

- aculeatus*) as an indicator of energy investment in vigour. *Evol. Ecol.* 7:439-450.
- GOODWIN, T. W. 1980. The biochemistry of carotenoids. Vol. 1, Plants (2nd ed.). Chapman and Hall, New York.
- GOODWIN, T. W. 1984. The biochemistry of carotenoids. Vol. 2, Animals (2nd ed.). Chapman and Hall, New York.
- GRINNELL, J. 1911. The linnet of the Hawaiian Islands: A problem in speciation. *Univ. Calif. Publ. Zool.* 7:79-95.
- HILL, G. E. 1990. Female House Finches prefer colourful males: Sexual selection for a condition-dependent trait. *Anim. Behav.* 40:563-572.
- HILL, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350:337-339.
- HILL, G. E. 1992. The proximate basis of variation in carotenoid pigmentation in male House Finches. *Auk* 109:1-12.
- HILL, G. E. 1993a. Geographic variation in carotenoid plumage pigmentation of House Finches. *Biol. J. Linn. Soc.* 49:63-86.
- HILL, G. E. 1993b. The proximate basis of inter- and intra-population variation in female plumage coloration in the House Finch. *Can. J. Zool.* 71:619-627.
- HILL, G. E. 1993c. House Finch. *In* Birds of North America (A. Poole, P. Stettenheim, and F. Gill, Eds.). No. 46. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- HILL, G. E. 1994. Geographic variation in male ornamentation and female mate preference in the House Finch: A comparative test of models of sexual selection. *Behav. Ecol.* 5:64-73.
- HIRAI, L. T. 1975. The Hawaiian House Finch. *Elepaio* 36:1-5.
- HUDON, J. 1994. Showiness, carotenoids, and captivity: A comment on Hill (1992). *Auk* 111:218-221.
- KOCH, E. L. 1939. Zur Frage der Beeinflussbarkeit der Gefiederfarben der Vögel. *Z. Wiss. Zool.* 152:27-82.
- LEE, W. L. 1966. Pigmentation of the marine isopod *Idotheamontereyensis*. *Comp. Biochem. Physiol.* 18:17-36.
- MURPHY, M. E., J. R. KING, AND J. LU. 1988. Malnutrition during the postnuptial molt of White-crowned Sparrows: Feather growth and quality. *Can. J. Zool.* 66:1403-1413.
- NEWTON, I. 1972. Finches. Collins, London.
- RUFF, M. D., W. M. REID, AND J. K. JOHNSON. 1974. Lowered blood carotenoid levels in chickens infected with coccidia. *Poult. Sci.* 53:1801-1809.
- SLAGSVOLD, T., AND J. T. LIJFELD. 1985. Variation in plumage coloration of the Great Tit *Parus major* in relation to habitat, season, and food. *J. Zool. (Lond.)* 206A:321-328.
- WEBER, H. 1953. Bewirkung des Fabwechsels bei männlichen Kreuzschnäbein. *J. Ornithol.* 94:342-346.
- WEBER, H. 1961. Über die Ursache des Verlustes der roten Federfarbe bei gekäfigten Birkenzeisigen. *J. Ornithol.* 102:158-163.
- WILLIAMS, J. H., G. BRITTON, AND T. W. GOODWIN. 1967. The biosynthesis of cyclic carotenes. *Biochem. J.* 105:99-105.
- ZUK, M., R. THORNHILL, AND J. D. LIGON. 1990. Parasites and mate choice in Red Jungle Fowl. *Am. Zool.* 235-244.

Received and accepted 7 December 1993.

The Auk 111(1):225-227, 1994

Use and Misuse of Bird Lists in Community Ecology and Conservation

J. V. REMSEN, JR.

*Museum of Natural Science, Foster Hall 119, Louisiana State University,
Baton Rouge, Louisiana 70803, USA*

Comparing lists of bird species among sites is an increasingly widespread practice for assessing patterns of species richness, particularly with the accelerating interest in conservation of tropical habitats. Because many researchers believe that problems in species identification and detectability are fewer in birds than in most other taxa, they believe that species richness of birds often can be assessed more quickly

and efficiently than for other taxa. Consequently, species richness of birds is frequently used as an index of overall "biodiversity," thereby assuming a prominent role in conservation decisions. Therefore, comparisons of inventories of avifaunas between sites take on a special significance.

A typical statement that one finds in comparisons of avifaunal surveys might be "341 species were re-

corded at site A, whereas 290 species were recorded at site B," with the conclusion that site A is richer than site B. Such blind comparisons of list totals have four primary flaws that I address below. I do not cite specific examples for each flaw because virtually every published comparison of bird lists contains one or more of these flaws, and so to single out individual publications for criticism is unwarranted.

1. *Failure to distinguish "core" members of avifauna from those species represented only by wandering or dispersing individuals.*—Species recorded at any site with a single habitat type include not only those that regularly breed, winter, or migrate through the site (the "core" avifauna) but also species not characteristic of that habitat and represented there by occasional, wandering or dispersing individuals (e.g. see Howell 1971). The latter species are of minimal interest to community ecology or conservation, yet they are accorded full "value" in a simple tally of the number of species recorded at the site. The number of species recorded through time in the core avifauna should approach an asymptote quickly, depending on observer skill and habitat complexity and homogeneity. The number of wanderers from other habitats or regions, however, depends more on observer effort and may not reach an asymptote within the time limits of most studies. Ability to distinguish core from noncore species depends on the familiarity of the observers with the local avifauna; unfortunately, such familiarity is often minimal in humid tropical habitats, where distributions are poorly known and where, in the absence of the dramatic seasonal changes of the temperate zone, distinguishing wanderers from low-density residents, and even breeding from nonbreeding species, is more difficult.

Failure to distinguish core from noncore species can lead to misleading comparisons of species richness. For example, if 341 species were recorded from site A and 290 from site B, the latter might actually be a richer area if of those 290 species, 275 were core species, whereas in A only 270 of its 341 species were core species, and the rest were only wanderers and occasional visitors recorded by virtue of sampling over a much longer period.

2. *Failure to take into account differences in quantity and quality of sampling effort.*—Although sampling effort is normally taken into account in comparisons among localities for any group of plants or animals, in no other group than birds are differences in sampling effort so critical, at least in densely vegetated areas. Wooded habitats, particularly at tropical latitudes, must be sampled in two ways for a reasonable assessment of species composition. First, unless the observers are thoroughly familiar with the voices of the birds of the area, the species list will be woefully incomplete and, even for those species detected, assessments of relative abundance will be extremely low for inconspicuous species (see Parker 1991). If an area has not been surveyed by an expert on that area's

bird vocalizations, then the survey cannot be considered comparable to one that has. For example, I was recently shown a report by a group who surveyed one of the richest areas in Amazonia for three weeks; the list of species in many families, especially Dendrocolaptidae, Formicariidae, Tyrannidae, and Tinamidae, contained far fewer species than would be expected to be heard from a single spot at that site in one morning. Surveys conducted by those not completely familiar with local voices should be augmented by extensive tape recordings, particularly of dawn choruses and of vocalizations from mixed-species flocks. These recordings should be examined in detail by an expert to complete the survey.

Second, any survey of areas with well-developed undergrowth must be accompanied by intensive mist-net sampling. Many secretive species of the undergrowth will be underrepresented in surveys not supplemented by mist-net sampling. However, it must be kept in mind that mist nets are not a substitute for over-all sampling. For example, the intensive mist-net sampling program in tropical forest near Manaus (seven years, 24,957 captures of 14,026 individuals, and 136,000 net-hours) captured only 41% of all bird species recorded there (Bierregaard 1990).

Also, comparisons between surveys that did not include similar spans of seasons must be treated with caution. In addition to the seasonal presence of long-distance migrants and altitudinal migrants (e.g. Blake et al. 1990), some "sedentary" tropical species show seasonal patterns of presence or abundance (e.g. Bierregaard 1990).

Additionally, surveys in tropical areas are being conducted with increasing frequency by persons not even familiar with the visual identification of the species of the region, and even by persons unfamiliar with bird identification in general. The frequency of misidentifications, even of hand-held mist-netted birds, is almost certainly much higher than realized by those who survey birds with mist nets.

Failure to take into account such differences in sampling effort could produce erroneous assessments of diversity. For example, 341 species might be recorded from site A and 290 from site B, but site B might actually be a richer area if those who surveyed the site were not familiar with voices and did not use mist nets to sample undergrowth species.

3. *Failure to take into account number of habitat types within areas compared.*—Comparisons of species totals among areas that include different numbers of habitats are flawed. Nevertheless, such comparisons are regularly encountered in the literature. For example, the numbers of bird species from Amazonian localities have been compared directly in several publications without noting that some sites include the gradient of successional habitats associated with major rivers, each of which has species found nowhere else in Amazonia (Remsen and Parker 1983, Terborgh et al. 1984, Rosenberg 1990), whereas others do not.

Continuing the comparison of hypothetical sites, if site A, with its 341 species, contains three distinct habitat types, say terra firme forest, varzea forest, and human-created second growth, whereas site B has only a single habitat type, terra firme forest, then comparison of the total species numbers must take this difference into account. The only comparable totals are the numbers of species in the terra firme forests.

4. *Failure to take into account proximity of other habitats.*—Because many bird species frequently range into habitats adjacent to their primary habitat that would not support them on a long-term basis, the proximity of different habitats to the study area must be taken into account. With increasing frequency, tropical sites with varying degrees of anthropogenic disturbances, such as lumbering or tree cultivation, are surveyed to determine how many forest species persist at such sites. Yet, these studies often do not describe or take into account the proximity of their sites to undisturbed habitats. If a tree plantation is adjacent to undisturbed forest, then many forest species may range regularly into the plantation. This, however, is not a true test of the plantation's ability to sustain populations of forest birds. Such sites must be beyond the daily cruising range of birds from nearby undisturbed habitats to even begin to qualify as an assessment of that site's ability to support species from undisturbed habitats, even over short-term periods.

I urge those responsible for designing comparisons of survey data, as well as funding agencies and reviewers of proposals and manuscripts, to address these concerns. The methodology section of papers that compare bird species richness among sites should include: (a) methods or criteria for distinguishing low-density residents that are truly part of the core avifauna from wandering species from other areas; (b) thorough documentation of sampling effort, including use of tape recorders, mist-net deployment pattern, and number of mist-net hours; (c) qualitative assessment of observer skills in visual and vocal iden-

tification; (d) description of the habitat types present within each area compared; and (e) distance to habitat types not represented in the sample areas.

Acknowledgments.—I thank S. W. Cardiff, R. T. Chesser, M. Cohn-Haft, G. Cox, J. W. Fitzpatrick, A. W. Kratter, M. Marín A., C. A. Marantz, D. C. Moyer, G. D. Schnell, and D. Wiedenfeld for comments on earlier versions of the manuscript.

LITERATURE CITED

- BIERREGAARD, R. O., JR. 1990. Species composition and trophic organization of the understory bird community in a central Amazonian terra firme forest. Pages 217–236 in *Four Neotropical forests* (A. H. Gentry, Ed.). Yale Univ. Press, New Haven, Connecticut.
- BLAKE, J. G., F. G. STILES, AND B. A. LOISELLE. 1990. Birds of La Selva Biological Station: Habitat use, trophic composition, and migrants. Pages 161–182 in *Four Neotropical forests* (A. H. Gentry, Ed.). Yale Univ. Press, New Haven, Connecticut.
- HOWELL, T. R. 1971. An ecological study of the birds of the lowland pine savanna and adjacent rain forest in northeastern Nicaragua. *Living Bird* 10: 185–242.
- PARKER, T. A., III. 1991. On the use of tape recorders in avifaunal surveys. *Auk* 108:443–444.
- REMSEN, J. V., JR., AND T. A. PARKER, III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica* 15:223–231.
- ROSENBERG, G. H. 1990. Habitat specialization and foraging behavior by birds of Amazonian river islands. *Condor* 92:427–443.
- TERBORGH, J. W., J. W. FITZPATRICK, AND L. EMMONS. 1984. Annotated checklist of bird and mammal species of Cocha Cashu Biological Station, Manu National Park, Peru. *Fieldiana (Zool.)* No. 21.

Received 20 April 1993, accepted 22 November 1993.