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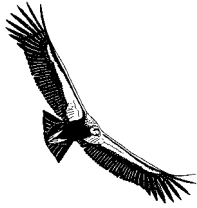
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COMMENTARY

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IS *SPIZELLA TAVERNERI* A SPECIES OR A SUBSPECIES?¹

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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.*

Es *Spizella taverneri* un especie o un subespecie?

Resumen. Usando datos de distribución, ecológicos, morfológicos, y de vocalización, Klicka y colaboradores (1999) argumentaron a favor de reconocer a nivel de especie la forma *taverneri*, la cual ha sido considerada por mucho tiempo una subespecie 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 alopatrica 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 y mantenimiento de parejas, es mejor considerar a *taverneri* y a *breweri* como subespecies 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 nonspecialist 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 suboscines 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*

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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 sympatry and strikingly different plumage signals (Johnson and Johnson 1985). Similarly, divergent vocal behavior (Borrer 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 de-

termine 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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THE TAXONOMIC RANK OF *SPIZELLA*
TAVERNERI: A RESPONSE TO MAYR AND
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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, tempora-

lidad de la reproducción, vocalizaciones y morfología apoyaban el reconocimiento de *S. taverneri* como una especie tanto filogenética como biológica. Nada en el comentario de Mayr y Johnson causa que cambiemos esa conclusión. Creemos que es probable que ese par de taxones alopatricos estén aislados. Contrariamente a Mayr y Johnson, creemos que se proporciona más información designando a *S. taverneri* como especie, pues revela el hecho de que ambos son taxones que evolucionan independientemente. La clasificación de *Spizella* debe mostrar el estatus de especies hermanas de *S. taverneri* y *S. breweri*, sin tomar en cuenta para el balance el grado de divergencia de las secuencias entre las especies, como fue sugerido por Mayr y Johnson.

Mayr and Johnson (2001) do not dispute the evidence presented by Klicka et al. (1999) that corroborated the existence of a taxon named *taverneri*. The discussion instead concerns whether this taxon should be ranked as a species or a subspecies. Mayr and Johnson believe that our evidence is best interpreted to indicate that *taverneri* is a subspecies of the biological species *S. breweri*. We concluded that *taverneri* represents a newly evolved phylogenetic species, and probably a biological species as well. We believe that the arguments presented by Mayr and Johnson, grounded in the school of evolutionary systematics (Mayr and Ashlock 1991), are equivocal, and show why the biological species concept (BSC) has been losing favor in many disciplines (Wheeler and Meier 2000), including ornithology (Zink and Davis 1999). Below we respond to the issues raised by Mayr and Johnson.

Evidence for reproductive isolation. Mayr and Johnson state that if genetic independence cannot be determined by direct observation (i.e., a "test of sympatry"), it must be inferred. This, in fact, has long been recognized as a critical flaw in the biological species concept: the main criterion for ranking taxa as species must be inferred in the thousands of cases (such as the present one) in which diagnosable populations or groups of populations are allopatric. The methods of inference are vague and vary among taxonomists. Today, analyses of DNA are used to discover genetically isolated groups of populations and to recover their phylogenetic relationships. In modern systematics, the phylogeny is used for classification (Gutiérrez et al. 2000), including the assignment of species limits (Zink and Davis 1999). Furthermore, it is now known that the pattern of reproductive compatibility is not necessarily an accurate predictor of phylogenetic relationship because non-sister taxa often hybridize (Zink and McKittrick 1995, Klicka et al. in press). Thus, species limits based on recovered patterns of evolutionary history (e.g., phylogenetic analyses of DNA) can conflict with those based on patterns of reproductive compatibility. Zink and Davis (1999) suggested that the appropriate research program was to map patterns of reproductive compatibility and isolation onto a phylogeny. In this way, one can understand which characteristics contribute to reproductive compatibility and isolation among taxa, rather than to use these categories as ambiguous characters to diagnose species.

Our DNA analyses suggested that *S. breweri* and *S.*

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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 (McKittrick and Zink 1988), the vocal differences are more convincing than Mayr and Johnson suggest. *Spizella taverneri* songs from populations separated by thousands of kilometers are more similar to each other than they are to *S. breweri* songs of only a few hundred kilometers away. Misinterpretation of individual variation as representative of population-level differences would not produce this pattern. Nevertheless, we agree that taken alone, the vocal evidence is insufficient for establishing unambiguously the species status of *taverneri* (a comprehensive geographic survey is needed).

We concluded that the combined vocal, morphological, behavioral, and ecological evidence presented is consistent with the genetic evidence in suggesting that *Spizella breweri* and *S. taverneri* are on independent evolutionary trajectories. We believe that using these combined sources of evidence to assess taxonomic rank is preferable to inferring reproductive isolation among allopatric populations. The most appropriate hypothesis, when the facts (including eight years of field experience with these birds) are considered, is that *taverneri* is both a phylogenetic and a biological species.

Information. According to Mayr and Johnson, information is lost if *S. taverneri* is elevated to species level. Using similar logic, we suggest that more important information is lost by not elevating *S. taverneri* to species status, namely that *S. taverneri* and *S. breweri* are independently evolving units. Ranking very closely related (i.e., young) taxa as species is standard in classifications, and few seem to be perplexed with questions concerning sister relationships and allopatry. Established procedures (Nelson and Platnick 1981) for translating a phylogeny into a classification would convey the fact that *S. breweri* and *S. taverneri* are sister species; however, such information is often lost in avian classifications (Barrowclough and Cracraft 1984). The notion that information about the allopatry of *S. breweri* and *S. taverneri* is lost by making them separate species is irrelevant because classifications are not intended to reveal geographic distributions.

A second problem with their argument involves the taxonomic inconsistency of subspecies. The position

taken by Mayr and Johnson would have more validity if all subspecies were as clearly defined as *S. taverneri* (although this would still not be an argument in favor of keeping the BSC, Zink and Davis 1999). Unfortunately, all subspecies are not created equal. The literature is fraught with poorly defined and indistinguishable subspecies. A growing body of evidence indicates that as many as 50% of avian subspecies are not corroborated by mtDNA data, presumably because they are based on arbitrary divisions of single morphological character clines (Zink et al. 2000). For example, Curve-billed Thrashers (*Toxostoma curvirostre*) have been divided into two morphologically distinct subspecies clusters (the Curvirostre and Palmeri 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, Withgott 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 genus *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 $4N_e$ 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 biological species (Avice and Walker 1998). Even after this time, species can continue to diverge without subsequent splitting. Hence, "species" of whatever ilk can be very similar or very different from congeners 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. breweri* are irreversible. We believe that the preponderance of the evidence suggests that *S. taverneri* is evolving independently, 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 describing patterns of biodiversity when following the BSC (Peterson and Navarro-Sigüenza 1999).

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