sional result of studies aimed at understanding the patterns and processes associated with geographic variation.

LITERATURE CITED

JOHNSON, N. K. 1980. Character variation and evolution of sibling species in the *Empidonax difficilis-flavescens* complex (Aves: Tyrannidae). Univ. Calif. Publ. Zool. 112: 1–151.

WILSON, E. O., & W. L. BROWN, JR. 1953. The subspecies concept and its taxonomic application. Syst. Zool. 2: 97–111.

THE SUBSPECIES CONCEPT: THEN, NOW, AND ALWAYS

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While President of the A.O.U., I encouraged the Chairman of the Check-list Committee seriously to consider restricting the next edition of the Check-list to the species level, and I was relieved when the Committee voted to do just that. My action was not prompted by disaffection with the subspecies concept, but rather by the conviction that a meaningful revision with subspecies could not be produced for at least another decade and that it was imperative that a revised check-list of species appear with reasonable dispatch. Those who have read the early volumes of *Systematic Zoology* realize that a debate over the concept of subspecies is not a novel idea. Nonetheless, the Editor of *The Auk* has suggested that many of his readers may not be aware of the arguments. He may be right. There certainly is the possibility that his readership has not accepted the arguments, for colleagues' responses to my position on the A.O.U. Check-list varied from delight to chagrin with what they initially perceived as my "abandonment" of subspecies.

One useful attribute of subspecies, sometimes overlooked in the heat of such debates, is the fact that they *can* be omitted from a check-list, field guide, atlas, or whatever. Subspecific names are not essential, and can be regarded as optional if deemed burdensome.

Subspecies have a more positive utility for those interested in geographical variation within species, as I hope to demonstrate with examples from my own research. Though my primary objective in revising the genus *Myiarchus* was to define species limits within this difficult group, some of the more interesting findings were those relating to differences in the biology of infraspecific units, including morphology, vocalizations, breeding and molt chronology, and migratory behavior. The trinomial system was indispensable as a means of describing this variability.

Swainson's Flycatcher (*Myiarchus swainsoni*) is a widespread South American species found east of the Andes and southward into the subtropical zone of Uruguay and central Argentina. The two southernmost subspecies are nominate *swainsoni*, which breeds in southern Brazil, Uruguay, and northeastern Argentina, and *ferocior*, which breeds over much of the remainder of Argentina, western Paraguay, and southeastern Bolivia. Because they differ substantially in morphology and vocalizations, it is not surprising that they were formerly considered specifically distinct, and I was able to demonstrate experimentally that *ferocior* in Argentina and Bolivia and nominate *swainsoni* in Brazil do not respond to the playback of one another's vocalizations. Under these conditions of "sympatry" created by experimental playback, the two forms show the same indifference to each other that they show to other species of *Myiarchus*. Had an ecological barrier developed to prevent secondary contact of these forms, it is probable that they would have continued to be treated as allopatric species. But we know now that there is a relatively narrow zone of secondary intergradation extending from central Paraguay south

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through eastern Argentina to western Uruguay. Birds within this zone are not only intermediate morphologically and vocally; they respond indiscriminately to the playback of the vocal characters typical of these forms in allopatry. Because they interbreed freely where their breeding ranges come together, as evidenced by complete morphological intergradation, they should be regarded as conspecific. I can not imagine how one might *effectively* discuss the comparative morphology and behavior of these two infraspecific units without recourse to trinomials.

The utility of the subspecies concept becomes even more self-evident when one appreciates that these two southern *Myiarchus, M. s. swainsoni* and *M. s. ferocior,* are migratory and spend the austral winter months in northern South America, where they are seasonally sympatric with resident conspecifics. Consequently, one may find some individuals of Swainson's Flycatcher in Venezuela in June that are breeding (*M. s. phaeonotus*), while others are in heavy molt (nominate *swainsoni*). To complicate the picture further, the wintering *swainsoni* are more similar morphologically to the resident *Myiarchus* of another species, *M. ferox,* than they are to the resident subspecies *M. s. phaeonotus.* Sorting out *Myiarchus* flycatchers in northern South America from June through August admittedly taxes the patience of the most experienced museum curator, but in the absence of the trinomial, all would be chaos.

Even more challenging is the Dusky-capped Flycatcher (*Myiarchus tuberculifer*), unique within the genus because of the circular arrangement of its South American subspecies, with reproductive isolation nearly, but not quite, complete at the southern end of this "open ring." Physical and ecological barriers effectively isolate the subspecies on either side of the Andes from Venezuela to southern Ecuador, while asynchronous breeding cycles prevent interbreeding between the two most divergent subspecies from southern Ecuador to central Bolivia. In the Yungas of Bolivia, however, the breeding seasons are more compatible, and it is possible to demonstrate a transition, morphologically and vocally, from nominate *tuberculifer* in the tropical lowlands to *atriceps* in the subtropical highlands. Consequently, all populations must be treated as conspecifics, though the "pure" forms on both ends of this altitudinal transition zone are more different from one another than are many species within the genus. But to argue against the retention of the name *atriceps* as an effective means of designating and discussing the very distinct temperate and subtropical populations of Argentina, Bolivia, and Peru would be utterly absurd.

Excesses and abuses in the application of the subspecies concept have led to indiscriminate naming of infraspecific units in the past, the cause of disillusionment among many biologists. But surely the solution is to "clean up our act," not abandon it. If and when the A.O.U. does issue a check-list with subspecies, careful analysis unquestionably will eliminate many of the currently recognized subspecific names, e.g. those designating arbitrary segments of north-south clines in eastern North America. This is as it should be.

Just as in the case of recent attacks by some colleagues on the biological species concept, prompted by frustration over problems of application, I would insist upon a more infallible and workable substitute before abandoning subspecies. When not abused, the trinomial system does work and can be of great value in discussing infraspecific variation in morphology and behavior. To paraphrase something said by someone, sometime—perhaps the deficiencies attributed to the subspecies concept are more to be viewed as deficiencies of the taxonomist rather than of the taxon. In any event, I look forward (with telescope, perhaps) to the eventual appearance of an A.O.U. Check-list of carefully evaluated subspecies.