IS SPIZELLA TAVERNERI A SPECIES OR A SUBSPECIES?

Authors: Ernst Mayr, and Ned K. Johnson
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COMMENTARY

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IS SPIZELLA TAVERNERI A SPECIES OR A
SUBSPECIES?!

ERNST MAYR,1 Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138
NED K. JOHNSON,3 Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, CA 94720-3160

Abstract. Based on distributional, ecologic, morphologic, and vocal data, Klicka et al. (1999) argued in favor of species status for the form taverneri, long regarded as a subspecies of the Brewer’s Sparrow (Spizella breweri). For several reasons we disagree with their conclusion: lack of evidence for the reproductive isolation of taverneri from breweri, loss of information on the close relationship and allopatric distribution of the two taxa that would accompany their elevation to species, and violation of the principle of taxonomic balance. Until the demonstration of vocal or display differences relevant to pair formation and maintenance, taverneri and breweri are best regarded as reproductively compatible subspecies.

Key words: Brewer’s Sparrow, reproductive isolation, species concepts, Spizella breweri, Spizella taverneri, taxonomic principles, Timberline Sparrow.

Is Spizella taverneri una especie o un subspecie?

Resumen. Usando datos de distribución, ecológicos, morfológicos, y de vocalización, Klika y colaboradores (1999) argumentaron a favor de reconocer a nivel de especie la forma taverneri, la cual ha sido considerada por mucho tiempo una subspecie del gorrión de Brewer (Spizella breweri). Nosotros diferimos de esta conclusión por varias razones: ausencia de evidencia de aislamiento reproductivo entre taverneri y breweri, pérdida de información sobre la relación evolutiva íntima y la distribución alopátrica de los dos taxones que acompañarían su elevación a nivel de especie, y violación del principio de balance taxonómico. Hasta que no se demuestre la existencia de diferencias relevantes en vocalización y formación de mantenimiento de parejas, es mejor considerar a taverneri y a breweri como subspecies reproductivamente compatibles.

In 1925, in the days when most new avian taxa were described as binomina, Spizella taverneri was described by Swarth and Brooks as a new species. Grinnell et al. (1930) ranked it as a subspecies of Spizella breweri and this rank was accepted by all subsequent AOU checklists. Recently Klicka et al. (1999) raised the question again and decided, even though somewhat hesitatingly, that the taxon deserved full species rank. Their analysis of the differences between S. breweri and S. taverneri is exemplary in the amount of detail and information provided, so that even a non-specialist is enabled to evaluate the situation.

S. taverneri is apparently completely geographically isolated from breweri, and all efforts to find an area of interbreeding or overlap have so far failed. The closest approach of the two taxa is about 150 km. The rank of taverneri, according to recognition criteria for species and subspecies under the biological species concept, therefore, cannot be determined by direct observation, but must be inferred, making use of the traditional criteria of such an inference (Mayr and Ashlock 1991:100–105). S. taverneri clearly is an incipient species, as are all geographically isolated populations, and we must infer whether or not it has already reached species level. Several considerations help us in making our decision.

Evidence for reproductive isolation. The analyses of distribution, ecology, and morphology provided by Klicka et al. (1999) usefully defined the allopatric distributions and size characters by which taverneri clearly differs from breweri. Unfortunately, these features have little or nothing to do with reproductive isolation, the only valid criterion by which to infer genetic independence and species status. Instead, information on pairing behavior is required as a basis for inference. Displays used in pair formation are apparently unknown in these sparrows. Thus we are left with possible differences in vocalizations as the chief potential reproductive isolating mechanism. Vocal characteristics in sparrows, as in other oscines, are apparently learned. Because such cultural transmission allows for considerable copying error, levels of variability are enhanced well beyond those seen in subspecies with innate, stereotyped voices (Kroodsma 1996).

Increased variability presents a formidable obstacle in any attempt to establish differences in songs between these closely related forms of sparrows. In our opinion the preliminary analysis of advertising song by Klicka et al. (1999) has not begun to describe even intra-individual variation, let alone population differences, and until such analyses are completed taverneri

1 Received 8 December 1999. Accepted 9 November 2000.
2 E-mail: emayr@oeb.harvard.edu
3 Corresponding author. E-mail: neddo@socrates.berkeley.edu

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is best viewed as a subspecies, reproductively compatible with S. breweri.

**Information.** Considering that a classification is an information storage system, we must ask, would it provide more information if taverneri were treated as a species or as a subspecies? When taverneri is treated as a species, all one learns is that it is different from breweri, but not even how different. Indeed, one might be misled into believing that taverneri is as different from breweri as are the other species of Spizella from each other. By contrast, when taverneri is treated as a subspecies one is at once provided with two pieces of important information. The first is that breweri is its nearest relative, a piece of information of considerable value in a genus with several other species. The other is that subspecies status of taverneri provides valuable geographical information by telling us that taverneri and breweri are allopatric. Both advantages are lost if taverneri is raised to full species rank.

**The principle of balance.** All entities (taxa) within a Linnaean category should be as equally different from each other as possible. For instance, one should not raise a genus to family rank when this family would be far less distinct than the other related families are from each other. When one compares the ranking criteria in different classes and phyla, one notices that this principle is often violated, but it is usually adhered to in the ranking within a class. The question then is, is taverneri as distinct from breweri as the other species of Spizella are from each other, and if not, does this justify treating it as a subspecies? In the base pairs of the mitochondrial DNA, taverneri and breweri differ on the average by only 0.13%. By contrast, two other species pairs of Spizella differ by 5.9% or 6.1%. Hence, the difference between taverneri and breweri for this character is more than an order of magnitude smaller than that between other species of Spizella.

In a recent survey of subspecies differences in sexual vertebrates, Avise and Walker (1999) found that subspecies often differed by more than 2% and sometimes even more than 3% of their mitochondrial base pairs. Is the small difference in the base pairs of the mitochondrial DNA of taverneri and breweri necessarily proof of only subspecific difference? Not necessarily! For example, Johnson and Zink (1983) and Cicero and Johnson (1995) found that relatively minuscule genetic distances separate the Red-breasted Sapsucker (Sphyrapicus ruber) and Red-naped Sapsucker (Sphyrapicus nuchalis), two taxa best defined as species on the basis of assortative mating in sympathy and strikingly different plumage signals (Johnson and Johnson 1985). Similarly, divergent vocal behavior (Borror 1972, James 1981) distinguishes the Cassin's Vireo (Vireo cassinii) from the Blue-headed Vireo (Vireo solitarius), despite the relatively trivial genetic distances that separate them (Murray et al. 1994, Johnson 1995, Cicero and Johnson 1998). In both of these examples, the crucial question for deciding species status was whether the differences provided evidence for essential reproductive isolation. We propose that the same question should be asked in attempting to determine the systematic status of S. taverneri. Lack of data proving essential reproductive isolation, therefore, rather than slight genetic difference, is the paramount reason supporting the conclusion that taverneri should continue to be listed as a subspecies of breweri.

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**LITERATURE CITED**


THE TAXONOMIC RANK OF *SPIZELLA TAVERNERI*: A RESPONSE TO MAYR AND JOHNSON

JOHN KICKA,1,2 Marjorie Barrick Museum of Natural History, Box 454012, University of Nevada Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154-4012

ROBERT M. ZINK, J. F. Bell Museum of Natural History, 100 Ecology Building, University of Minnesota, St. Paul, MN 55108

JON C. BARLOW, Royal Ontario Museum, 100 Queen’s Park, Toronto, ON M5S 2C6, Canada

W. BRUCE MCGILLIVRAY, Provincial Museum of Alberta, 12856-102 Avenue, Edmonton, AB T6N 0M6, Canada

TERRY J. DOYLE, Ten Thousand Islands National Wildlife Refuge, 3860 Tollgate Blvd., Suite 300, Naples, FL 34114

Abstract. Mayr and Johnson suggest that Spizella taverneri should be a subspecies of the biological species *S. breweri*, because it is possibly not reproductively isolated. We originally concluded that evidence from mitochondrial DNA sequences, habitat preferences, timing of breeding, vocalizations, and morphology supported the recognition of *S. taverneri* as a phylogenetic and biological species. Nothing in the commentary by Mayr and Johnson causes us to change that conclusion. We believe that it is probable that these two allopatric taxa are isolated. Contrary to Mayr and Johnson, we believe that more information is given by ranking *S. taverneri* as a species, because it reveals the fact that they are independently evolving taxa. The classification of *Spizella* should convey the sister-species status of *S. taverneri* and *S. breweri*, without regard for balancing the degree of sequence divergence among species, as suggested by Mayr and Johnson.

Key words: Brewer’s Sparrow, classification, DNA sequences, species concepts, Timberline Sparrow.

El Estatus Taxonómico de *Spizella taverneri*: una Respuesta a Mayr y Johnson

Resumen: Mayr y Johnson sugieren que *Spizella taverneri* debe ser una subespecie de la especie biológica *S. breweri*, porque posiblemente no se encuentra aislada reproductivamente. Nosotros originalmente concluimos que la evidencia de las secuencias del ADN mitocondrial, preferencias de hábitat, temporad
taverneri are recently isolated sister taxa. Whether they are reproductively isolated is of interest, but is only relevant to determining whether *S. taverneri* is a biological species. Mayr and Johnson speculate that there is insufficient evidence to predict whether pairings between individual *S. taverneri* and *S. breweri* would yield viable offspring, were they to encounter each other during the breeding season. We think that some of the differences that help diagnose *S. taverneri* are relevant to the question of reproductive compatibility. For example, Mayr and Johnson disregard substantial differences in the timing of breeding. *Spizella taverneri* does not return to the breeding grounds until 4–6 weeks after *S. breweri* has begun nesting, reducing the likelihood of interbreeding. Mayr and Johnson also emphasized the lack of information on pairing behavior of the two taxa. In particular, they focused on our discussion of the differing vocal characteristics. Although differences in advertising song might or might not be important in assessing reproductive isolation among allopatric populations (McKitrick and Zink 1988), the vocal differences are more convincing than the mtDNA analyses (Zink and Blackwell-Rago 2000). We think that some subspecies (the Curvirostrum and Palmieri groups) that correspond to an east-west division in southwestern North America, yet seven subspecies are generally accepted. Recent morphometric (Rojas-Soto 1998) and mtDNA analyses (Zink and Blackwell-Rago 2000) support division into only two (or possibly three) evolutionary units, which we consider species. Indeed, a loss of information occurs when all 7 subspecies are given equal rank. Similarly inappropriate is the classification of *S. taverneri* as a subspecies.

The principle of balance. Nothing in the formal taxonomic code mandates that taxonomists follow this so-called “principle” of balance. Classifications are systems for the storage and retrieval of information (although the nature of this is under debate, Widgott 2000), but this information should reveal evolutionary patterns, not degrees of sequence divergence. *Spizella taverneri* need not be as different from *S. breweri* as *S. breweri* is from other congeners. In fact, we know of no molecular studies that find all congeners equally related, including the species *Vireo*, which Mayr and Johnson discuss. Mayr and Johnson’s implication that congeners should be morphologically and genetically equidistant (a “star phylogeny”) is inconsistent with the way we understand evolution to occur; some species (within a clade) are older than others. Evolution need not produce balanced clades, and classifications should not be constructed to make them so. The classification of *Spizella* should convey that *S. taverneri* and *S. breweri* are sister species. Reference to the original paper (Klicka et al. 1999) will show interested readers the degree of sequence differentiation.

When does a species become a species? At the center of the current discussion is identifying the point in the process of evolutionary divergence at which an isolated taxon becomes a species (Avise and Walker 1998). Klicka and Zink (1999) reviewed the stages that occur when a single population is divided into two daughter lineages. For a considerable period, mtDNA haplotypes are paraphyletic with respect to the splitting of the lineage; this is partly true in the present discussion, as the haplotype identifying *S. taverneri* is embedded within the clade belonging to *S. breweri* (Klicka et al. 1999). After approximately 4N generations of isolation, the mtDNA haplotype tree is reciprocally monophyletic (membership in either daughter species is unambiguous based on DNA). Because haplotypes representing *S. breweri* and *S. taverneri* are not mutually reciprocally monophyletic, we believe that the speciation event was very recent. How we recognize species depends on the species concept employed. At
the point of reciprocal monophyly, one could consider
the two lineages to be phylogenetic (and evolutionary)
species. More divergence (anagenesis) typically must
occur before the lineages are reproductively isolated
and subsequently recognized by taxonomists as biolog-
ical species (Avise and Walker 1998). Even after
this time, species can continue to diverge without sub-
sequent splitting. Hence, “species” of whatever ilk can
be very similar or very different from congeneras as a
logical consequence of the evolutionary process.

_Spizella taverneri_ represents a very young species,
displaying precisely the morphological and genetic
characteristics we would expect to see in a newly
evolved species. Indeed, we think it is one of the most
likely examples of a Late Pleistocene speciation event in
a North American bird (Klicka and Zink 1999).

Mayr and Johnson, following the BSC, would prefer
to wait until there is evidence that the independent
evolutionary trajectories of _S. taverneri_ and _S. brewei_
are irreversible. We believe that the preponderance of
the evidence suggests that _S. taverneri_ is evolving in-
dependently, and that recognition of this independence
is more important than burying it at the subspecific
level. The philosophical underpinnings of alternative
species concepts allow for multiple interpretations of
the same evidence. In particular, reducing _S. taverneri_
to a subspecies reveals the problems inherent in de-
scribing patterns of biodiversity when following the
BSC (Peterson and Navarro-Siguenza 1999).

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