Why so many kinds of passerine birds?

Raikow and Bledsoe (2000), in embracing the null model of Slowinski and Guyer (1989a, 1989b), may perhaps be said literally to have added nothing to the list of suggestions for why there are so many species of passerine birds. When Raikow (1986) addressed this problem previously and could find no key morphological adaptations to explain the diversity of Passeriformes, the so-called songbirds or perching birds, he despaired and suggested that the problem may be only "an accident of classificatory history," which brought on a storm of protest (*Systematic Zoology* 37: 68-76; 41: 242-247). Now, Raikow and Bledsoe have substituted one form of nihilism for another. The null model formulation deals merely with numerical probability and lacks any explanatory value in this case, unless perhaps it could be shown that no evolutionary forces influenced patterns of speciation in birds.

What is known about the dynamics and timing of the radiation of the order Passeriformes does not support the success of these birds being due to random processes. Similar early and middle Eocene avifaunas from the United States (Wyoming), England, and Germany show that by about 50 million years ago, Europe and North America were inhabited by a diverse array of arboreal birds, some of very small size, but not one of which was a passerine (Olson 1989, Mayr 1998a, 1998b, 2000). Although passerines occured in the early Eocene of Australia (Boles 1997), the earliest evidence of the order in the Northern Hemisphere is from the latest Oligocene (about 25 million years ago) of France (Mourer-Chauviré et al. 1996). Passerines do not become an important component of the avifaunas of the Northern Hemisphere until the Miocene (about 20 to 5 million years ago), when they radiated explosively. Passerines are now the numerically dominant group of birds in virtually all geographical areas of the globe (see Slud 1976). It is unreasonable to assume that there is no underlying biological reason for this pattern and for the major turnover in avifaunas in the Northern Hemisphere in favor of passerines after the Oligocene.

Reproductive adaptations presumably made the holometabolous insects (Coleoptera, Diptera, Hymenoptera, Lepidoptera, and so on) the dominant clade of organisms on earth. Likewise, it appears that reproductive adaptations, not morphology, are responsible for the dominance of passerine birds over other orders of birds.

Most arboreal nonpasserine birds are obligate cavity nesters that rely on holes in trees, earthen banks, or termite nests. This automatically restricts them to habitats where those features are present and at the same time makes competition for nest sites severe. Cavities cannot be readily concealed and numerous predators exploit the vulnerability of cavity-dwelling organisms (snakes, certain hawks, and so on). On the other hand, passerine birds, both oscines and suboscines, have an extraordinary ability to fashion nests out of a wide variety of materials, to place them in an equally wide variety of situations, and, when need be, to camouflage or conceal them with unusual "resourcefulness." That the ability of passerines to protect their eggs and young in this manner may have led to their success as a group is not a new idea, having been advanced clearly and in some detail by Irwin (1962) in an otherwise obscure publication that has since been widely overlooked. Collias (1997) added nest-building behavior to the list of possible reasons for passerine success, but I would place more emphasis on it than he did.

It is difficult to discuss the nest-building capabilities of passerines without resorting to anthropomorphisms such as "clever" or "ingenious." Is it not marvelous, however, that a highly specialized aerial feeder such as a cliff swallow (*Hirundo pyrrhonota*), with tiny, weak bill and feet, can fashion a complex nest out of gobs of mud fastened to a flat, vertical surface? What adjective suffices to describe the nest of tailorbirds (*Orthotomus*), which actually stitch the edges of two leaves together with plant fibers to provide a concealed cup in which to place their nest? The long woven bags of oropendulas and relatives (Icteridae) and the various complex woven structures made by weaverbirds (Ploceidae) are well-known examples of the complexity of passerine nest types. The delicate cup nests of gnatcatchers (*Polioptila*), made of spider webs covered with lichens and fastened to a horizontal limb, or the cup nest of the Australian sitellas (*Sitella*), placed in an acutely angled crotch and covered with minute, vertically-oriented strips of bark, are exquisite uses of camouflage among passerines.

Baptista and Trail (1992) emphasized the ability of passerines to move into new environments as a key factor in the success of the order. If there is any single attribute that would make this possible, it is the ability of passerines to adapt their breeding regimen to locally available nest sites and nesting materials. The brain in the entire order appears to be "hard-wired" for nest-building inventiveness. The next most successful order of birds in terms of number of species is the Apodiformes (swifts and hummingbirds), species which also have complex and diverse nest-building habits. This is unlikely to be coincidental.

Letters to the Editor
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The staff of *BioScience* reserves the right to edit letters for length or clarity without notifying the author. Letters are published as space becomes available.

As a morphologist, I am quite willing to concede that morphology is not going to provide the answer to the numerical dominance of the Passeriformes. Morphology will still be useful, in tandem with molecular studies, in providing much-needed improvements in our understanding of relationships within the Passeriformes, which, in contrast to the impression given by Raikow and Bledsoe, is still very imperfect. At the same time, a detailed analysis of nest types could also contribute materially to a better phylogenetic framework and lead to fascinating insights into divergence and convergence in nest-building behavior. Another fruitful avenue of investigation would be descriptive and experimental studies of the neuroanatomy and neurophysiology of nest-building behavior, along the lines of the studies of vocalizations that have generated so much attention in ornithology in recent years. It is time for the analysis of passerine success to progress beyond disheartened sorties into semantics and probability statistics and enter the realm of enthusiastic biological exploration.

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Response from Raikow and Bledsoe

Olson makes two main points in his letter. He criticizes our application of a null model to the study of the diversity of passerine birds, and he offers the hypothesis that the great diversity of passerine birds results from their nest-building capabilities. In presenting the latter as an alternative to a null model explanation of passerine diversity, Olson conflates two different questions. The first asks whether the passerines are significantly different from their sister group in number of species. The second asks whether such a difference may be attributed to a particular cause—in this instance, according to Olson, the possession of a particular reproductive adaptation. We argue, as have others (e.g., Bond and Opell 1998, Chan and Moore 1999), that before asking this second question, one should first demonstrate that a group is indeed unusually species rich. Null model approaches are designed specifically for this purpose.

To understand the value of null model approaches, consider the question "How different do sister taxa need to be in species richness to cause a search for a deterministic explanation for the difference?" Would sister groups of, say, 100 and 110 species, respectively, differ sufficiently to warrant a search for an explanation like the one Olson proposes for passerine diversity? Exactly how different must groups be in species richness before one would be willing to invoke a deterministic, as opposed to stochastic, cause for the difference?

As noted in our article, and contrary to Olson's implication at the end of his first paragraph, we are not arguing here that the number of species in a given clade has no antecedent causes. It of course must. Instead, we merely ask by how much sister groups must differ in species richness to prompt a search for an explanation for the difference in the adaptations possessed by the groups. We reiterate that the null model approach is designed precisely to answer the question of whether such a search is required.

Gotelli and Graves (1996) identify five important features of null models. With respect to Olson's statement that the null model we used "lacks any explanatory value," we believe its most important features are (1) that it allows for the possibility that no deterministic mechanism is operating to produce an observed result; (2) that stochastic processes may be responsible for a result; and (3) that parsimony dictates that we favor simple explanations over complex explanations. If a properly constructed null model predicts a pattern seen in nature, then we are obligated under the principle of parsimony to favor the simple explanation that stochastic processes have produced the pattern.

We believe that, in a real sense, there is explanatory power in such a result. We would argue that a random branching process is sufficient to explain the difference in species richness between passerines and their sister group. This stochastic explanation is indeed an explanation, contrary to what Olson implies. It is also important to note that null models have basic biological principles at their core; they are far from being a form of "nihilism." In the model we used, these principles are imbedded in the model's assumptions—among others, that speciation events are essentially instantaneous, that they are independent, even that speciation occurs at all. Any of the model's assumptions are open for inspection of how violations of them would affect our interpretation of species richness in sister clades. But null models should not be dismissed out of hand.

Null model assessment is increasingly recognized as a critical first step in analyses of species richness. Bond and Opell (1998; araneoid spiders), Pearson (1998; planktonic foraminifera, nannofossils, and graptoloids), Purvis et al. (1995; primates), and Wollenberg et al. (1996; columbine plants, cranes, and *Drosophila*) all have used a null model as a starting point to investigate patterns of species richness. Sometimes null models are sufficient to explain the diversity of sister groups (e.g., *Drosophila virilis* species group; Wollenberg et al. 1996). In other instances, they are not (e.g., cercopithecid primates; Purvis et al. 1995). Regardless, all of these authors have started with a null model analysis, recognizing, as did Slowinski and Guyer in their seminal paper (1989, p. 190), that "a random branching pattern *inherently produces sister taxa of disparate size*" (their emphasis).

We would be more enthusiastic had Olson mounted serious potential objections to our analysis: that the assumptions of the null model might be incorrect, that violations of these assumptions might seriously undermine our result, that the Sibley-Ahlquist phylogeny might be flawed and hence that we are making an inappropriate comparison, to name a few. But Olson mounts no such serious objections. Furthermore, we would be delighted to see a rigorous, compelling demonstration that the possession of an adaptation like nest-building capabilities causally explains passerine diversity. But that demonstration has not occurred. Far from consisting of "disheartened sorties into semantics and probability statistics," our analysis, we hope, has introduced an important consideration into the debate about passerine diversity.

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Pricing Biodiversity and Ecosystem Services

I agree with Marino Gatto and Giulio de Leo: It would be desirable to base estimates of the benefits of biodiversity and ecosystem services (environmental assessment) on the knowledge of an interdisciplinary team that could "investigate all possible environmental, social, and economic consequences of a proposed activity" (Gatto and de Leo 2000, p. 353). However, this ideal-sounding approach invites some practical questions. For example, how large and diverse should such an interdisciplinary team be? Also, is it possible for any team, however large and diverse, to investigate *all* the possible environmental, social, and economic consequences of an activity?

Eight years ago, my colleagues and I assessed the environmental and economic costs incurred for bird losses caused by pesticide use, taking into account the different value of birds to different observers. Our review (Pimentel et al. 1993) suggested that individual birds were valued at 40¢ per bird by bird watchers, $216 per bird by hunters, and $800 per bird based on the costs of replacement. We estimated the value of an adult bird, then, to be approximately $30. Some reviewers thought this amount too low, and others too high. Data in the literature suggest that about 67 million birds are killed in the field with pesticides, and this number does not even include the young birds that die in the nest because their parents are killed by pesticides or the young birds that were killed when they were fed pesticide-contaminated insects.

Gatto and de Leo say that a contingent valuation method—whereby respondents to a questionnaire state how much they would be willing to pay for some environmental resource—is the only pricing technique "capable of providing an estimate of existent values" (Gatto and de Leo 2000, p. 348). In my view, however, it would be a mistake to use willingness to pay to assess the value of birds killed by pesticides. The general public simply does not know how many birds are killed by pesticides, so any valuation based on the public's willingness to pay must be suspect.

Our papers (Pimentel et al. 1992, 1993) give details and sources and describe how we arrived at our estimates of the value of species and ecosystems. Scientists, decisionmakers, and the public are very much interested in these environmental and economic data, because this type of accounting gives them some idea of the magnitude of a particular ecological and economic problem. Certainly, we all hope that better data will be forthcoming, supplied through the type of interdisciplinary investigations suggested by the authors. But until those investigations are achieved, let us use current data to inform scientists, decisionmakers, and the public of the magnitude of ecosystem problems.

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Response from Gatto and De Leo:

Professor Pimentel's comments on our article provide us with a further opportunity to clarify our viewpoints on valuing biodiversity and ecosystem services. In particular, he raises four points that we would like to address.

First, he asks how large and diverse an interdisciplinary team should be to conduct an evaluation that meets the standards set forth in our article—that is, an evaluation that accounts for the full range of environmental, social, and economic consequences of an activity. The answer, simply put, is that the size of an interdisciplinary team depends on the importance of the proposed project, plan, or policy. The requirements for environmental impact assessments (EIAs) usually vary according to expected impacts, which can be determined roughly by looking at the size of the proposed project (as noted in European Directive 97/11/EC; European Union 1997) or by conducting a preliminary study (as called for in US regulations; Council on Environmental Quality 1978). Then, if a comprehensive study is deemed necessary, the so-called scoping process (Council on Environmental Quality 1978, Canter 1996, European Union 1997) will identify the critical social and environmental problems to be analyzed, depending on the vulnerability of the territory and the frequency, type, and magnitude of the potential impacts. The size of the interdisciplinary team and the types of expertise it should encompass are calibrated on the basis of these findings. According to Canter (1996, p. 50), "The number of members of an interdisciplinary team can vary from as few as 2 to perhaps as many as 8 or 10 individuals, depending on the size and complexity of the study. Typically a team comprises three to four members."

In any case, the question is not posed properly in the context of our article. The right question would be "Given a limited budget to evaluate a proposed activity, would it be better to spend the money on an interdisciplinary study that explicitly incorporates multiple evaluation criteria or on a cost–benefit analysis conducted by economic consultants who employ monetary pricing techniques?"

Suppose Professor Pimentel is granted $100,000 to assess whether, and in what amount, a new pesticide can be introduced into our environment. A first option would be for him to use those dollars to hire an interdisciplinary team consisting of, for example, an ecotoxicologist, an agronomist, and an economist, who will provide independent evaluations from three different perspectives: The ecotoxicologist will estimate how different amounts of pesticide per unit of crop area (measured, e.g., as kg of pesticide per square km) will translate into different increases of mortality (measured, e.g., as percentage mortality per year) in birds and mammals; the agronomist will suggest how these amounts translate into different increases of harvested biomass (measured, e.g., as tons per square km); and the economist will figure how the farmer's budget (measured as thousands dollars per square km) is affected. Then Professor Pimentel can use multicriteria analysis to assess the tradeoff between the monetary net benefit to the farmer and the mortality of birds and mammals, an analysis that will help the decisionmaker and the citizens reach an informed conclusion about how many kilograms of pesticide per square kilometer can be allowed.

A second option is to use the grant money to hire economists to prepare questionnaires asking some citizens the dollar value they attach to one unit of animal mortality. Because the economists calculate that a good deal of the grant money must go toward preparing, printing, and mailing the questionnaires—and toward paying themselves—they have to behave in the following way: They do not consult an agronomist, but make their own rough estimate of increased harvests based on previous similar case studies. They give a little money to an ecotoxicologist to conduct a study and estimate the pesticide effects on just one charismatic species of bird. Thus the questionnaire recipients learn nothing of the pesticide effects on mammals and other birds, and the returns in terms of increased crop production are not known precisely. The economists collect the questionnaires and, for each unit of pesticide sprayed per square kilometer, compute the difference between benefits and costs.

Even though the costs include only the noxious effects on one charismatic species, not the many other animal species that will undoubtedly be affected, and the farmer's production is estimated only imprecisely, Professor Pimentel would nonetheless calculate the amount of pesticide that corresponds to the maximum estimated net monetary benefit and communicate this figure to decisionmakers. Honestly, we believe that it would be better for the citizens and taxpayers for Professor Pimentel to use the first option rather than the second—that is, he should hire an interdisciplinary team and conduct a multicriteria analysis.

Second, Professor Pimentel wonders whether it is possible to investigate all the possible consequences of a proposed activity. We did not mean to imply that *all* the consequences could be investigated; what we meant was that the interdisciplinary team should do its best to forget no significant consequences of a proposed activity. How to ensure that nothing significant is omitted in environmental impact assessments (EIAs) has been the subject of much debate. The simple solution is to employ "checklists" for different categories of projects or plans (Canter 1996, pp. 86 ff). Checklists compiled on the basis of accumulated experience have been extensively reported in, for example, the *EIA Guidelines* published in 1995 by the European Union Centre for EIA in Manchester, United Kingdom (*www.art.man.ac.uk/eia/lf12.htm#lf12*). Of course, humans are fallible and cannot forecast everything, but we can try to do our best within reasonable constraints set by time and resources. One of the advantages of undertaking this effort is that the possible conflicts between environmentalists and developers over debated questions will emerge before a decision is taken, not afterward. Thus less time and money are spent on the whole decision process.

Third, Pimentel says we claim that contingent evaluation is the only technique capable of providing an estimate of existence values, and such techniques would be inappropriate for assessing, for instance, the value of birds killed by pesticides. Let us point out that we did not say a contingent evaluation method is the *only* technique capable of providing an estimate of existence values. We said that *among pricing techniques*, the contingent evaluation methods approach is considered by economists to be the only one capable of providing an estimate of existence values, and we added that other problems undermined the effectiveness of any pricing technique. Indeed, a good deal of our paper is devoted to convincing the reader that existence values cannot be consistently estimated via pricing techniques. Professor Pimentel's example on the value of the existence of birds (40¢ or $216 or $800 per bird) is a beautiful demonstration of this fact.

Fourth, until data collected through the type of interdisciplinary investigations we suggest are available, Professor Pimental comments, let us use current data—presumably gathered through traditional accounting techniques—to give the public some idea of the magnitude of ecosystem problems. This point seems to contradict Professor Pimentel's third point, that "it would be a mistake to use willingness to pay to assess the value of birds killed by pesticides," or, in general terms, to assess the existence value of a species. Why does Professor Pimentel claim, at the end of his letter, that these accounting exercises are useful, while in the previous paragraph he maintained that they are not? Moreover, it must be considered that even pricing techniques, if properly used (Portney 1994), require interdisciplinary investigation. In fact, respondents to questionnaires that are used to derive estimates of willingness to pay must be properly informed about the significant consequences of a proposed activity. Such information can be provided only after an investigation that explores the different social, environmental, technical, and economic aspects of the problem. As we said above, pricing techniques and EIA-like techniques must be compared *ceteris paribus*. There is no doubt that we must "use current data to inform scientists, decision-makers, and the public of the magnitude of ecosystems problems." But should we convey information on the magnitude of an ecosystem problem as a single number (net monetary benefit) or as a more inclusive array of information? We believe that the monetary solution is simplistically attractive but very misleading in most cases.

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