypothesis, or a theory. A refutation is a criticism of the conjecture that is so severe that the conjecture must be rejected as false. Note that by pseudo-science Popper generally meant metaphysics (see below). His critique of evolutionary biology and especially of natural selection (which he considered to be largely tautological) has been incorrectly interpreted by some

biologists to mean that evolutionary biology is not science. What Popper (1972b: 241–242) really said was: “... the trouble about evolutionary *theory* [his italics] is its tautological, or almost tautological, character ...” But he also stated that Darwinian evolutionary theory was not a perfect theory. He did not say that it was not a scientific theory. He then (1972b: 242–244) went on to attempt a 12-point restatement of evolutionary theory to make it less vague.

Deduction. The American Heritage Desk Dictionary defines deduction as: “The act or process of reasoning, esp. a logical method in which a conclusion necessarily follows from the propositions stated.” This method is the one used by physicists.

Empirical. According to Webster’s II New Collegiate Dictionary: “1.a. Relying upon or gained from experiment or observation <empirical technique>; 1.b. Capable of proof or verification by means of experiment or observation <empirical knowledge>; 2. Relying solely on practical experience and without regard for theory or system.” Neotropical ornithologists clearly work along empirical lines as described above in 1.a, 1.b, and 2, and very few indeed use Popper’s method of “conjectures and refutations.”

Empiricism. “An ensemble of theories of explanation, definition and justification to the effect that our concepts or knowledge are derived from or to be explicated (or justified) in terms of *sense-experience* (or introspection).”

Epistemology. “The philosophical theory of knowledge concerned with its nature, varieties, origins, objects and limits.”

Explanation. “The process or account by which something is made intelligible, where

the account is called the ‘*explanans*’ and the thing, which may be a statement, event, state, process, law, theory, etc. is called the ‘*explanandum*’.”

Fact. Dictionary definitions are usually straightforward (example: a fact is “that which is actual, real” and “a true description of what is happening or of what has happened” (Angeles 1992: 103). As I argued earlier in the text, however, “fact” is a very fluid entity or concept. In his classic analysis of a “scientific fact” in medicine, for instance, Fleck (1979) has shown that the notion of fact depends on the interactions between the amount of knowledge of a particular subject and our understanding of what constitutes a “description,” of how we judge what “truth” is, and of how we interpret “reality.” Thus, facts are not necessarily fixed and objective items, but things that evolve.

Falsificationism. “The methodology ... of conjectures and refutations” according to Popper.

Hypothetico-deductive method. A method proposed “by some philosophical opponents of induction.” “It is based on the idea that hypotheses cannot be derived from observation, but once having been put forward (as a result of an imaginative leap) may be tested against observation. The method consists of (a) putting forward a hypothesis, (b) conjoining it with a statement of ‘initial conditions’, (c) deducing from the two a prediction, (d) finding whether or not the prediction is fulfilled.” According to Cassirer (1950: 130, 200–201) one of the early proponents and exponents of deduction in biology was Cuvier: “Deduction [previously mostly a method used in physics] was no longer absolutely out of the question, even if it had to assume a special form to correspond with the nature of its object [biological entities].”

Induction. “... a process of reasoning establishing general truths from particular instances,” which goes back to Bacon. According to Cassirer (1950), Darwin’s theory of evolution by natural selection “is a model of genuinely inductive research and proof”. Most biologists reason by induction.

Metaphysics. Either “(a) philosophy *per se*, including ontology or theory of being, epistemology or theory of knowledge and the relations between them or (b) more broadly, any more or less synoptic world-view...”

Ontology. “... the branch of metaphysics concerned with the nature of existence or being as such...”

Paradigm. “Usually defined as a pattern or exemplar. For the historian of science the word is most often used in connection with T. S. Kuhn’s ... *The Structure of Scientific Revolutions* (1962), where it is a specific scientific achievement embodying experimental results and procedures, patterns of theoretical interpretation and methodological interpretation.”

Prediction. “A proposition or assertion about the future.” “... falsificationists, such as K. R. Popper ... have seen the acid test of a theory in its predictive power.”

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