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The Song Sparrow, *Melospiza melodia*, as a ring species: patterns of geographic variation, a revision of subspecies, and implications for speciation

Abstract Identification and analysis of ring species are important to our understanding of evolution and speciation. We review geographic variation in the Song Sparrow (*Melospiza melodia*) in the context of a ring species, one of few known from the highly vagile class Aves. Although 52 subspecies have been named, our reassessment of morphological variation across the entire species reveals that 25 subspecies are diagnosable throughout the species' range, which includes much of the North American continent. We include an analysis of plumage variation in *M. m. heermanni* of coastal California and *M. m. fallax* of the Sonoran Desert and a description of the contact zone between these subspecies, which forms the contact points of a ring centred around the Sierra Nevada and Mojave Desert. These two subspecies come into contact in a narrow hybrid zone, where interbreeding is limited. In addition to substantial differences in plumage, songs of these subspecies vary concomitantly with differences in the structure of occupied habitat. Females tend to exhibit assortative preferences for plumage and song and males exhibit assortative recognition (and associated agonistic behaviour) of song. Plumage variation across the Song Sparrow varies according to climate and habitat, suggesting both geographical and ecological components to the species' diversification.

Key words geographic variation, *Melospiza melodia*, ring species, subspecies, speciation

We question whether study of geographic variation in song sparrows leads to insights concerning speciation.

Zink and Dittmann (1993)

Introduction

The study of geographic variation has formed, in animals at least, the basis for our understanding of speciation (Mayr, 1942). Ring species exemplify perhaps the most interesting pattern of variation. A 'ring species' is a species comprised of multiple subspecies whose connected ranges form a circle or ring (Mayr, 1942; Irwin *et al*., 2001a; Irwin & Irwin, 2002) and whose subspecies at opposite poles of the ring behave like good biological species (or nearly so), in that they are reproductively isolated (and, typically, morphologically or behaviourally distinct from each other). Subspecies connecting these endpoints grade into each other to form a continuous set of intermediate forms. The pattern of variation in ring species demonstrates that intraspecific variation can be great enough to lead to species formation – that the microevolutionary processes that lead to population differentiation are related to the processes that lead to speciation (Irwin *et al*., 2001a; Irwin & Irwin, 2002). In other words, differences among individuals are of the same kind as differences among populations, which in turn are of the same kind as differences among species. These differences are only a matter of degree.

Classic ring species are well documented in the mouse *Peromyscus maniculatus* (Murie, 1933), the salamander *Ensatina eschscholtzii* (Moritz *et al*., 1992; Alexandrino *et al*., 2005; Kuchta, 2005; Wake, 2006; cf. Highton, 1998; Wake & Schneider, 1998), and the millipede *Rhymogona montivaga* (Pedroli-Christen & Scholl, 1996), with more contentious examples in the pocket mouse *Perognathus longimembris/P. amplus* (McKnight, 1995), the mouse *Mus musculus* (Bonhomme, 1994), the tree *Acacia karroo* (Brain, 1989), and the butterfly *Junonia lavinia* (Mayr 1942:181). See Irwin *et al*. (2001a, b) for reviews and critiques of these and other claimed ring species.

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Mayr's (1942:182) comment that ring species are 'rather frequent' in birds notwithstanding, most evolutionary biologists have assumed that they would be rare in birds, if not impossible, principally because birds are so mobile. Indeed, various examples in birds do not hold up to scrutiny. The textbook case of the Herring Gull (*Larus argentatus*) complex encircling the North Pole (Mayr, 1940; Ridley, 1993:41), for example, does not appear to constitute a true ring species: neighbouring subspecies are allopatric or different biological species (Cramp & Simmons, 1983; Kennerley *et al*., 1995; American Ornithologists' Union, 1998), and recent genetic research supports a model of divergence by vicariance in glacial refugia rather than isolation by distance in a ring (Liebers *et al*., 2004). The Great Tit (*Parus major*) was also thought to be a ring species across Eurasia (Mayr, 1940; Martens, 1996), but this example is confounded by recent sympatry resulting from habitat alteration by humans (Nazarenko *et al*., 1999), and the purported 'ring' may be comprised of three reproductively isolated species (Päckert *et al*., 2005). None of the various examples of 'ring species' mentioned by Phillips (1959), including the Mallard (*Anas platyrhynchos*) complex in the USA and Canada, seems plausible, chiefly because they do not form rings – there are no taxa behaving as good species at the endpoints. Even by his own standards Mayr's (1940, 1942) additional examples – *Halcyon* kingfishers in Micronesia, the *Phylloscopus collybita* complex (now split into 3–4 allospecies), *Zosterops* white-eyes in the Lesser Sunda Islands, *Lalage* trillers in the southern Celebes (Sulawesi), and *Pernis* honey-buzzards in the Philippines – require further study. Easily the best possibility for a true ring species in birds is offered by populations of the Greenish Warbler (*Phylloscopus trochiloides*) in Asia (Ticehurst, 1938; Mayr, 1942; Irwin & Irwin, 2002), with recent research showing introgression between neighbouring populations in the ring and subspecies acting as biological species at the contact point of the ring (Irwin, 2000; Irwin *et al*., 2001a, b; Irwin & Irwin, 2002; Irwin *et al*., 2005).

We present evidence that Song Sparrow (*Melospiza melodia*) populations of southwestern North America constitute a ring species. The Sierra Nevada and Mojave Desert lie at the ring's centre. The connecting point is between *M. m. heermanni* and *M. m. fallax* in the southern Coachella Valley (Patten *et al*., 2004b), which extends southeast across a steep ecological gradient through the San Gorgonio Pass, a deep rift that separates the Transverse and Peninsular Ranges of southern California. This pass is the site of various other meeting points between coastal and desert taxa (e.g. see Patten *et al*., 2003, 2004a). Despite differences in plumage, *M. m. heermanni* and *M. m. fallax* interbreed sparingly in the Coachella Valley (Patten *et al*., 2003, 2004b), yet females exhibit assortative mate preference for consubspecific song and plumage, and males have stronger reactions to consubspecific song and thus exhibit assortative song recognition (Patten *et al*., 2004b).

As a necessary first step in describing patterns of geographic variation in the Song Sparrow, we undertook a taxonomic revision and detailed synopsis of all named subspecies, including creating complete lists of synonymies. At the outset we summarise the overall patterns, dividing the species into five groups of subspecies. The pattern of geographic variation

and the evidence from the connecting points of the ring are strongly associated with ecological factors (e.g. habitat structure, temperature, rainfall). In this respect, the Song Sparrow is an excellent species in which to study the process of speciation, from both geographical and ecological perspectives.

Geographic variation in the Song Sparrow

The Song Sparrow is generally of medium build, though its size varies substantially, ranging from as large as a California Towhee (*Pipilo crissalis*; ± 50 g) in the Aleutian Islands of Alaska to as small as a Savannah Sparrow (*Passerculus sandwichensis*; ± 18 g) on the Channel Islands of California (Aldrich, 1984; Rising, 1996). Its plumage is generally characterised by a streaked breast and mantle, although populations on the Mexican Plateau are spotted below, with the white throat unstreaked, away from Alaska and the Pacific Northwest, ventral streaking typically coalesces into a central breast spot. Streaking or spotting is generally well defined on a whitish, grey, olive, or pale brown background; streak colour varies from black to pale rufous. Broad lateral crown stripes border a pale central stripe, but a contrasting central crown is often inconspicuous. Irides and other bare parts are dark brown to blackish.

The Song Sparrow is often regarded as the most polytypic and variable species in North America (Miller, 1956) and vies with the Horned Lark (*Eremophilus alpestris*) and Yellow Wagtail (*Motacilla flava*) as the most polytypic bird species in the northern hemisphere, though each is less so than the Golden Whistler (*Pachycephala pectoralis*) of Australasia, the most polytypic in the world (Mayr & Diamond, 2001). Variation across the Song Sparrow's range is substantial and complex in both size (Aldrich, 1984) and plumage (Dickerman, 1963; Rising, 1996), with little apparent association between mitochondrial DNA (mtDNA) and morphological differentiation (Zink, 1991; Zink & Dittmann, 1993; Fry & Zink, 1998), although recent studies using more rapidly evolving microsatellite loci have detected a correlation between morphology and genes (Chan & Arcese, 2002, 2003; Patten *et al*., 2004; Pruett & Winker, 2005; Pruett *et al*., 2008b). We feel that subspecies are an excellent surrogate for underlying variation in the nuclear genome.

Patterns of geographic variation in the Song Sparrow follow Gloger's rule, a common trend in North American birds (Zink & Remsen, 1986), with the darkest, most heavily pigmented birds in cold, humid northwest areas and the palest, least heavily pigmented in hot, dry southwestern areas. Geographic variation also appears to follow Bergmann's rule, with the largest birds in the cold Northwest and the smallest in the warm Southwest (Aldrich, 1984). There are 52 subspecific names, including *M. m.* '*alleghanii*' Bailey, 1936, a *nomen nudum* (Hubbard & Banks, 1970). Of the remaining 51 properly named subspecies, generally 38–40 are recognised (e.g. American Ornithologists' Union, 1957; Dickerman, 1963; Paynter, 1970; Rising, 1996), although only 15 possess unique characters (Marshall, 1964), and we recognise only 25 herein.

Geographic variation in the Song Sparrow can be partitioned readily into five subspecies groups:

(1) Eastern North America through the Great Basin – medium to small; brownish; wings long; breast streaked blackish (*M. m. melodia*, *M. m. atlantica*, *M. m. montana*).
(2) Alaska and the Pacific Northwest – large to medium; dark; breast streaks ruddy, diffuse (*M. m. maxima*, *M. m. sanaka*, *M. m. insignis*, *M. m. kenaiensis*, *M. m. caurina*, *M. m. rufina*, *M. m. morphna*, *M. m. merrilli*, *M. m. cleonensis*). The last subspecies is intermediate between *M. m. morphna* and *M. m. gouldii*, so it might just as easily be placed in the California group.
(3) California – medium to small; greyish olive; wings short; breast streaked black (*M. m. gouldii*, *M. m. samuelis*, *M. m. maxillaris*, *M. m. pusillula*, *M. m. heermanni*, *M. m. graminea*).
(4) Desert Southwest and northwestern Mexico – small to medium; pale; breast streaked rufous (*M. m. fallax*, *M. m. rivularis*, *M. m. goldmani*).
(5) Mexican Plateau – small to medium; breast spotted; throat clean white (*M. m. zacapu*, *M. m. adusta*, *M. m. villai*, *M. m. mexicana*).

Synopsis of the subspecies

The study of geographic variation in the Song Sparrow has the potential to teach us much about the process of speciation (*cf.* Zink & Dittmann, 1993), particularly if we are interested in the role ecology plays in the process. First, however, it is important to ensure that we are not dealing with an inflated number of taxa. Inclusion of invalid subspecies gives a false impression of real geographic variation and thus confuses our ideas of where species may be forming. Second, it is evident that ecological factors have shaped much of the geographic variation in this species, with such factors appearing to largely explain variation around the ring (see below). Failure to detect concordance between subspecific and mtDNA genetic variation (Zink, 1991; Zink & Dittmann, 1993; Fry & Zink, 1998) is confounded by two considerations. In the first case, if we restrict genetic analyses to mtDNA then we risk biasing results against detecting genetic variation resulting from natural selection. If all variation is the result of drift during periods of geographic isolation, then mtDNA, assuming it is shielded from selection (see Ballard & Whitlock, 2004), is a perfect molecule for genetic analysis. If, however, ecological factors played a substantial role in generating variation, then nearly all resultant genetic variation is ignored by focusing on mtDNA, particularly if divergence was rapid and recent. In the second case, including invalid subspecies as separate groups in analyses biases results in favour of failing to reject the null hypothesis. These separate groups are not real, so treating them as such means we should expect no differences between them. For these two reasons, it is not surprising that these studies did not report a strong positive concordance between morphology and genetics. Studies using rapidly evolving neutral markers report concordance with morphology (Chan & Arcese, 2002, 2003; Patten *et al.*, 2004; Pruett & Winker, 2005; Pruett *et al.*,

2008b) and thus show that evolutionarily recent events (e.g. Pruett *et al.*, 2008a), too recent for mtDNA to track, are likely to have structured Song Sparrow subspecies.

Detailed study of the nuclear genome of the Song Sparrow will doubtless reveal a great deal of genetic control for the species' substantial morphological variation. There may come a time when we have identified the appropriate genes and can readily analyse their variation. In the interim we are limited to examining morphology. Although the environment plays a role in geographic variation (James, 1983), plumage and mensural characters are an effective and appropriate surrogate for measuring the nuclear genome, and many of these characters are known to be heritable in Song Sparrows (Smith & Zach, 1979; Schluter & Smith, 1986).

Taxonomic methods

To begin a study of speciation in the Song Sparrow, we provide details for the taxonomic treatment presented above, including the myriad of synonymies. We recognise only 25 subspecies, half of the 51 valid names that have been assigned to different Song Sparrow populations but closer to the 15 on the basis of unique characters (Marshall, 1964). We emphasise diagnosability rather than mean differences, the latter having dominated subspecific taxonomy, to its detriment, for decades (Rand & Traylor, 1950; Patten & Unitt, 2002). For mensural data, we used a statistical application of the 75% rule (Patten & Unitt, 2002); this rule is the standard for defining a subspecies (Amadon, 1949; Mayr, 1969). Certain groups of Song Sparrow subspecies already have received adequate treatment in literature. In particular, Marshall (1948) provided a detailed quantitative study of subspecies in the San Francisco Bay region of California that we follow completely. We also follow Gibson and Kessel's (1997) assessment of Alaskan subspecies and generally follow Dickerman's (1963) detailed study of Mexican subspecies. For all other subspecies, we present an assessment of specimens (nearly 5000 in total) and an interpretation of the literature.

Plumage patterns of the Song Sparrow are exceedingly complex, with multiple colours frequently appearing on the same feathers and some coloured areas extremely narrow (<1 mm). Because the measurement aperture is 3–8 mm on all available devices, we could not use spectroradiometry (colourimetry) to quantify colour. By necessity, therefore, differences between various subspecies were qualified using a colour scheme (e.g. Munsell soil colour book). Specimens of like age and wear were used for assessment of most subspecies, virtually always being specimens with relatively unworn plumage (i.e. generally from September through January, after the pre-basic moult). Specimens of birds in juvenal plumage and with excessively worn feathers (usually taken from May into August) were avoided. When needed for proper assessment, size was quantified using calipers following standard methods to measure avian specimens (Baldwin *et al.*, 1931). For plumage variation in *M. m. heermanni* and *M. m. fallax*, we used most available specimens at SDNHM, MVZ and WFVZ (see Table 1), augmented by ±70 wild-caught birds, and

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
BMNH	Bell Museum of Natural History, University of Minnesota
CAS	California Academy of Sciences, San Francisco
CMNH	Cleveland Museum of Natural History, Cleveland
DEL	Delaware Museum of Natural History, Greenville
FMNH	Field Museum of Natural History, Chicago
LACM	Natural History Museum of Los Angeles County, Los Angeles
MCZ	Museum of Comparative Zoology, Harvard University
MNHN	Muséum National d'Histoire Naturelle, Paris
MVZ	Museum of Vetrebrate Zoology, University of California–Berkeley
PM	Peale's Museum, Boston
RBCM	Royal British Columbia Museum, Vancouver
SDNHM	San Diego Natural History Museum, San Diego
UMNH	Utah Museum of Natural History, University of Utah
USNM	National Museum of Natural History, Washington, DC.
WFVZ	Western Foundation of Vertebrate Zoology, Camarillo, California

Table 1 Abbreviations for museums holding cited specimens.

quantified plumage colour and pattern using a scoring system described below. On the basis of our analyses, we recognise 25 subspecies (Fig. 1), as detailed in the following accounts.

Eastern/Great Basin Group

Melospiza melodia melodia (Wilson)

Fringilla melodia Wilson, 1810, *Am. Ornithol.* 2:125, pl. 16, fig. 4

Fringilla fasciata (not Müller) Gmelin, 1788, *Syst. Nat.* 1(2):922 [preoccupied; *Auk* 16:183, 1899]

Emberiza? melodia Jardine, 1832, *Wilson's Am. Ornithol.* 1:269

Zonotrichia melodia Bonaparte, 1838, *Geogr. Comp. List* 31

Melospiza melodia Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:477, part

Melospiza melodia var. *melodia* Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Birds* 2:18

Melospiza fasciata Scott, 1876, *Am. Nat.* 10:18

Melospiza meloda [sic] Henshaw, 1879, *Bull. Nuttall Ornithol. Club* 4:156

Melospiza fasciata juddi Bishop, 1896, *Auk* 13:132

Melospiza melodia melodia Oberholser, 1899, *Auk* 16:183

Melospiza cinerea melodia Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):354

Melospiza melodia juddi American Ornithologists' Union, 1908, *Auk* 25:379

Melospiza melodia beata Bangs, 1912, *Proc. New England Zool. Club* 6:87

Melospiza melodia acadica Thayer & Bangs, 1914, *Proc. New England Zool. Club* 5:67

Passerella melodia acadica Linsdale, 1928, *Condor* 30:349

Passerella melodia beata Linsdale, 1928, *Condor* 30:349

Passerella melodia juddi Linsdale, 1928, *Condor* 30:350

Passerella melodia melodia Linsdale, 1928, *Condor* 30:350

Melospiza melodia euphonia Wetmore, 1936, *Smithsonian Misc. Coll.* 95(17):1

Melospiza melodia beata Todd, 1930, *Auk* 47:257, part

Zonotrichia melodia euphonia Paynter, 1970, *Check-list Birds World* 13:46

Zonotrichia melodia melodia Paynter, 1970, *Check-list Birds World* 13:46

Zonotrichia melodia juddi Paynter, 1970, *Check-list Birds World* 13:47

Melospiza melodia callima Oberholser, 1974, *Bird Life Texas* 2:957

Melospiza melodia melanchra Oberholser, 1974, *Bird Life Texas* 2:958

HOLOTYPE: MCZ 67860 (ex. PM 6573); sex?; Canada to Georgia [=Philadelphia, Pennsylvania, USA]; date?; collector?.

DIAGNOSIS: Size moderate ($\male$ 18.0–25.3 g, $\bar{x} = 21.8$ g, $n = 28$; $\female$ 18.8–24.0 g, $\bar{x} = 21.1$ g, $n = 27$); wing length moderate ($\male$ 63–72.5 mm, $\bar{x} = 66.5$ mm, $n = 171$; $\female$ 59–71.5 mm, $\bar{x} = 64.1$ mm, $n = 88$); tail length moderate ($\male$ 62–74 mm, $\bar{x} = 67.7$ mm, $n = 49$; $\female$ 55.5–72 mm, $\bar{x} = 64.4$ mm, $n = 44$); bill length moderate (8.5–10.3 mm, $\bar{x} = 9.3$ mm, $n = 52$); bill deep (7.4–8.4 mm, $\bar{x} = 7.8$ mm, $n = 73$); underparts white; throat flecked; ventral streaks brown, fringed chestnut, contrast sharply with ground colour; upperparts medium brown, feathers edged buff; dorsal streaks brown, narrow; supercilia whitish; malar reddish-brown.

RANGE: Migratory. Except for parts of the middle Atlantic Coast, breeds throughout eastern North America, from Newfoundland south to northern Georgia and west through the Prairie Provinces and eastern Great Plains (Fig. 1). Winters in the southeast, south to Florida and southern Texas (Oberholser, 1974:958).

REMARKS: Wilson (1810) listed the type specimen of *Fringilla* [=*Melospiza*] *melodia* as 'Peale's Museum 6573'. Most birds in that museum's collection were transferred to the Boston Society of Natural History, where the type, apparently a live mount lacking the original label, was housed until the early 1910s (Bangs, 1912). Within a few years the type specimen was transferred to MCZ (Thayer & Bangs, 1914), where it remains (as a live mount). The exact type locality has long been fixed at Philadelphia, but whether the bird was of the local breeding population has generated some dispute, with Thayer and Bangs (1914) suggesting it was perhaps a winter visitor from the Allegheny Plateau. If Thayer and Bangs are correct, and if additional subspecies are recognised, then the bird was from the population the American Ornithologists' Union (1957) called *M. m. euphonia*, meaning that *M. m. euphonia*
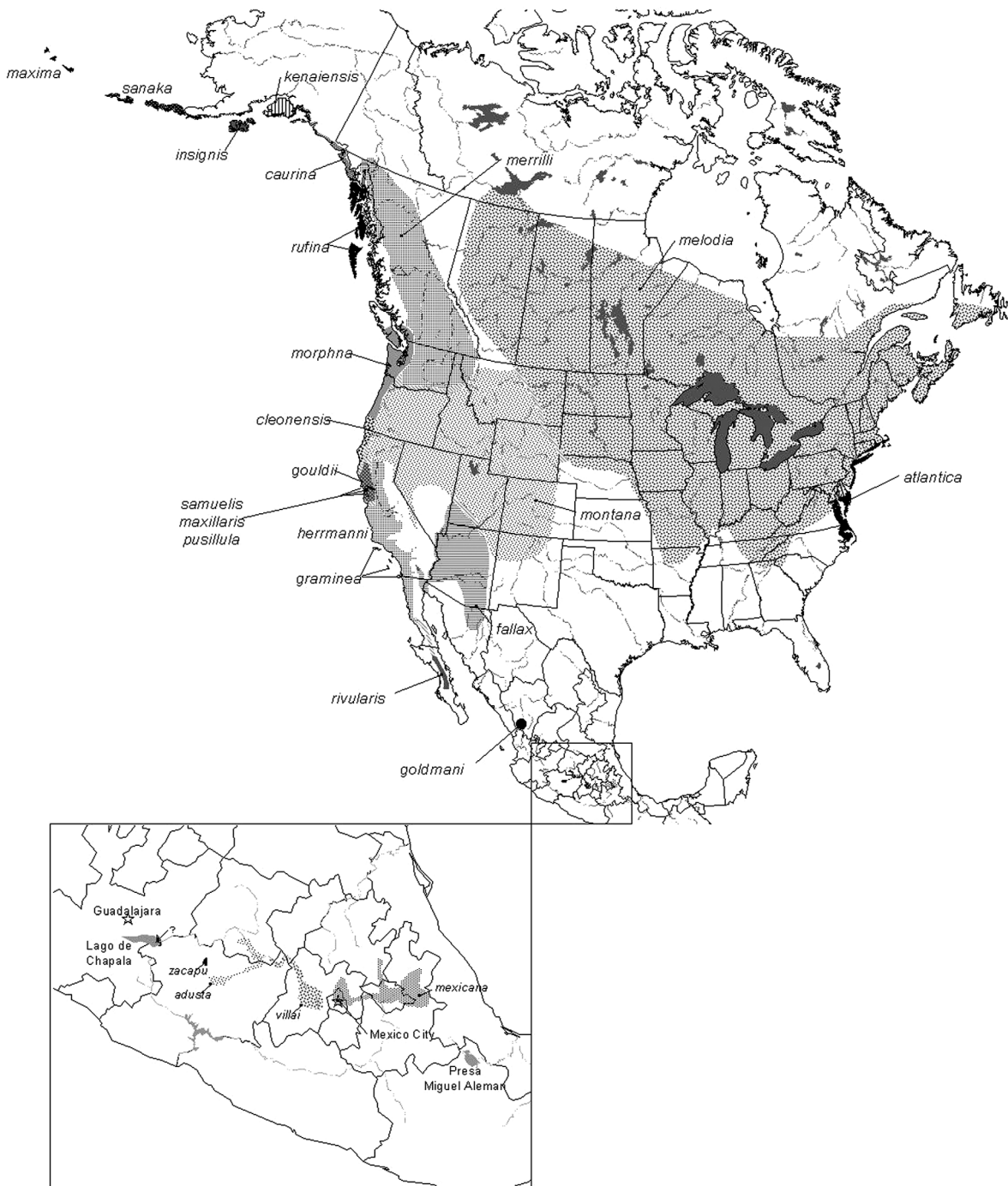
Figure 1   Subspecific breeding ranges in the Song Sparrow, with an inset for those on the Mexican Plateau. Crosshatching signifies zones of intergradation and borders between subspecies, by definition, are not as sharp as (heuristic) range boundary lines would suggest.

would become a synonym of the nominate subspecies, while the nominate subspecies would take the name *M. m. acadica*. As it stands, *M. m. acadica* (holotype: MCZ 320554 [ex. MCZ 65643]; adult ♂; Wolfville, Nova Scotia, Canada; 22 April 1914; R. W. Tufts) is a synonym of the nominate subspecies (Todd, 1963:710) even though Bangs (1930:386) continued to recognise it.

Oberholser's (1974) magnum opus on the Texas avifauna included numerous newly described taxa based on trifling differences, including *M. m. callima* (holotype: USNM 310402;

adult ♂; West Point, Orange County, New York, USA; 15 April 1909; Wirt Robinson 1352). This subspecies was subsequently determined to be synonymous with the nominate (Browning, 1978). Browning also determined that *M. m. melanchra* (holotype: CMNH 29986; adult ♂; Bay Point, 3 miles n. of Sandusky, Ottawa County, Ohio; 30 June 1931; John Dittrick and J. W. Aldrich) is a synonym of *M. m. euphonia* (holotype: USNM 348887; adult ♂; Cranberry Glades, Pocahontas County, West Virginia, USA; 8 June 1936; W. M. Perrygo and C. Lingebach 393), which we in turn consider

a synonym of *M. m. melodia*. Bull (1974:600) recognised neither *M. m. euphonia* nor *M. m. juddi*; instead, he called the 'poorly differentiated' *M. m. euphonia* 'merely part of an east-west cline extending from New England and New York . . . through several slightly differentiated populations including the more western . . . *juddi* (itself part of the cline).' This cline is especially weak from *M. m. melodia* through *M. m. euphonia*, with numerous specimens from their respective ranges indistinguishable from one another. For example, birds from Prince Edward Island (e.g. AMNH 817591, taken 6 June 1986) are indistinguishable from ones from Alleghany County in northwestern North Carolina (e.g. AMNH 825955, taken 19 May 1988).

Ridgway (1901:358) synonymised *M. m. juddi* (holotype: FMNH 124043; adult ♂; Rock Lake, Towner County, North Dakota, U.S.A.; 11 May 1895; Louis B. Bishop) with *M. m. melodia* before *M. m.* '*euphonia*', the geographically intermediate subspecies, was described. He remarked that specimens from the Atlantic Coast and Great Plains 'average slightly greyer than those from the intermediate region, but the difference is so slight and inconstant that subspecific separation seems to me unjustifiable'. Todd (1963:711), by contrast, recognised *M. m. juddi* as being greyer dorsally, with 'less reddish brown and more black' and more contrasting streaking, trends which generally hold for the mantle and crown. He noted that the malar streak tended to be black rather than brown, a trend that was confirmed on various specimens (AMNH, MCZ, SDNHM). But, after comparing birds from the Prairie Provinces of Canada to birds from eastern Ontario, he also noted that 'eastern birds of this race are slightly different from the western, and are not quite typical . . . with less contrast between the dorsal stripes and the general colour' Todd (1963:712). The pattern of variation is evidently clinal (Bull, 1974:600). In colour and dorsal streaking, specimens from Ontario, although attributed to *M. m. juddi* (Fleming & Snyder, 1939; Todd, 1963), are almost perfectly intermediate between birds from farther west and *M. m. melodia* from farther east (e.g. AMNH 788392, Barrie 16 September 1966). So, too, are specimens from Minnesota (e.g. AMNH 55863, Ft. Snelling 17 October 1890). Moreover, some winter specimens from Texas (e.g. AMNH 405586, Ingram, Kerr County, 27 November 1914) cannot be distinguished from birds from New England (e.g. AMNH 821142, Newfane, Vermont, 14 November 1937). Likewise, some specimens from well within the range of *M. m.* '*juddi*' are indistinguishable from a typical *M. m. melodia*, being redder and paler (e.g. AMNH 84052, Boggy River, Indiana, 18 December 1884). This last specimen is a near-perfect match for the Minnesota specimen cited above. We thus concur that recognition of subspecies through much of eastern North America 'extend[s] the trinomial system to the limits of utility' (Mengel, 1965:511). Curiously, although Mengel (1965:513) saw 'no Kentucky specimen typical of *juddi* as it appears in its most highly developed form on the Great Plains,' he 'somewhat arbitrarily' attributed various specimens from the state to that subspecies. More importantly, he re-identified as *M. m. juddi* three Kentucky specimens (USNM 353304, Trigg County 1 November 1938; USNM 353288, Hopkins County 21 October 1938; USNM 353296, Butler County 11

November 1938) identified as *M. m. euphonia* by Wetmore, *M. m. euphonia*'s describer! This action underscores the extreme similarity between various eastern 'subspecies'.

Lastly, *M. m. beata* (holotype: MCZ 44704; adult ♂; Enterprise, Florida, USA; 17 April 1859; Henry Bryant) is widely considered a synonym of *M. m. juddi* (Wetmore, 1936; American Ornithologists' Union, 1957), and thus of *M. m. melodia*, although Oberholser (1974:1013) championed its validity. In summary, Song Sparrows from the Midwest average blacker dorsal streaking (*M. m.* '*beata*' and *M. m.* '*melanchra*') and birds from the eastern Great Plains average slightly greyer dorsally, with blacker streaking (*M. m.* '*juddi*'), but individual variation is substantial. As a result, birds from throughout the range of *M. m. melodia*, as recognised herein, can match birds from anywhere else in that range; i.e. no populations are separate from others under the 75% rule, in that extreme colouration of one population overlaps the average colouration of others (even at a qualitative level). With the exception of *M. m. atlantica*, all subspecies of the Song Sparrow from eastern North America are best synonymised under that nominate, while recognising some clinal variation in characters.

Incidentally, despite Bailey's (1936) arguments, his '*M. m. alleghanii*' was never a properly named subspecies (it is a *nomen nudum*), which is why the name was never used for the Appalachian population (Hubbard & Banks, 1970). He had referenced the name previously in print (e.g. Bailey, 1925) and catalogued his own specimens under the name, but neither served as a proper type description.

Melospiza melodia atlantica Todd

Melospiza melodia atlantica Todd, 1924, *Auk* 41:147
Melospiza melodia Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:477, part
Melospiza melodia var. *melodia* Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Birds* 2:18, part
Melospiza fasciata Scott, 1876, *Am. Nat.* 10:18, part
Melospiza cinerea melodia Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):354, part
Passerella melodia atlantica Linsdale, 1928, *Condor* 30:349
Melospiza melodia rossignolii Bailey, 1936, *Bailey Mus. Lib. Nat. Hist. Bull.* 11
Zonotrichia melodia atlantica Paynter, 1970, *Check-list Birds World* 13:46

HOLOTYPE: USNM 294442; adult ♂; Smith's Island, Northampton County, Virginia, U.S.A.; 25 May 1898; William Palmer 4979.

DIAGNOSIS: Size of *M. m. melodia* (♂ 21.6–23.2 g, $\bar{x} = 22.2$ g, $n = 3$; ♀ 19.8–21.2 g, $\bar{x} = 20.5$ g, $n = 2$); wing length moderate (♂ 67–73 mm, $\bar{x} = 67.3$ mm, $n = 17$; ♀ 63–71 mm, $\bar{x} = 64.8$ mm, $n = 15$); tail length moderate (♂ 65–73 mm, $\bar{x} = 66.4$ mm, $n = 17$; ♀ 66–72 mm, $\bar{x} = 64.8$ mm, $n = 15$); bill length moderate ($\bar{x} = 9.5$ mm, $n = 25$); bill deep ($\bar{x} = 8.3$ mm, $n = 25$); plumage like *M. m. melodia* but upperparts greyer, mantle feathers edged pale grey (not buff).

RANGE: Migratory. Breeds in salt marshes along the middle Atlantic Coast from Long Island, New York, south to central

North Carolina, including at a few points in Chesapeake Bay (Fig. 1). Birds along Long Island Sound from western Connecticut to Cape Cod are intermediate, but more like *M. m. atlantica* (Fig. 1). Winters coastally from Maryland to Georgia.

REMARKS: Remarkably, the type locality of *M. m. rossignolii* (holotype: USNM 525744; ♀; Hogg [=Hog] Island, Northampton County, Virginia, USA; 22 May 1936; Harold H. Bailey 5562) is along the Atlantic Coast < 25 km north of the type locality of *M. m. atlantica*, essentially making it a synonym the moment it was described. Bailey (1936) apparently based its type description on a comparison of its type specimen with insufficient material (Hubbard & Banks, 1970). Although this subspecies was merged with *M. m. melodia* by various authorities (e.g. Ridgway, 1901; Bull, 1974), we agree with Mengel (1965:511) who, in a footnote, observed that '*M. m. atlantica* is clearly more distinct and more uniform than the other eastern races here discussed', of which he meant *M. m. melodia*, *M. m. euphonia* and *M. m. juddi*.

Melospiza melodia montana Henshaw

Melospiza fasciata montana Henshaw, 1884, *Auk* 1:224

Zonotrichia fasciata (not *Fringilla fasciata* Gmelin) Gambel, 1847, *J. Acad. Nat. Sci. Philadelphia* 1:49, part

Melospiza fasciata Sharpe, 1888, *Cat. Birds Brit. Mus.* 12:701, part

Melospiza melodia (not *Fringilla melodia* Wilson) Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:477, part

Melospiza fallax (not *Zonotrichia fallax* Baird) Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:481, part

Melospiza heermanni (not Baird) Butcher, 1868, *Proc. Acad. Nat. Sci. Philadelphia*, p. 149, part

Melospiza melodia var. *fallax* Coues, 1872, *Key N. Am. Birds*, p. 139, part

Melospiza melodia var. *heermanni* Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Birds* 2:24, part

Melospiza melodia heermanni Ridgway, 1875, *Bull. Essex Inst.* 7:11, part

Melospiza melodia fallax Ridgway, 1875, *Bull. Essex Inst.* 7:19, part

Melospiza fasciata var. *fallax* Ridgway, 1877, *Field For.* 2:198, part

Melospiza fasciata var. *heermanni* Ridgway, 1877, *Ornithol. 40th Parallel*, p. 481, part

Melospiza fasciata fallax Mearns, 1879, *Bull. Nuttall Ornithol. Club* 4:169, part

Melospiza fasciata heermanni American Ornithologists' Union, 1886, *Check-list N. Am. Birds*, no. 581c, part

Melospiza montana Salvin & Godman, 1886, *Biol. Centr.-Am., Aves* 1:387, part

Melospiza melodia montana Oberholser, 1899, *Auk* 16:183

Melospiza cinerea montana Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):358

Melospiza melodia fisherella Oberholser, 1911, *Proc. Biol. Soc. Washington* 24:251

Passerella melodia fisherella Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia fisherella Paynter, 1970, *Check-list Birds World* 13:49

Zonotrichia melodia montana Paynter, 1970, *Check-list Birds World* 13:47

HOLOTYPE: USNM 11222; adult ♂; Fort Bridger, Utah [=Wyoming, Uinta County], U.S.A.; 18 June 1858; Constantin Drexler 650.

DIAGNOSIS: Size of *M. m. melodia* (♂ 15.5–25.5 g, x̄ = 21.3 g, n = 262; ♀ 16.0–26.7 g, x̄ = 20.6 g, n = 162), though wings average longer; wing relatively long (♂ 65.5–74 mm, x̄ = 69.3 mm, n = 43; ♀ 62.5–71 mm, x̄ = 66.2 mm, n = 34); tail relatively long (♂ 63.5–77 mm, x̄ = 69.7 mm, n = 43; ♀ 62.5–73 mm, x̄ = 67.0 mm, n = 33); bill length moderate (8–11.1, x̄ = 9.2 mm, n = 70); bill depth moderate (6.8–8.1, x̄ = 7.2 mm, n = 69); plumage like *M. m. melodia* but upperparts greyish brown, upperpart feathers edged grey (not buff). Also note longer wing and more slender bill.

RANGE: Partly migratory. Breeds throughout the Rocky Mountain and Great Basin regions from southeastern Washington east to north-central Montana south to northern and eastern California east to northern New Mexico. Many individuals are resident, but northernmost birds migrate south to southeastern California and north-central Mexico (eastern Sonora east to, at least, Coahuila).

REMARKS: Neither the year nor the collector was supplied in the original description of the type, but Deignan (1961:666) rectified these omissions. There has been some confusion about this subspecies' range and, consequently, its characters. It is not a synonym of *M. m. fallax* (*contra* Oberholser, 1911) and differs radically from that subspecies in plumage colour. Indeed, it is Oberholser's own *M. m. fisherella* (holotype: USNM 203507; adult ♂; Honey Lake, near Millford [=Milford], Lassen County, California, U.S.A.; 18 June 1906; A. S. Bunnell) that is most similar to *M. m. montana*. Alleged differences between these named forms are slight and inconsistent, with only an apparently weak clinal tendency toward less grey and more red in the western portion of the range.

Alaska/Pacific Northwest Group

Melospiza melodia maxima Gabrielson & Lincoln

Melospiza melodia maxima Gabrielson & Lincoln, 1951, *Condor* 53:251

Melospiza insignis (not of Baird) Dall, 1873, *Proc. Calif. Acad. Sci.* 5:27, part

Melospiza cinerea cinerea Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):377, part

Zonotrichia melodia maxima Paynter, 1970, *Check-list Birds World* 13:49

HOLOTYPE: USNM 230692; adult ♂; Kiska Harbor, Kiska Island, Alaska, USA; 17 June 1911; Alexander Wetmore 518.

DIAGNOSIS: With *M. m. sanaka*, the largest subspecies (size of a *Pipilo* towhee); wing extremely long (♂ 82–87.5 mm,

$\bar{x} = 83.0$ mm, $n = 26$; ♀ 78–85.5 mm, $\bar{x} = 79.2$ mm, $n = 19$); tail extremely long (♂ 78–87 mm, $\bar{x} = 77.6$ mm, $n = 26$; ♀ 71–82 mm, $\bar{x} = 75.3$ mm, $n = 19$); bill extremely long (13.4–15.1 mm, $\bar{x} = 13.7$ mm, $n = 9$); bill deep (7.6–9.0 mm, $\bar{x} = 7.8$ mm, $n = 39$); underparts grey; throat flecked; ventral streaks brown, long, and diffuse, with little fringe and contrast weakly with ground colour; upperparts medium brownish grey, fringed slightly paler; dorsal streaks brown, diffuse; supercilia grey; malar brown.

RANGE: Resident. Alaska in the western Aleutian Islands from Attu Island to Atka Island.

REMARKS: Recognition of this subspecies and various others from Alaska follows Gabrielson and Lincoln (1951) and Gibson and Kessel (1997); we examined minimal specimen material for this study, although we have determined that *M. m. maxima* is genetically distinct (Pruett *et al.*, 2008a, b).

Melospiza melodia sanaka McGregor

Melospiza sanaka McGregor, 1901, *Condor* 3:8

Fringilla cinerea Gmelin, 1788, *Syst. Nat.* 1(2):922 [preoccupied; *Auk* 25:380, 1908]

?*Emberiza unalaschensis* (?not of Gmelin) Brandt, 1836, *Descr. Anim. Ross.*, pl. 2, fig. 4

Zonotrichia cinerea Gray, 1849, *Gen. Birds* 2:373

Melospiza cinerea Finsch, 1872, *Abh. Nat. Ver. Bremen* 3:20

Melospiza insignis (not of Baird) Dall, 1873, *Proc. Calif. Acad. Sci.* 5:27, part

Melospiza melodia var. *insignis* Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Bird* 2:30, part

Melospiza melodia cinerea Grinnell, 1901, *Condor* 3:20

Melospiza cinerea cinerea Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):377

Melospiza melodia semidiensis Brooks, 1919, *Proc. New England Zool. Club* 7:27

Melospiza melodia sanaka American Ornithologists' Union, 1908, *Auk* 25:379

Passerella melodia sanaka Linsdale, 1928, *Condor* 30:350

Passerella melodia semidiensis Linsdale, 1928, *Condor* 30:350

Melospiza melodia amaka Gabrielson & Lincoln, 1951, *Condor* 53:253

Zonotrichia melodia sanaka Paynter, 1970, *Check-list Birds World* 13:49

Zonotrichia melodia amaka Paynter, 1970, *Check-list Birds World* 13:49

HOLOTYPE: AMNH 405699; sex unknown [♂ on tag]; Sanak Island, Alaska, USA; 13 June 1894; C. Littlejohn.

DIAGNOSIS: Size of *M. m. maxima* (♂ 44.5–52.7 g, $\bar{x} = 47.8$ g, $n = 9$; ♀ 41.5–44.1 g, $\bar{x} = 42.7$ g, $n = 4$); wing extremely long (♂ 82–86.5 mm, $\bar{x} = 83.6$ mm, $n = 33$; ♀ 77–84 mm, $\bar{x} = 80.2$ mm, $n = 18$); tail extremely long (♂ 76–86 mm, $\bar{x} = 80.8$ mm, $n = 33$; ♀ 75–81 mm, $\bar{x} = 77.3$ mm, $n = 18$); bill long (10.9–14.0 mm, $\bar{x} = 12.8$ mm, $n = 28$); bill deep (7.6–9.1 mm, $\bar{x} = 7.8$ mm, $n = 44$); plumage like *M. m. maxima* but greyer overall. Also note shorter bill (*M. m. sanaka* generally < 13.0 mm, *M. m. maxima* generally > 13.5 mm).

Birds on the Semidi Islands average slightly greyer. A weakly defined subspecies.

RANGE: Resident. Alaska from the eastern Aleutian Islands (Seguam to Unimak, including Amak), the Alaska Peninsula east to Stepovak Bay, and islands south of the peninsula (Sanak Island to Semidi Island).

REMARKS: Birds from the Semidi Islands, named *M. m. semidiensis* by Brooks (holotype: MCZ 67069; adult ♂; North Semidi Island, Semidi Islands, Alaska, USA; 19 April 1913; Winthrop Sprague Brooks 33), average slightly greyer than *M. m. sanaka* but are basically inseparable from that subspecies (Gabrielson & Lincoln 1951). *Melospiza m. amaka* Gabrielson & Lincoln, 1951 (holotype: USNM 298522; adult ♂; Amak Island, Alaska, USA; 13 July 1925; Olaus J. Murie 3103) was described as being like *M. m. sanaka* but browner; however, there is little specimen material, and what exists indicates that it cannot be distinguished from *M. m. sanaka* (Gibson & Kessel, 1997; Pruett *et al.*, 2004).

Melospiza melodia insignis Baird

Melospiza insignis Baird, 1869, *Trans. Chicago Acad. Sci.* 1:319, pl. 29, fig. 2

Zonotrichia insignis Gray, 1870, *Hand-list* 2:94

Melospiza melodia var. *insignis* Coues, 1872, *Key N. Am. Birds*, p. 140

Melospiza cinerea (not *Fringilla cinerea* Gmelin) Ridgway, 1880, *Proc. U. S. Natl. Mus.* 3:3

Melospiza melodia insignis Goode, 1883, *Bull. U. S. Natl. Mus.* 25:328

Melospiza fasciata rufina (not *Passerella rufina* Bonaparte) Nelson, 1887, *Rep. Nat. Hist. Coll. Alaska*, p. 192, part

Melospiza cinerea insignis Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):376

Passerella melodia insignis Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia insignis Paynter, 1970, *Check-list Birds World* 13:49

HOLOTYPE: USNM 52476; adult, ♀? Kadiak [=Kodiak Island], Alaska, USA; 27 May 1868; Ferdinand Bischoff. Baird selected this specimen as the lectotype, although the entire series of six skins collected on Kodiak Island by Bischoff in 1868 must be considered cotypes (Deignan, 1961:663), the other being USNM 52477 (adult ♂, 24 May), USNM 52478 (lost), USNM 52479 (adult ♂, 10 June), USNM 54536 (adult, 25 September), and USNM 54537 (adult, 12 August).

DIAGNOSIS: Slightly smaller than *M. m. maxima*; wing extremely long (78.5–86.5 mm, $\bar{x} = 82.5$ mm, $n = 28$; ♀ 76–80 mm, $\bar{x} = 78.5$ mm, $n = 3$); tail extremely long (♂ 73.5–83 mm, $\bar{x} = 80.3$ mm, $n = 8$; ♀ 72.5–79 mm, $\bar{x} = 75.2$ mm, $n = 3$); bill long (11.6–13.1 mm, $\bar{x} = 12.3$ mm, $n = 11$); bill depth moderate (6.9–8.1 mm, $\bar{x} = 7.5$ mm, $n = 29$); plumage like *M. m. sanaka* but darker overall.

RANGE: Mainly resident. Alaska on the Kodiak Islands (Barren Islands to Sitkalidak Island) and Alaska Peninsula at Kukak and Katmai; some migrate south in winter along Alaskan coast.

Melospiza melodia kenaiensis Ridgway

Melospiza melodia kenaiensis Ridgway, 1900, *Auk* 17:29

?*Melospiza insignis* Finsch, 1872, *Abh. Nat. Ver. Bremen* 3:44, part

Melospiza fasciata rufina Bean, 1882, *Proc. U. S. Natl. Mus.* 5:152, part

Melospiza cinerea (not *Fringilla cinerea* Gmelin) Turner, 1886, *Contr. Nat. Hist. Alaska*, p. 174, part

Melospiza cinerea kenaiensis Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):375

Passerella melodia kenaiensis Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia kenaiensis Paynter, 1970, *Check-list Birds World* 13:49

HOLOTYPE: USNM 131730; adult ♂; Port Graham, Cook's Inlet, Alaska, USA; 9 April 1892; Charles H. Townsend.

DIAGNOSIS: Much smaller than *M. m. maxima* and *M. m. sanaka*, averages smaller than *M. m. insignis* (♂ 28.6–31.4 g, x̄ = 29.7 g, *n* = 5; ♀ 29.6 g, *n* = 1); wing long (♂ 76.5–80 mm, x̄ = 78.2 mm, *n* = 2; ♀ 78.2 mm, *n* = 1); tail long (72–73 mm, x̄ = 72.5 mm, *n* = 2;. 75.4 mm, *n* = 1); bill long (10.5–11.3 mm, x̄ = 10.9 mm, *n* = 3); bill depth moderate (7.1–7.6 mm, x̄ = 7.4 mm, *n* = 2); underparts grey; throat flecked; ventral streaks sooty, long, and diffuse, with little fringe, contrast weakly with ground colour; upperparts dark dusky, fringed slightly paler; dorsal streaks sooty, diffuse; supercilia grey; malar sooty. Darker and browner (less grey) than *M. m. insignis*.

RANGE: Mainly resident. Alaska on Pacific coast of Kenai Peninsula and islands in Prince William Sound; some winter coastally south to British Columbia.

Melospiza melodia caurina Ridgway

Melospiza fasciata caurina Ridgway, 1899, *Auk* 16:36

Melospiza rufina Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:480, part

Melospiza fasciata rufina (not *Passerella rufina* Bonaparte) Nelson, 1887, *Rep. Nat. Hist. Coll. Alaska*, p. 192, part

Melospiza melodia caurina Oberholser, 1899, *Auk* 16:183

Melospiza cinerea caurina Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):375

Passerella melodia caurina Linsdale, 1928, *Condor* 30:349

Zonotrichia melodia caurina Paynter, 1970, *Check-list Birds World* 13:50

HOLOTYPE: USNM 138367; adult ♂; Yakutat, Alaska, U.S.A.; 6 July 1895; Clark P. Streator.

DIAGNOSIS: Smaller than *M. m. kenaiensis* (♂ 24.8–32.2 g, x̄ = 28.7 g, *n* = 9; ♀ 25.5–30.0 g, x̄ = 27.0 g, *n* = 6); wing long (♂ 69–80 mm, x̄ = 72.6 mm, *n* = 23; ♀ 67–71 mm, x̄ = 68.8 mm, *n* = 5); tail long (♂ 63.5–73 mm, x̄ = 68.0 mm, *n* = 23; ♀ 62.5–67 mm, x̄ = 64.8 mm, *n* = 5); bill length moderate (9.1–11.3 mm, x̄ = 10.0 mm, *n* = 11); bill depth moderate (6.2–7.6 mm, x̄ = 6.8 mm, *n* = 11); underparts grey; throat flecked; ventral streaks sooty, long, and diffuse, with little fringe, contrast weakly with ground colour; upperparts medium dusky, fringed slightly paler; dorsal streaks sooty, diffuse; supercilia grey; malar sooty. Distinguished from *M. m. kenaiensis* by smaller size, paler colouration overall.

RANGE: Partly migratory. Resident on coast of northern Gulf of Alaska; many winter in Pacific Northwest, with records south to northwestern California.

Melospiza melodia rufina (Bonaparte)

Passerella rufina Bonaparte, 1850, *Consp. Generum Avium* 1:477, sig. 60

Melospiza rufina Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:480

Zonotrichia rufina Gray, 1870, *Hand-list* 2:94

Melospiza melodia var. *rufina* Coues, 1872, *Key N. Am. Birds*, p. 139

Melospiza guttata (not *Fringilla guttata* Nuttall) Finsch, 1872, *Abh. Nat. Ver. Bremen* 3:41

Melospiza meloda [*sic*] var. *rufina* Henshaw, 1879, *Bull. Nuttall Ornithol. Club* 4:159

Melospiza fasciata rufina Ridgway, 1880, *Proc. U. S. Natl. Mus.* 3:3

Melospiza melodia rufina Finsch, 1883, *J. Ornithol.* 24:271

Melospiza cinerea rufina Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):373

Passerella melodia rufina Linsdale, 1928, *Condor* 30:350

Melospiza melodia kwaisa Cumming, 1933, *Murrelet* 14:78

Zonotrichia melodia rufina Paynter, 1970, *Check-list Birds World* 13:48

HOLOTYPE: MNHN lost; sex?; Sitka, Alaska, USA; date?; collector?. Virtually all of the type specimens of taxa described by Charles Bonaparte were deposited at the National Museum of France, but the type of *M. m. rufina* does not appear to be there and 'has probably disappeared' (E. Pasquet *in litt.*).

DIAGNOSIS: Averages smaller than *M. m. caurina*; wing long (66–77 mm, x̄ = 71.6 mm, *n* = 42; ♀ 64–70.5 mm, x̄ = 67.2 mm, *n* = 18); tail long (♂ 60–76 mm, x̄ = 68.6 mm, *n* = 42; ♀ 58–70.5 mm, x̄ = 63.6 mm, *n* = 29); bill length moderate (9.1–11.9 mm, x̄ = 10.4 mm, *n* = 26); bill depth moderate (6.2–7.8 mm, x̄ = 6.9 mm, *n* = 27); underparts grey; throat flecked; ventral streaks sooty brown, long, and diffuse, with little fringe, contrast weakly with ground colour; upperparts dark reddish brown, fringed slightly paler; dorsal streaks sooty brown, diffuse; supercilia grey; malar sooty brown. Distinguished from *M. m. caurina* by smaller size, darker, redder (less grey) colouration overall.

RANGE: Partly migratory. Resident on outer islands of Alexander Archipelago, southeastern Alaska, and on Queen Charlotte Islands, British Columbia; some birds move south in winter.

REMARKS: *M. m. kwaisa* (holotype; RBCM 7319; ♂; Langara Island, Canada; 7 July 1930; R. A. Cumming 2141) of the Queen Charlotte Islands has long been regarded as a synonym (Hellmayr, 1938).

Melospiza melodia morphna Oberholser

Melospiza melodia morphna Oberholser, 1899, *Auk* 16:183

Fringilla cinerea (not Gmelin) Audubon, 1839, *Ornithol. Biogr.* 5:22, pl. 390, fig. 1

Passerella cinerea Bonaparte, 1838, *Geogr. Comp. List*, p. 31

Fringilla guttata Nuttall, 1840, *Man. Ornithol.* 1:581, 2nd edn. [=*Melospiza fasciata guttata*], debarred because *Fringilla guttata* Vieillot, 1817, *Nouv. Dict. d'Hist. Nat.* 12:233 was preoccupied

Zonotrichia guttata Gambel, 1847, *J. Acad. Nat. Sci. Philadelphia*, ser. 2, 1:50, part

Zonotrichia cinerea Heermann, 1852, *J. Acad. Nat. Sci. Philadelphia*, ser. 2, 2:266, part

Melospiza rufina (not *Emberiza rufina* Brandt) Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:480, part

Melospiza fallax (not of Baird) Sclater, 1859, *Proc. Zool. Soc. London*, p. 235

Melospiza melodia var. *guttata* Coues, 1872, *Key N. Am. Birds*, p. 139

Melospiza guttata Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Birds* 2, pl. 27, fig. 12

Melospiza fasciata var. *guttata* Ridgway, 1878, *Bull. Nuttall Ornithol. Club* 3:66, part

Melospiza meloida guttata Henshaw, 1879, *Ornithol. Rep. Wheeler's Surv.*, p. 299, part

Melospiza meloda [*sic*] var. *guttata* Henshaw, 1879, *Bull. Nuttall Ornithol. Club* 4:158

Melospiza fasciata guttata Ridgway, 1880, *Proc. U. S. Natl. Mus.* 3:180

Melospiza fasciata rufina Fisher, 1893, *N. Am. Fauna* 7:100, part

Melospiza cinerea morphna Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):372

Melospiza cinerea phaea Fisher, 1902, *Condor* 4:36, part

Melospiza melodia phaea Grinnell, 1915, *Pac. Coast Avifauna* 11:123

Passerella melodia morphna Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia morphna Paynter, 1970, *Check-list Birds World* 13:48

HOLOTYPE: USNM 1860; adult ♀; no locality provided [=Fort Vancouver, Clark County, Washington, USA]; 18 January 1836; John K. Townsend 59. The exact type is disputable, although Baird annotated the old tag of USNM 1860 with '*Fringilla cinerea* of Audubon. Type of his description and figure.' An adult of unknown sex, taken by Townsend on an unknown date at the type locality (USNM 1942), is probably a cotype of *F. cinerea* but 'presumably has no connection' with the names *F. guttata* Nuttall or *M. m. morphna* (Deignan, 1961:664). A cotype of *F. guttata* Nuttall [=*M. m. morphna*] is a . that Townsend collected in similarly mysterious circumstances; it is now ANSP 24028 (Stone, 1899:19).

DIAGNOSIS: Smaller than *M. m. rufina* (♂ 20.3–27.7 g, x̄ = 23.6 g, *n* = 27; ♀ 16.5–29.9 g, x̄ = 22.1 g, *n* = 30); wing length moderate (♂ 61.5–71.5 mm, x̄ = 67.1 mm, *n* = 96; ♀ 62–69 mm, x̄ = 65.0 mm, *n* = 26); tail length moderate (♂ 58–73 mm, x̄ = 65.2 mm, *n* = 96; ♀ 57.5–68 mm, x̄ = 63.0 mm, *n* = 26); bill length moderate (8.1–10.9 mm, x̄ = 9.4 mm, *n* = 89); bill shallow (6.0–7.0 mm, x̄ = 6.4 mm, *n* = 56); underparts grey; throat flecked; ventral streaks brown, long, and diffuse, with little fringe, contrast weakly with ground colour; upperparts dark reddish brown, fringed slightly paler; dorsal streaks brown, diffuse; supercilia grey; malar brown. Distinguished from *M. m. rufina* by smaller size, browner (less sooty) colouration overall.

RANGE: Mainly resident. Central and southwestern British Columbia southward west of the Cascades to northwestern Oregon. Slight movement southward in winter, to northwestern California.

REMARKS: At least two different species names, *Fringilla cinerea* and *F. guttata*, were applied to this taxon before it was learned that both were preoccupied by Old World taxa. The name *M. m. morphna* was not applied until 1899. This confusion led to questions about designation of the type. Subspecific limits between *M. m. morphna*, *M. m. inexspectata*, *M. m. phaea* and *M. m. rufina* have been questioned, with Swarth (1912:60, 1922:255) merging all into *M. m. rufina*. Swarth (1923) subsequently recognised *M. m. morphna* and *M. m. rufina*, but merged *M. m. inexspectata* into the former and suggested that *M. m. merrilli* was perhaps not worthy of recognition. Most important, he properly noted that *M. m. phaea* (holotype; MVZ 35954; adult ♂; Gardiner, mouth of Umpqua River, Oregon, USA; 1 December 1901; Edmund Heller) was nothing more than a name for a narrow hybrid zone between *M. m. morphna* and *M. m. cleonensis*. Its type is nearer the former.

Melospiza melodia merrilli Brewster

Melospiza fasciata merrilli Brewster, 1896, *Auk* 13:46

Melospiza melodia var. *guttata* Ridgway, 1875, *Bull. Essex Inst.* 7:37, part

Melospiza fasciata var. *guttata* (not *Fringilla guttata* Nuttall) Ridgway, 1877, *Ornithol. 40th Parallel*, p. 482, part

Melospiza melodia var. *rufina* (not *Emberiza rufina* Brandt) Bendire, 1877, *Proc. Boston Soc. Nat. Hist.* 25:119, part

Melospiza fasciata guttata Brewster, 1882, *Bull. Nuttall Ornithol. Club* 7:229, part

Melospiza fasciata mexicana (not *M. melodia* var. *mexicana* Ridgway) Allen, 1893, *Bull. Am. Mus. Nat. Hist.* 5:39

Melospiza fasciata ingersolli McGregor, 1899, *Bull. Cooper Ornithol. Club* 1:35

Melospiza melodia ingersolli McGregor, 1899, *Bull. Cooper Ornithol. Club* 1:88

Melospiza cinerea merrilli Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):361

Melospiza melodia merrilli American Ornithologists' Union, 1908, *Auk* 25:379

Melospiza melodia inexspectata Riley, 1911, *Proc. Biol. Soc. Washington* 24:234

Melospiza melodia inexpectata [*sic*] Stone, 1912, *Auk* 29:117

Passerella melodia inexspectata Linsdale, 1928, *Condor* 30:350

Passerella melodia merrilli Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia inexspectata Paynter, 1970, *Check-list Birds World* 13:48

Zonotrichia melodia merrilli Paynter, 1970, *Check-list Birds World* 13:48

HOLOTYPE: MCZ 246026; adult ♂; Fort Sherman, Idaho, USA; 6 March 1895; J. C. Merrill.

DIAGNOSIS: Size of *M. m. morphna* (♂ 17.8–30.5 g, x̄ = 23.4 g, n = 59; ♀ 17.7–28.0 g, x̄ = 21.8 g, n = 41), though tail averages longer; wing length moderate (♂ 63–72 mm, x̄ = 67.4 mm, n = 36; ♀ 61–68.5 mm, x̄ = 66.1 mm, n = 30); tail length moderate (♂ 63–74 mm, x̄ = 68.2 mm, n = 36;. 60–71 mm, x̄ = 64.8 mm, n = 30); bill short (8.0–9.3 mm, x̄ = 8.5 mm, n = 43); bill shallow (5.5–6.8 mm, x̄ = 6.2 mm, n = 43); underparts grey; throat flecked; ventral streaks dark brown and somewhat diffuse, with little fringe, contrast moderately with ground colour; upperparts dark ashy brown, with feathers moderately edged grey; dorsal streaks dark brown, relatively crisp; supercilia grey; malar brown. Distinguished from *M. m. morphna* by ashier (less reddish) colouration overall and darker, more contrasting streaking. The plumage of *M. m. merrilli* is intermediate between *M. m. morphna* and *M. m. montana*, although its characters are fairly constant (see below). There is a slight cline toward greyer birds in the northern part of the range.

RANGE: Partly migratory. Resident in eastern British Columbia south through southeastern Washington east to northwestern Montana; some winter farther south, with records to southeastern California in the Anza-Borrego Desert and along the lower Colorado River (Patten *et al*., 2003).

REMARKS: Ridgway (1901:361) 'hesitated to recognise' *M. m. merrilli* because the name 'covers a series of 'intergrades' between *M. c.* [=*m.*] *montana* and *M. c.* [=*m.*] *morphna*.' The intermediacy of *M. m. merrilli*, however, is consistent and definable. *M. m. ingersolli* (holotype: AMNH 405733; adult ♂; Battle Creek, Tehama County, California, U.S.A.; 19 October 1898; Richard C. McGregor 2222) is a synonym of *M. m. merrilli* (Ridgway, 1901:362; Grinnell, 1932). It was collected near the western edge of that subspecies' range.

Swarth (1923) merged *M. m. inexspectata* (holotype: USNM 222829; adult ♀; Fraser River, 3 miles e. of Moose Lake, Mount Robson National Park, British Columbia, Canada; 21 August 1911; J. Harvey Riley 2268) into *M. m. morphna*, from which it differs in being larger, greyer, and having the dorsal and ventral streaks blacker. Munro and Cowan (1947:236) noted the dissimilarity between it and *M. m. morphna*, and correctly drew attention to the similarity between *M. m. inexspectata* and *M. m. merrilli*, yet they failed to note that no characters of *M. m. inexspectata* differ consistently from those of *M. m. merrilli*. The misspelling ('inexpectata') of the subspecific epithet of *M. m. inexspectata*, begun by Witmer Stone shortly after the type description, was continued by Gabrielson and Lincoln (1951), American Ornithologists' Union (1957), Rising (1996), Fry and Zink (1998) and others.

Birds found along the coastal mainland of southeastern Alaska and inner islands of the Alexander Archipelago were treated as *M. m. inexspectata* by Gibson and Kessel (1997). These birds differ genetically from *M. m. morphna* (Pruett *et al*., 2008a; Wilson *et al*., 2008) and differ morphologically from *M. m. rufina*. More work is needed on this population.

Melospiza melodia cleonensis McGregor

Melospiza melodia cleonensis McGregor, 1899, *Bull. Cooper Ornithol. Club* 1:87

Melospiza cinerea cleonensis Ridgway, 1901, *Bull. U. S. Natl. Mus*. 50(1):371

Melospiza cinerea phaea Fisher, 1902, *Condor* 4:36, part

Melospiza melodia phaea Grinnell, 1915, *Pac. Coast Avifauna* 11:123, part

Passerella melodia cleonensis Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia cleonensis Paynter, 1970, *Check-list Birds World* 13:50

HOLOTYPE: AMNH 39223; ♀; Westport, Mendocino County, California, USA; 28 May 1889; Richard C. McGregor 288.

DIAGNOSIS: Smaller than *M. m. morphna* (♂ 18.1–23.5 g, x̄ = 21.0 g, n = 17; ♀ 17.2–21.4 g, x̄ = 19.0 g, n = 19); wing short (♂ 58.5–68 mm, x̄ = 62.3 mm, n = 38; ♀ 54.5–65 mm, x̄ = 60.0 mm, n = 23); tail short (♂ 56–65 mm, x̄ = 60.4 mm, n = 38; ♀ 52.5–63 mm, x̄ = 58.4 mm, n = 23); bill short (7.7–9.2 mm, x̄ = 8.6 mm, n = 24); bill somewhat shallow (5.6–7.4 mm, x̄ = 6.6 mm, n = 22); underparts greyish; throat flecked; ventral streaks blackish brown and relatively crisp, with little fringe, contrast moderately with ground colour; upperparts dark reddish brown, with feathers thinly edged grey; dorsal streaks blackish brown, somewhat crisp; supercilia greyish; malar fuscous. Distinguished from *M. m. morphna* by smaller size and crisper, darker streaking, from *M. m. merrilli* by smaller size and redder colouration overall. Generally intermediate between *M. m. morphna* and *M. m. gouldii*.

RANGE: Resident. West of the Cascades in southwestern Oregon and northwestern California.

REMARKS: Regarding *M. m. phaea*, see remarks under *M. m. morphna*.

California Group

Melospiza melodia gouldii Baird

Melospiza gouldii Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:479

Melospiza melodia santaecrucis Grinnell, 1901, *Condor* 3:92

Melospiza cinerea samuelis Ridgway, 1901, *Bull. U. S. Natl. Mus*. 50(1):369, part

Melospiza melodia gouldii Grinnell, 1909, *Univ. Calif. Publ. Zool*. 5:267

Passerella melodia gouldii Linsdale, 1928, *Condor* 30:350

Passerella melodia santaecrucis Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia gouldii Paynter, 1970, *Check-list Birds World* 13:50

HOLOTYPE: USNM 8053; sex?, probably ♀ (Grinnell, 1909); California [=5 miles w. of Inverness, toward Point Reyes, Marin County,] USA; prior to 27 February 1858 (Grinnell, 1932; Deignan, 1961); unknown (donated to USNM by John Gould).

DIAGNOSIS: Size similar to *M. m. cleonensis* (♂ 15.6–24.0 g, x̄ = 19.8 g, *n* = 331; ♀ 15.1–25.0 g, x̄ = 18.3 g, *n* = 182), though tail much longer; wing short (♂ 58–64 mm, x̄ = 61.2 mm, *n* = 99;. 55.5–59 mm, x̄ = 58.4 mm, *n* = 12); tail length moderate (♂ 63.5–69 mm, x̄ = 67.4 mm, *n* = 18; ♀ 56–67 mm, x̄ = 64.7 mm, *n* = 12); bill short (7.8–9.4 mm, x̄ = 8.6 mm, *n* = 267; Marshall, 1948); bill somewhat shallow (6.1–7.1 mm, x̄ = 6.6 mm, *n* = 260; Marshall, 1948); underparts white; throat flecked; ventral streaks black and crisp, fringe olive-yellow and contrasting sharply with ground colour; upperparts medium reddish brown, with an olive cast; dorsal streaks broad, black, crisp; supercilia ashy; malar blackish. Distinguished from *M. m. cleonensis* by crisper, blacker streaking, paler and more olivaceous overall colouration, and longer tail. Note that the streaks of *M. m. gouldii* lack a rufous or ruddy halo, unlike those of *M. m. heermanni*, *M. m. melodia* and *M. m. montana*. Birds between San Francisco Bay and Monterey Bay are somewhat intermediate toward *M. m. heermanni*.

RANGE: Resident. Central coastal California, excepting San Francisco Bay. Recorded south of this range on Santa Cruz Island (SDNHM).

REMARKS: Birds ranging from the north end of Monterey Bay to south of *M. m. pusillula* on the San Francisco Bay were named *M. m. santaecrucis* (holotype: MVZ 35969; adult ♂; San Francisquito Creek, near Palo Alto, Santa Clara County, California, USA; 2 June 1900; Joseph Grinnell 4292). Grinnell (1932), Grinnell and Miller (1944), and Marshall and Dedrick (1994) subsequently recognised this subspecies. It averages slightly browner above than *M. m. gouldii*, but it is not consistently diagnosable from that subspecies. Its mantle colour matches *M. m. heermanni*, but it is finely streaked like *M. m. gouldii*. It thus appears that *M. m. 'santaecrucis'* is a name for a hybrid zone between *M. m. gouldii* and *M. m. heermanni*. Because it shares more similarities with *M. m. gouldii*, we merge it with that taxon. On the basis of the range ascribed to *M. m. gouldii*, the American Ornithologists' Union (1957) implicitly merged *M. m. santaecrucis* in the same manner.

Melospiza melodia samuelis (Baird)

Ammodramus samuelis Baird, 1858, *Proc. Boston Soc. Nat. Hist.* 6:379

Melospiza gouldii Baird, 1858, *Rep. Pac. R. R. Surv*. 9:479, part

Zonotrichia gouldii Gray, 1870, *Hand-list* 2:64

Melospiza melodia var. *gouldii* Coues, 1872, *Key N. Am. Birds*, p. 139

Melospiza melodia var. *samuelis* Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Birds* 2:26

Melospiza samuelis Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Birds* 2, pl. 27, fig. 7

Melospiza meloda [sic] var. *samuelis* Henshaw, 1879, *Bull. Nuttall Ornithol. Club* 4:157

Melospiza fasciata samuelis Ridgway, 1880, *Proc. U. S. Natl. Mus*. 3:3

Melospiza melodia samuelis Goode, 1883, *Bull. U. S. Natl. Mus*. 25:328

Melospiza melodia gouldii McGregor, 1899, *Bull. Cooper Ornithol. Club* 1:87

Melospiza cinerea samuelis Ridgway, 1901, *Bull. U. S. Natl. Mus*. 50(1):369

Passerella melodia samuelis Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia samuelis Paynter, 1970, *Check-list Birds World* 13:50

HOLOTYPE: USNM 5553; adult ♂; Petaluma, Sonoma County, California, USA; 9 May 1856; Emanuel Samuels 775. Baird designated USNM 7098, another adult ♂ taken by Samuels (orig. no. 773) from the same location and date (not 9 August) as the type, but Charles W. Richmond declared USNM 5553 the type, a move followed by Grinnell (1932). The two specimens must be considered cotypes (Deignan, 1961:664).

DIAGNOSIS: Smaller than *M. m. gouldii* (♂ 16.4–21.6 g, x̄ = 18.9 g, *n* = 132; ♀ 14.8–19.4 g, x̄ = 17.7 g, *n* = 83); wing short (55–64 mm, x̄ = 59.6 mm, *n* = 55; ♀ 56–59 mm, x̄ = 57.8 mm, *n* = 13); tail short (♂ 53–62 mm, x̄ = 59.9 mm, *n* = 25; ♀ 53–60 mm, x̄ = 58.3 mm, *n* = 13); bill somewhat short (8.3–9.8 mm, x̄ = 9.0 mm, *n* = 102; Marshall, 1948); bill depth moderate (6.3–7.3 mm, x̄ = 6.8 mm, *n* = 86; Marshall, 1948); underparts white; throat flecked; ventral streaks fuscous and crisp, fringed brown and contrasting sharply with ground colour; upperparts medium dusky olive; dorsal streaks medium width, fuscous, crisp; supercilia ashy; malar fuscous.

RANGE: Resident. California in salt marshes skirting northern San Francisco Bay and in San Pablo Bay.

REMARKS: Even though their distributions are small and highly localised, the morphology of *M. m. samuelis* and the other two subspecies endemic to San Francisco Bay (*M. m. maxillaris*, *M. m. pusillula*) are remarkably distinct (Marshall, 1948; Marshall & Dedrick, 1994; Chan & Arcese, 2002, 2003).

Melospiza melodia maxillaris Grinnell

Melospiza melodia maxillaris Grinnell, 1909, *Univ. Calif. Publ. Zool.* 5:265

Passerella melodia maxillaris Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia maxillaris Paynter, 1970, *Check-list Birds World* 13:50

HOLOTYPE: MVZ 5476; adult ♂; tule marsh [within 2 miles] w. of Suisun, Solano County, California, USA; 1 January 1909; L. Kellogg.

DIAGNOSIS: Size of *M. m. gouldii* (♂ 17.3–22.8 g, x̄ = 20.3 g, *n* = 73; ♀ 17.0–22.3 g, x̄ = 18.8 g, *n* = 43), though with bill longer and deeper, tail shorter; wing short (59–66 mm, x̄ = 62.5 mm, *n* = 36; Marshall, 1948); tail short (62 mm, *n* = 1); bill length moderate (8.6–10.1 mm, x̄ = 9.4 mm, *n* = 178; Marshall, 1948); bill deep (7.2–8.4 mm, x̄ = 7.8 mm, *n* = 171; Marshall, 1948); underparts white; throat flecked;

ventral streaks fuscous and crisp, fringed brown and contrasting sharply with ground colour; upperparts dark, rich brown; dorsal streaks crisp, fuscous edged with buff-grey; supercilia ashy; malar reddish fuscous. Also note the distinctive swollen base of the bill, recalling McCown's Longspur (*Calcarius mccownii*).

RANGE: Resident. California in brackish marshes of Suisun Bay.

REMARKS: Specimens to the east of Suisun Bay, particularly in the northern Sacramento Valley (*M. m. 'mailliardi'*, in part), provide evidence of introgression in having the base of the bill slightly more swollen than on typical *M. m. heermanni*, although the subspecies is somewhat distinct genetically (Pruett *et al.*, 2008b).

Melospiza melodia pusillula Ridgway

Melospiza fasciata pusillula Ridgway, 1899, *Auk* 16:35
Melospiza fasciata samuelis (not *Ammodramus samuelis* Baird) Coues, 1884, *Key N. Am. Birds*, 2nd edn., part
Melospiza melodia pusillula Oberholser, 1899, *Auk* 16:183
Melospiza cinerea pusillula Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):370
Passerella melodia pusillula Linsdale, 1928, *Condor* 30:350
Zonotrichia melodia pusillula Paynter, 1970, *Check-list Birds World* 13:51

HOLOTYPE: USNM 105324; adult ♂; 'salt marsh,' Alameda County, California, USA; 18 April 1885; W. Otto Emerson 552.

DIAGNOSIS: Size of *M. m. samuelis* (♂ 15.3–20.6 g, x̄ = 18.7 g, *n* = 66; ♀ 15.3–18.5 g, x̄ = 16.9 g, *n* = 49), but smallest subspecies in overall dimensions; wing extremely short (♂ 54.5–63 mm, x̄ = 58.7 mm, *n* = 81; ♀ 53.5–61.5 mm, x̄ = 55.9 mm, *n* = 26); tail short (♂ 50–63 mm, x̄ = 59.8 mm, *n* = 32; ♀ 52–61 mm, x̄ = 57.4 mm, *n* = 26); bill short (7.6–9.0 mm, x̄ = 8.3 mm, *n* = 206; Marshall, 1948); bill shallow (5.5–6.8 mm, x̄ = 6.2 mm, *n* = 226; Marshall, 1948); underparts yellowish; throat flecked; ventral streaks fuscous and crisp, fringed brown and contrasting sharply with ground colour; upperparts medium yellowish grey; dorsal streaks fuscous, crisp; supercilia yellowish; malar brown.

RANGE: Resident. California in salt marshes skirting southern San Francisco Bay.

REMARKS: Grinnell (1932) asserted that the type was collected 'doubtless not far from, and west of, Hayward', Alameda County. In addition to being the only Song Sparrow with yellow underparts, *M. m. pusillula* is also genetically distinct (Chan & Arcese, 2002, 2003; Pruett *et al.*, 2008a, b; Wilson *et al.*, 2008).

Melospiza melodia heermanni Baird

Melospiza heermanni Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:478
?*Zonotrichia fasciata* (not *Fringilla fasciata* Gmelin) Gambel, 1847, *J. Acad. Nat. Sci. Philadelphia*, ser. 2, 1:49

?*Zonotrichia guttata* (not *Fringilla guttata* Nuttall) Heermann, 1859, *Rep. Expl. Surv. Pac. R. R.* 10:47, part
Zonotrichia heermanni Gray, 1870, *Hand-list* 2:94
Melospiza melodia var. *heermannii* [*sic*] Coues, 1872, *Key N. Am. Birds*, p. 139
Melospiza melodia var. *heermanni* Coues, 1873, *Check List*, no. 169d
Melospiza melodia heermanni Ridgway, 1874, *Bull. Essex Inst.* (Oct.), p. 171
Melospiza meloda [*sic*] var. *heermanni* Henshaw, 1879, *Bull. Nuttall Ornithol. Club* 4:157
Melospiza fasciata var. *heermanni* Ridgway, 1877, *Ornithol. 40th Parallel*, p. 481
Melospiza fasciata heermanni Ridgway, 1880, *Proc. U. S. Natl. Mus.* 3:3
Melospiza fasciata samuelis (not *Ammodramus samuelis* Baird) Belding, 1883, *Proc. U. S. Natl. Mus.* 5:528, part
?*Melospiza fasciata guttata* (not *Fringilla guttata* Nuttall) Evermann, 1886, *Auk* 3:182
Melospiza fasciata graminea (not of Townsend) Fisher, 1893, *N. Am. Fauna* 7:100, part
Melospiza fasciata cooperi Ridgway, 1899, *Auk* 16:35
Melospiza melodia cooperi Oberholser, 1899, *Auk* 16:183
Melospiza cinerea heermanni Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):364
Melospiza cinerea cooperi Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):367
Melospiza melodia mailliardi Grinnell, 1911, *Univ. Calif. Publ. Zool.* 7:197
Passerella melodia cooperi Linsdale, 1928, *Condor* 30:350
Passerella melodia heermanni Linsdale, 1928, *Condor* 30:350
Passerella melodia mailliardi Linsdale, 1928, *Condor* 30:350
Zonotrichia melodia mailliardi Paynter, 1970, *Check-list Birds World* 13:50
Zonotrichia melodia cooperi Paynter, 1970, *Check-list Birds World* 13:51
Zonotrichia melodia heermani [*sic*] Paynter, 1970, *Check-list Birds World* 13:51

HOLOTYPE: USNM 6227; adult ♂; Tejon Valley, Kern County, California, USA; 1853, probably September or October (Grinnell, 1932); Adolphus L. Heermann.

DIAGNOSIS: Size of *M. m. gouldii* (♂ 17.2–22.7 g, x̄ = 20.3 g, *n* = 126; ♀ 17.0–26.0 g, x̄ = 19.3 g, *n* = 89), though tail shorter; wing short (♂ 57.5–71.5 mm, x̄ = 63.1 mm, *n* = 124; ♀ 57–64 mm, x̄ = 59.7 mm, *n* = 26); tail length moderate (♂ 55.5–74.5 mm, x̄ = 64.8 mm, *n* = 121; ♀ 57–65.5 mm, x̄ = 64.8 mm, *n* = 14); bill length moderate (8.5–10.6 mm, x̄ = 9.6 mm, *n* = 22); bill depth moderate (6.1–7.4 mm, x̄ = 6.9 mm, *n* = 35); underparts white; throat flecked; ventral streaks fuscous and crisp, fringed reddish brown and contrasting sharply with ground colour; upperparts dark greyish brown, with olive tone; dorsal streaks crisp, fuscous bordered by warm brown; mantle feathers edged thinly (and variably) with grey; supercilia ashy; malar reddish fuscous. Distinguished from *M. m. maxillaris* by greyer colouration overall and shallower bill (*M. m. heermanni* generally < 7.2 mm, *M. m. maxillaris* generally > 7.5 mm), from *M. m. montana* by darker colouration overall, olive

tone to plumage, and blacker streaking. Weak clinal variation from south to north in reduced greyish fringes to mantle feathers and reduced brown between black medial streak and fringe, but most specimens not safely assignable to specific localities.

RANGE: Resident. Central and southwestern California (including the Central Valley) and northwestern Baja California. Some winter dispersal into southeastern California (e.g. the southern Salton Sink; Patten *et al.*, 2003, 2004a).

REMARKS: Despite being recognised by the American Ornithologists' Union (1957) and Paynter (1970), *M. m. mailliardi* (holotype: MVZ 16687; adult ♂; Rancho Don Dios, near Modesto, Stanislaus County, California, USA; 6 April 1910; Joseph Mailliard 7200) cannot be diagnosed (see Marshall, 1948). Most specimens are indistinguishable from comparable specimens of either *M. m. heermanni* or *M. m.* '*cooperi*'. Its range is attributed to the Sacramento Valley of California. *Melospiza m. cooperi* (holotype: USNM 31895 [not 51895; see Deignan 1961:665]; adult, sex undetermined; San Diego, San Diego County, California, USA.; 18 April 1862; James G. Cooper 261C) of cismontane central and southern California and northwestern Baja California is also widely recognised. In general, fringes on the mantle feathers of this population average slightly wider brownish grey than on *M. m. heermanni sensu stricto*, but there is considerable overlap and most specimens cannot be safely assigned to the correct population using this character. The subspecies are otherwise identical and are thus best synonymised.

Of note, spring specimens from the southernmost part of the range of *M. m. heermanni*, as recognised herein, have the breast streaking ruddier and finer and the dorsum redder. Some (e.g. SDNHM 34960, ♂ 2 km e. of El Rosario 21 May 1925) could pass for *M. m. heermanni* × *M. m. fallax* hybrids (as described below). These birds range in Baja California from El Rosario southeast through San Fernando. Song Sparrows were recently discovered farther south and east at Cataviña and Santo Dominguito, north of Rosarito (pers. obs., R. A. Erickson pers. comm.), with some birds appearing to be 'typical' *M. m. rivularis* (T. E. Wurster pers. comm.). An analysis of fresh fall and early winter specimens, apparently none of which exist in collections, is needed to determine whether Song Sparrows from El Rosario to at least Santo Dominguito (a) are an undescribed subspecies or, perhaps more likely, (b) exhibit undocumented introgression with the 'allopatric' *M. m. rivularis*.

Melospiza melodia graminea C. H. Townsend

Melospiza fasciata graminea C. H. Townsend, 1890, *Proc. U. S. Natl. Mus.* 13:139

Melospiza fasciata clementae C. H. Townsend, 1890, *Proc. U. S. Natl. Mus.* 13:139

Melospiza melodia var. *heermanni* (not *Melospiza heermanni* Baird) Henshaw, 1876, *Ornithol. Rep. Wheeler's Surv.*, p. 244, part

Melospiza melodia clementae Oberholser, 1899, *Auk* 16:183

Melospiza melodia graminea Oberholser, 1899, *Auk* 16:183

Melospiza cinerea clementae Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):368

Melospiza cinerea graminea Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):369

Melospiza coronatorum Grinnell & Daggett, 1903, *Auk* 20:34

Melospiza melodia micronyx Grinnell, 1928, *Proc. Biol. Soc. Washington* 41:37

Passerella melodia clementae Linsdale, 1928, *Condor* 30:350

Passerella melodia coronatorum Linsdale, 1928, *Condor* 30:350

Passerella melodia graminea Linsdale, 1928, *Condor* 30:350

Passerella melodia micronyx Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia micronyx Paynter, 1970, *Check-list Birds World* 13:51

Zonotrichia melodia clementae Paynter, 1970, *Check-list Birds World* 13:51

Zonotrichia melodia graminea Paynter, 1970, *Check-list Birds World* 13:51

Zonotrichia melodia coronotorum Paynter, 1970, *Check-list Birds World* 13:51

HOLOTYPE: USNM 117634; ♂; Santa Barbara Island, California, USA; 13 February 1889; Charles H. Townsend.

DIAGNOSIS: Slightly larger than *M. m. heermanni* (♂ 20.0–25.4 g, $\bar{x} = 22.2$ g, $n = 21$; ♀ 19.0–25.0 g, $\bar{x} = 21.5$ g, $n = 18$), though tail and bill shorter; wing short (♂ 57–66.5 mm, $\bar{x} = 63.0$ mm, $n = 145$; ♀ 58–63.5 mm, $\bar{x} = 60.9$ mm, $n = 39$); tail short (♂ 53–68.5 mm, $\bar{x} = 61.8$ mm, $n = 108$; ♀ 55.5–69.5 mm, $\bar{x} = 61.2$ mm, $n = 23$); bill somewhat short (8–8.7 mm, $\bar{x} = 8.3$ mm, $n = 12$); bill depth moderate (6.4–7.6 mm, $\bar{x} = 7.0$ mm, $n = 26$); underparts white; throat flecked; ventral streaks fuscous and crisp, fringed reddish brown and contrasting sharply with ground colour; upperparts medium greyish brown; dorsal streaks blackish and crisp, fringed pale silvery grey; supercilia whitish; malar reddish fuscous. Distinguished from *M. m. heermanni* by generally smaller size, distinctive silvery grey fringes to mantle feathers, narrow ventral streaks. Average size varies between islands, being smallest on Santa Barbara Island, largest on San Clemente Island and Islas Los Coronados. Mantle colour is best developed on Santa Barbara (van Rossem, 1924), San Clemente, and Santa Rosa (Willet, 1945) Islands. Birds on Santa Cruz Island are much closer to *M. m. heermanni*.

RANGE: Resident. Islands off southern California (San Miguel, Santa Rosa, Anacapa, Santa Barbara [formerly], and San Clemente) and off northern Baja California (Los Coronados). Claimed on mainland at Santa Barbara (A.O.U. 1957), but the record instead may pertain to individual variation in *M. m. heermanni*.

REMARKS: Birds on Santa Cruz Island are generally intermediate between *M. m. graminea* and *M. m. heermanni* of the adjacent coast (van Rossem, 1924; SDNHM specimens), with many specimens indistinguishable from typical *M. m.*

	Culmen length (mm)	Tarsus length (mm)
San Clemente Island ($\male$, $n = 10$)	10.77 ± 0.48 (10.1–11.7)	20.64 ± 0.62 (19.8–21.7)
Islas Los Coronados ($\male$, $n = 10$)	10.61 ± 0.46 (9.7–11.2)	19.50 ± 0.75 (18.3–20.8)
San Clemente Island ($\female$, $n = 3$)	10.77 ± 0.38 (10.4–11.3)	19.97 ± 0.12 (19.8–20.1)
Islas Los Coronados ($\female$ $n = 10$)	10.22 ± 0.47 (9.4–11.0)	18.51 ± 0.82 (17.4–19.8)

Table 2 Mensural characters [mean ± SD (range)] of *Melospiza melodia* from San Clemente Island, California, and Islas Los Coronados Islands, Baja California.

heermanni in both colouration and size, although a few match typical *M. m. graminea*. These birds are thus best treated as comprising an intergrade population, providing a morphological 'bridge' between the mainland and island subspecies. Ridgway (1901:369) called the population on Santa Cruz *M. m. graminea sensu stricto*, attesting to its generally darker colouration, but most other authorities have called it *M. m. clementae*. It is possible that Santa Cruz Island was only recently colonised: Willett (1945) considered Song Sparrows rare on the island and knew of only one specimen (at CAS) from it.

Song Sparrows resident on Islas Los Coronados were named *M. m. coronatorum* (holotype: MVZ 35969; adult $\male$; Los Coronados Islands (North Island), Baja California, México; 7 August 1902; Joseph Grinnell 5232). This subspecies purportedly differed only in having a smaller bill and shorter legs, but mean differences are slight (Table 2). Only ±10% of males and ±40% of females are diagnosable on culmen length and ±55% of males and ±75% of females are diagnosable on tarsus length. Recognition of *M. m. coronatorum* therefore clearly violates the 75% rule. Although not originally described as differing in plumage, fringes on the mantle feathers of birds on Islas Los Coronados average slightly browner (van Rossem, 1924).

Both *M. m. micronyx* (holotype: MVZ 51535; adult $\male$; San Miguel Island, California, U.S.A.; 21 September 1927; Chester C. Lamb 7930) and *M. m. clementae* (holotype: USNM 117620; adult $\male$; San Clemente Island, California, USA; 25 January 1889; Charles H. Townsend) suffer similar fates. Apart from minor deviations in colour, plumages of these alleged subspecies are basically the same as *M. m. graminea*, particularly accounting for substantial individual and inter-island variation. *Melospiza m. micronyx* was distinguished principally on its short hind claw and short tail. Tail length broadly overlaps with birds from Santa Rosa Island (Willett, 1945) and has no taxonomic value. The hind claw of birds from San Miguel Island does average shorter, but even mean differences are slight (0.7–1.1 mm; Willett, 1945) and the smallest *M. m. graminea* (7.2 mm) is smaller than the mean *M. m.* 'micronyx' (7.3 mm; Grinnell, 1928a). It is thus impossible, using the 75% rule, to diagnose these populations on the basis of the length of the hind claw.

During a February 1889 excursion, Townsend (1890) noted that Song Sparrows were 'extremely abundant on the small island of Santa Barbara'. Less than a century later the population was extinct. Like birds from San Miguel Island,

birds initially taken on San Clemente Island (and later various other northerly Channel Islands) were distinguished from *M. m. graminea* by their larger size, showing little overlap in wing or tail length, sex for sex (Ridgway, 1901:368). Our examination of pertinent published data, however, belies these claims. In his survey of male Song Sparrows of the Channel Islands, van Rossem (1924) documented that maximal wing length in *M. m. graminea sensu stricto* (62.5 mm) exceeded the mean for *M. m.* 'coronatorum' (62.3 mm) from Islas Los Coronados and was close to the mean for other islands sampled. Likewise, mean wing chord for *M. m.* 'micronyx' (62.0 mm) overlaps the maximum for *M. m. graminea sensu stricto* (Grinnell, 1928a), again violating the 75% rule. Willett (1945) provided wing chord measurements showing that <50% of females were diagnosable on this measure (the smallest birds from San Miguel, San Clemente, and Santa Rosa Islands were smaller than the largest from Santa Barbara), whereas ±5% of males are diagnosable. It seems highly unlikely that only one sex would differ in size, particularly in light of van Rossem's (1924:219) observation that 'Measurements of the females parallel those of the males in all proportions. They average about 5 per cent smaller' (see also Aldrich, 1984:115). The claimed shorter tail is similarly problematic, as the smallest *M. m.* 'micronyx', *M. m.* 'coronatorum' and *M. m.* 'clementae' (59.0–60.5 mm) extend below the mean of *M. m. graminea sensu stricto* (61.0 mm in van Rossem, 1924; 60.7 mm in Willett, 1945), again automatically failing the 75% rule.

Willett (1945:54) effectively captured the hodgepodge of minor characters across the Channel Islands when he concluded that Song Sparrows from Santa Rosa Island are 'nearest to *clementae* in colour, and length of hind claw; nearest to *micronyx* in length of tail; and intermediate between the two in wing length. The culmen measures about the same in birds from all four [San Clemente, Santa Barbara, Santa Rosa, San Miguel] islands.'

It would be logical and convenient to maintain the name *M. m. clementae* for the Song Sparrows of the Channel Islands, as its etymology refers to one of the islands and its name has been applied to more island populations. However, Townsend (1890) named both species in the same paper, but *M. m. graminea* has page priority (it appeared one-half page sooner). Moreover, it could also be interpreted that Marshall (1964) acted as first reviser when he provided his simplified key that merged *M. m. clementae* into *M. m. graminea*. If all subspecies are merged into one, then the latter's name must apply to the entire group.

Southwest Group

Melospiza melodia fallax (Baird)

Zonotrichia fallax Baird, 1854, *Proc. Acad. Nat. Sci. Philadelphia* 7:119

Melospiza fallax Baird, 1858, *Rep. Expl. Surv. Pac. R. R.* 9:481, part

Melospiza melodia var. *fallax* Coues, 1872, *Key N. Am. Birds* p. 139, part

Melospiza fasciata var. *fallax* Ridgway, 1877, *Ornithol. 40th Parallel*, p. 482, part

Melospiza meloda [sic] var. *fallax* Henshaw, 1879, *Bull. Nuttall Ornithol. Club* 4:156, part

Melospiza fasciata fallax Ridgway, 1880, *Proc. U. S. Natl. Mus.* 3:3, part

Melospiza melodia fallax Goode, 1883, *Bull. U. S. Natl. Mus.* 25:328

Melospiza cinerea fallax Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):362

Melospiza melodia saltonis Grinnell, 1909, *Univ. Calif. Publ. Zool.* 5:268

Passerella melodia fallax Linsdale, 1928, *Condor* 30:350

Passerella melodia saltonis Linsdale, 1928, *Condor* 30:350

Melospiza melodia virginis Marshall & Behle, 1942, *Condor* 44:123

Melospiza melodia bendirei Phillips, 1943, *Auk* 60:247

Zonotrichia melodia fallax Paynter, 1970, *Check-list Birds World* 13:47

Zonotrichia melodia saltonis Paynter, 1970, *Check-list Birds World* 13:47

HOLOTYPE: USNM 10281; adult, sex?; Pueblo Creek, New Mexico [=Walnut Creek, n. of Prescott, Yavapai County, Arizona, U.S.A.]; 22 January 1854; Caleb B. R. Kennerly 51.

DIAGNOSIS: Smaller than *M. m. montana* (♂ 16.0–23.0 g, $\bar{x}$ = 18.6 g, n = 52;. ♀ 13.5–20.5 g, $\bar{x}$ = 17.0 g, n = 30), though wings shorter; wing length moderate (♂ 58.5–71.5 mm, $\bar{x}$ = 67.2 mm, n = 61; ♀ 60–69.5 mm, $\bar{x}$ = 63.9 mm, n = 25); tail length moderate (♂ 65.5–73.5 mm, $\bar{x}$ = 69.8 mm, n = 26; ♀ 60.5–71.5 mm, $\bar{x}$ = 66.4 mm, n = 26); bill length moderate (8.0–9.0 mm, $\bar{x}$ = 8.6 mm, n = 12); bill depth moderate (6.5–7.4 mm, $\bar{x}$ = 7.1 mm, n = 28); underparts white; throat flecked; ventral streaks crisp, brown fringed broadly chestnut, contrasting moderately with ground colour; ventral streaks sometimes wholly chestnut, lacking brown centre; upperparts pale brownish grey; dorsal streaks brown and crisp, fringed greyish chestnut; supercilia whitish; malar chestnut.

RANGE: Resident. Sonoran Desert south to the Gulf of California and parts of the eastern Mojave Desert north to southern Nevada (vicinity of Henderson) and southwestern Utah (Virgin River valley) and east to southeastern Arizona. Some dispersal westward into Mojave Desert in winter (Death Valley, Victorville; MVZ).

REMARKS: The range and nomenclature of many Song Sparrow subspecies have suffered a history of chaos, but perhaps none more so than *M. m. fallax*. Deducing this distinctive taxon's type locality was problematic enough (Phillips, 1943), let alone determining its range. Baird himself applied the range to a mixture of *M. m. fallax sensu lato* and the then-unnamed *M. m. montana*. Grinnell (1909) mistakenly considered *M. m. fallax* an older name for *M. m. montana* and so considered the former to apply to the Rocky Mountain population. He went so far as to assert that *M. m. fallax* 'has been shown to be incorrectly employed for the 'desert' song sparrow *resident* along the Gila and Colorado rivers' (Grinnell, 1914:174; emphasis in original). He apparently never examined Baird's type specimen, which is essentially a perfect match for *M. m. saltonis* and unlike the black-streaked *M. m. montana*. Grinnell's confusion likely explains why he was so certain that *M. m. saltonis* was a valid subspecies, 'sharply defined both geographically and specifically' (Grinnell, 1914:175). In actuality, most specimens of *M. m. saltonis* and *M. m. fallax sensu lato* are not separable (see below).

M. m. virginis (holotype: UMNH 6534; adult ♂; near junction of Virgin and Santa Clara Rivers, 3 miles s. of Saint George, Washington County, Utah, USA; 16 May 1940; William H. Behle 2091) was synonymised by Marshall (1942) himself shortly after the original description. Phillips was not so clear with his synonymy of *M. m. bendirei* (holotype: DEL 18510; immature ♂; Salt River near Tempe Butte, Maricopa County, Arizona, USA; 11 November 1941; Lewis D. Yaeger), although he implicitly synonymised it (Phillips *et al.*, 1964; Monson & Phillips, 1981) when describing the range of *M. m. fallax* as including all of the range he originally ascribed to *M. m. bendirei*.

No authors previously have questioned the validity of *M. m. saltonis* Grinnell, 1909 (holotype: MVZ 599; adult ♂; the [then] edge of Salton Sea, one mile SE of Mecca, Colorado Desert, Riverside County, California, USA; 13 March 1908; Charles H. Richardson, Jr. 1155). As noted above, Grinnell (1909, 1914) was certain of its validity because he conflated *M. m. fallax* and *M. m. montana*. Even such critical taxonomists as Allan R. Phillips recognised *M. m. saltonis*, although he referred to it as 'weakly characterised' (Phillips *et al.*, 1964). That he attributed specimens of this sedentary subspecies to various locales in Arizona, including as far east as near the New Mexico border (Phillips *et al.*, 1964:210), belies its true nature: it is not diagnosable from *M. m. fallax*. Plumage and measurements overlap broadly, with, perhaps, slight *mean* differences in paler colouration and smaller size in the western Sonoran Desert, although the provenance of any given specimen could not be assigned with confidence beyond stating it was from the Sonoran Desert.

Melospiza melodia rivularis W. E. Bryant

Melospiza fasciata rivularis W. E. Bryant, 1888, *Proc. Calif. Acad. Sci.*, ser. 2, 1:197

Melospiza melodia rivularis Oberholser, 1899, *Auk* 16:183

Melospiza cinerea rivularis Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):363

Passerella melodia rivularis Linsdale, 1928, *Condor* 30:350

Zonotrichia melodia rivularis Paynter, 1970, *Check-list Birds World* 13:52

HOLOTYPE: CAS destroyed; ♂; Comondú, Baja California, México; 11 March 1888; Walter E. Bryant 3024. On the basis of the original description, a ♀ from the same locale 12 March 1888 (Bryant no. 3041) was a cotype. The great San Francisco fire of 1906 claimed the California Academy of Sciences and all of its holdings, including the cotypes and a series of topotypes of *M. m. rivularis* (Grinnell 1928b:177). Various topotypes are extant, e.g. MVZ 15516–15519 from April 1909 and 47 skins at MCZ taken late March–early May 1909.

DIAGNOSIS: Larger than *M. m. fallax* (♂ 19.3–28.6 g, x̄ = 23.9 g, *n* = 23; ♀ 19.9–27.1 g, x̄ = 22.7 g, *n* = 15); wing relatively long (♂ 68.5–73 mm, x̄ = 71.1 mm, *n* = 10; ♀ 64–69 mm, x̄ = 66.6 mm, *n* = 7); tail relatively long (♂ 70.5–75 mm, x̄ = 72.9 mm, *n* = 9; ♀ 66–73 mm, x̄ = 68.8 mm, *n* = 7); bill relatively long (9.5–10 mm, x̄ = 9.7 mm, *n* = 13); bill depth moderate (6.9–7.4 mm, x̄ = 7.1 mm, *n* = 4); plumage like *M. m. fallax*, but streaking slightly duller, less pronounced, and more restricted. Note the much longer bill (*M. m. rivularis* >9.5 mm nostril to tip, *M. m. fallax* < 9.0 mm nostril to tip).

RANGE: Resident. Baja California Sur from San Ignacio south to (but not including) the Sierra Laguna. May occur farther north (see *M. m. heermanni*).

REMARKS: The plumage of this subspecies matches the palest *M. m. fallax*. The similarity could stem from convergence or from shared common ancestry. The former requires only that the Song Sparrow conforms to Gloger's rule, the tendency for colouration to be more heavily pigmented in humid regions (Zink & Remsen, 1986). The latter is plausible in light of the multitude of shared flora and fauna between arid southern Baja California and arid western Sonora (Stager, 1960; Turner *et al.*, 1995).

Melospiza melodia goldmani Nelson

Melospiza goldmani Nelson, 1899, *Auk* 16:29
Melospiza melodia goldmani Oberholser, 1899, *Auk* 16:183
Melospiza cinerea goldmani Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):366
Passerella melodia goldmani Linsdale, 1928, *Condor* 30:350
Zonotrichia melodia goldmani Paynter, 1970, *Check-list Birds World* 13:52

HOLOTYPE: USNM 159182; adult ♂; El Salto, Durango, México; 17 July 1898; E. W. Nelson and E. A. Goldman 5662.

DIAGNOSIS: Slightly larger than *M. m. rivularis*, though bill shallower; wing relatively long (♂ 69–75.5 mm, x̄ = 71.7 mm, *n* = 13; ♀ 65–71 mm, x̄ = 67.3 mm, *n* = 7); tail relatively long (♂ 67–78 mm, x̄ = 72.1 mm, *n* = 12; ♀ 64–69 mm, x̄ = 66.6 mm, *n* = 7); bill relatively long (9–10.6 mm, x̄ = 9.6 mm, *n* = 17); bill shallow (5.9–6.6 mm, x̄ = 6.3 mm, *n* = 17); underparts whitish; throat flecked; ventral streaks diffuse, reddish brown and contrasting weakly with ground colour; upperparts dark reddish brown; dorsal streaks brown and diffuse, lacking a notable fringe; supercilia ashy; malar brown.

Overall plumage colour and pattern recalls *M. m. morphna* of the Pacific Northwest, though *M. m. goldmani*'s underparts are whiter and its streaking is crisper.

RANGE: Resident. Durango, in the vicinity of El Salto.

REMARKS: Despite extensive searches in the Sierra Madre Occidental of western Durango and eastern Sinaloa, *M. m. goldmani* remains known only from the vicinity of the type locality (Dickerman, 1963). The type specimen is actually a ♂, not a ♀ as reported in the original description (Deignan, 1961:666). Two controversial specimens from Bavispe, Chihuahua, where no Song Sparrows breed, have plumage colouration intermediate between *M. m. goldmani* and *M. m. montana* (Dickerman, 1963:36), hinting at past intergradation and/or a formerly more extensive range of *M. m. goldmani*. Alternatively, they might represent an extinct, undescribed subspecies.

Mexican Plateau Group

Melospiza melodia zacapu Dickerman

Melospiza melodia zacapu Dickerman, 1963, *Minn. Mus. Nat. Hist. Occas. Paper* 9:40
Melospiza melodia adusta Miller, Friedmann, Griscom, & Moore, 1957, *Pac. Coast Avifauna* 33:401, part
Zonotrichia melodia zacapu Paynter, 1970, *Check-list Birds World* 13:53

HOLOTYPE: AMNH 817694 (ex. BMNH 16678); immature ♀; Zacapu, Michoacán, México; 12 December 1956; Robert W. Dickerman 7772.

DIAGNOSIS: Size of *M. m. fallax*, though tail shorter; wing length moderate (♂ 63–71 mm, x̄ = 67.1 mm, *n* = 24; ♀ 61–67 mm, x̄ = 63.3 mm, *n* = 31); tail short (♂ 56–68 mm, x̄ = 63.1 mm, *n* = 22; ♀ 56–63 mm, x̄ = 60.0 mm, *n* = 29); bill length moderate (8.3–9.9 mm, x̄ = 9.1 mm, *n* = 55); bill shallow (5.7–6.7 mm, x̄ = 6.1 mm, *n* = 52); underparts white; throat clean white; ventral markings are crisp black spots, contrasting sharply with ground colour; upperparts dark reddish; dorsal streaks broad, black, lacking a fringe; supercilia white; malar black.

RANGE: Resident. Michoacán at Zacapu and 6–8 km north of Panindícuaro; also, perhaps, at Laguna Chapala, Jalisco.

REMARKS: Despite approaching *M. m. adusta* as close as 30 km, only ±2% of fall specimens ('one or two' of 51 total) that Dickerman (1963:41) examined showed any tendency toward intermediacy. The next nearest population is at Laguna Chapala. Birds there constitute either an undescribed subspecies (Dickerman, 1963) or an isolated population of *M. m. zacapu*; however, apparently no good specimens of Song Sparrow have been collected at the lake, so a taxonomic designation cannot be made at this time.

Melospiza melodia adusta Nelson

Melospiza adusta Nelson, 1899, *Auk* 16:28
Melospiza melodia adusta Oberholser, 1899, *Auk* 16:183

Melospiza cinerea adusta Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):366

Passerella melodia adusta Linsdale, 1928, *Condor* 30:349

Melospiza melodia yuriria Phillips and Dickerman, 1957, *Auk* 74:380

Zonotrichia melodia yuriria Paynter, 1970, *Check-list Birds World* 13:52

Zonotrichia melodia adusta Paynter, 1970, *Check-list Birds World* 13:53

HOLOTYPE: USNM 144046; adult ♂; [Lago] Pátzcuaro, Michoacán, México; 27 July 1892; E. W. Nelson and E. A. Goldman 261.

DIAGNOSIS: Size of *M. m. zacapu* (♂ 22.0 g, $n = 1$; ♀ 20.8 g, $n = 2$), though tail averages longer; wing length moderate (♂ 63–71 mm, $\bar{x} = 67.8$ mm, $n = 24$; ♀ 61–68 mm, $\bar{x} = 64.9$ mm, $n = 33$); tail length moderate (♂ 60–70 mm, $\bar{x} = 65.1$ mm, $n = 63$; ♀ 58–66 mm, $\bar{x} = 62.1$ mm, $n = 33$); bill length moderate (8.4–10.3 mm, $\bar{x} = 9.1$ mm, $n = 105$; Dickerman, 1963); bill shallow (5.6–6.9 mm, $\bar{x} = 6.3$ mm, $n = 97$; Dickerman, 1963); plumage like *M. m. zacapu* but upperparts medium reddish brown. Also distinguished from *M. m. zacapu* by paler colouration on nape and edges to inner secondaries. Clinal variation, with redder birds in the west and browner birds in the east.

RANGE: Resident. Along the Río Lerma drainage in Michoacán from Pátzcuaro upstream to Lago Yuriria, Guanajato.

REMARKS: Dickerman (1963) recognised *M. m. yuriria* (holotype: AMNH 817692 [ex. BMNH 12490]; adult [?] ♂; Yuriria, Guanajuato, México; 21 November 1956; Robert W. Dickerman 7723), the browner eastern birds, though he noted (Dickerman, 1963:fig. 19) an extensive population of birds of intermediate colouration. In considering the overlap in various plumage characters and this extensive population of intermediates, it seems unwise to recognise more than one subspecies in this region. It would be worthwhile to explore mesic habitats in northeastern Michoacán between Morelia and Lago Pátzcuaro to determine the extent of character variation in the region.

Melospiza melodia villai Phillips & Dickerman

Melospiza melodia villai Phillips & Dickerman, 1957, *Auk* 74:380

Melospiza cinerea mexicana Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):365, part

Melospiza melodia pectoralis Hellmayr, 1938, *Zool. Ser., Field Mus. Nat. Hist.* 13(11):608, part

Melospiza melodia mexicana Sutton & Burleigh, 1942, *Auk* 59:418, part

?*Passerella melodia pectoralis* Miller, 1956, *Evolution* 10:264, part

Zonotrichia melodia villai Paynter, 1970, *Check-list Birds World* 13:52

HOLOTYPE: AMNH 817693 (ex. BMNH 12500); adult [?] ♂; 6 miles nne. of Amoloya del Rio [=9 km sse. of Lerma],

Edo. México, México; 24 October 1956; Robert W. Dickerman 7560.

DIAGNOSIS: Larger than *M. m. adusta*; wing relatively long (♂ 68–78 mm, $\bar{x} = 71.4$ mm, $n = 78$; ♀ 61–72 mm, $\bar{x} = 67.5$ mm, $n = 35$); tail relatively long (♂ 65–75 mm, $\bar{x} = 68.8$ mm, $n = 75$; ♀ 60–72 mm, $\bar{x} = 66.0$ mm, $n = 30$); bill length moderate (8.3–10.1 mm, $\bar{x} = 9.2$ mm, $n = 115$; Dickerman, 1963); bill shallow (5.7–6.8 mm, $\bar{x} = 6.4$ mm, $n = 103$; Dickerman, 1963); plumage like *M. m. zacapu* but upperparts dark brown, lacking rich reddish tones. Distinguished from *M. m. adusta* by darker, sootier colouration overall and lack of reddish tones. Larger than other birds in the Río Lerma drainage, exhibiting little size overlap with other subspecies (Dickerman, 1963:63–66).

RANGE: Resident. México in upper Río Lerma drainage from near Toluca, Edo. México, north and west to Tarandacuao, Guanajato, and west to San Cayento, México.

REMARKS: Dickerman (1963:43) asserted that the break between *M. m. villai* and Song Sparrows farther west in the Río Lerma drainage was 'a sharp one in both size and colour, especially the latter, with little indication of 'introgression'' evident even where the populations approached each other.

Melospiza melodia mexicana Ridgway

Melospiza melodia var. *mexicana* Ridgway, 1874 *in* Baird, Brewer, & Ridgway, *Hist. N. Am. Birds* 2:18

?*Melospiza gouldii* Sclater, 1862, *Proc. Zool. Soc. London*, p. 368, part

Melospiza fallax Sclater, 1864, *Proc. Zool. Soc. London*, p. 172, part

?*Melospiza pectoralis* Müller, 1865, *Reise Mex.* 3:583

Melospiza meloda [sic] var. *mexicana* Henshaw, *Bull. Nuttall Ornithol. Club* 4:158

Melospiza fasciata mexicana Ferrari-Pérez & Ridgway, 1886, *Proc. U. S. Natl. Mus.* 9:144

Melospiza heermanni (not of Baird) Salvin & Godman, 1873, *Nomen. Avifauna Neotrop.*, p. 32, part

Melospiza heermanni Salvin & Godman, 1886, *Biol. Centr.-Am., Aves* 1:388, part

Melospiza cinerea mexicana Ridgway, 1901, *Bull. U. S. Natl. Mus.* 50(1):365, part

Melospiza melodia mexicana Oberholser, 1899, *Auk* 16:183

Passerella melodia mexicana Linsdale, 1928, *Condor* 30:350

Melospiza melodia pectoralis Hellmayr, 1938, *Zool. Ser., Field Mus. Nat. Hist.* 13(11):608, part

Passerella melodia pectoralis Miller, 1956, *Evolution* 10:264

Melospiza melodia azteca Dickerman, 1963, *Minn. Mus. Nat. Hist. Occas. Paper* 9:46

Melospiza melodia niceae Dickerman, 1963, *Minn. Mus. Nat. Hist. Occas. Paper* 9:51

Zonotrichia melodia niceae Paynter, 1970, *Check-list Birds World* 13:52

Zonotrichia melodia mexicana Paynter, 1970, *Check-list Birds World* 13:52

Zonotrichia melodia azteca Paynter, 1970, *Check-list Birds World* 13:52

HOLOTYPE: USNM 60046; adult, sex?; Puebla, Puebla, México; January 1866; unknown (donated to USNM by Adolphe Boucard).

DIAGNOSIS: Size of *M. m. adusta*; wing length moderate (♂ 61–72 mm, x̄ = 68.5 mm, *n* = 139; ♀ 60–70 mm, x̄ = 64.8 mm, *n* = 81); tail length moderate (♂ 58–71 mm, x̄ = 65.8 mm, *n* = 133; ♀ 58–68 mm, x̄ = 62.7 mm, *n* = 76); bill relatively short (7.7–9.9 mm, x̄ = 8.9 mm, *n* = 220); bill shallow (5.4–7.0 mm, x̄ = 6.3 mm, *n* = 210); plumage like *M. m. villai* but upperparts medium (paler) brown. Further distinguished from *M. m. villai* by smaller size. Some clinal variation, with birds paler, smaller, and more contrasting from Hidalgo south through the Valley of México and west to Edo. México.

RANGE: Resident. Eastern trans-Mexican volcanic belt from southern Hidalgo southeast to northern Puebla, and west through Tlaxcala to northern Edo. México and Distrito Federal (Fig. 1).

REMARKS: *Melospiza m. mexicana* (*sensu* Dickerman, 1963) is a heterogeneous subspecies. Even Dickerman (1963:49) commented that it showed so much geographic variation that 'were a name not available, it might best be considered a highly variable intermediate population' between his dark *M. m. nicea* (holotype: AMNH 817696 [ex. BMNH 16897]; immature? ♂; Tulancingo, Hidalgo, México; 22 September 1956; Robert W. Dickerman 7427) and his smaller, pale *M. m. azteca* (holotype: AMNH 817695 [ex. BMNH 16870]; adult ♀; Lago de Zumpango, Edo. México, México; 10 November 1956; Robert W. Dickerman 7640). Under Dickerman's scenario, the range size of the population with intermediate characters would be nearly twice that of the combined range sizes of his two 'valid' subspecies (see Dickerman, 1963:fig. 20). The best recourse is to recognise a single variable subspecies in the eastern trans-Mexican volcanic belt, with clinal variation from dark to pale and in decreasing size as one moves from Hidalgo through Puebla to Edo. México. If not, one is forced to consider most individual specimens as intermediate (i.e. not diagnosable).

Key to Song Sparrow subspecies

We present a dichotomous key to facilitate identification of individual specimens. A principal goal of defining diagnosable subspecies is that it allows one to assign migrants and dispersants to a particular named population. This key is founded on Marshall's (1948) key, which he based on unique characters (a 100% rule). We include more subspecies because we followed the 75%-rule (Amadon, 1949; Mayr, 1963; Patten & Unitt, 2002), an acknowledgement that morphological distinctiveness will be blurry where geographic ranges abut.

I. Shaft markings long and diffuse streaks, not greatly contrasting with ground colour; background colour of underparts grey; bill long and slender; size generally large.
   A. Streaks sooty; dorsal background dusky.
      1. Size huge (matching *Pipilo*; ±50 g); bill thicker . . . .*M. m. maxima*
      2. Smaller (±45 g); bill more slender; greyer . . . .*M. m. sanaka*
   B. Streaks brown.
      1. Dorsum grey; size large (±40 g).
         a. Paler; greyer . . . . *M. m. insignis*
         b. Darker; browner; smaller (±35 g) . . . .*M. m. kenaiensis*
      2. Dorsum reddish-brown; size medium (25–30 g).
         a. Bill long; greyer . . . . *M. m. caurina*
         b. Bill short; browner.
            i. Streaking brownish, not contrasting.
               (a) Sootier . . . . *M. m. rufina*
               (b) Redder . . . .*M. m. morphna*
            ii. Streaking blackish/darker, more contrasting.
               (a) Greyer; paler; streaks blacker . . . .*M. m. merrilli*
               (b) Browner; darker; streaks redder . . . . *M. m. cleonensis*

II. Shaft markings compact, sharply contrasting with ground colour; background colour of underparts white or yellow; bill short; size generally small (<25 g).
   A. Ventral markings are streaks; middle of throat finely marked.
      1. Streaks brown.
         a. Streaks dark reddish-brown; feather fringes sooty . . . . *M. m. goldmani*
         b. Streaks pale reddish-brown; feather fringes pale grey.
            i. Bill short; streaks wide . . . .*M. m. fallax*
            ii. Bill long; streaks narrow . . . .*M. m. rivularis*
      2. Streaks black.
         a. Dorsum greyish, lacking brown; bill slender; size very small (20 g).
            i. Venter yellow; dorsal background yellow-grey . . . . *M. m. pusillula*
            ii. Venter white.
               (a) Dorsum pale silvery-grey . . . . *M. m. graminea*
               (b) Dorsum olive-dusky . . . .*M. m. samuelis*
         b. Dorsum brownish; feathers fringed grey or buff.
            i. Wing long.
               (a) Dorsum reddish-brown
                  (i) Mantle fringes brownish . . . . *M. m. melodia*
                  (ii) Mantle fringes pale grey . . . .*M. m. atlantica*
               (b) Dorsum brownish-grey . . . .*M. m. montana*
            ii. Wing short.
               (a) Bill swollen at base; dorsum rich brown . . . .*M. m. maxillaris*
               (b) Bill not swollen.
                  (i) Dorsum rich olive-brown; no mantle fringes . . . . *M. m. gouldii*
                  (ii) Dorsum grey-brown; grey mantle fringes . . . . *M. m. heermanni*

B. Ventral markings are black splotches, forming a necklace; throat clean white.
  1. Dorsum reddish-brown.
    a. Dark; redder . . . . *M. m. zacapu*
    b. Pale; browner . . . . *M. m. adusta*
  2. Dorsum plain brownish.
    a. Darker; large (±25 g) . . . . *M. m. villai*
    b. Paler; smaller (±20 g), greyer . . . .
       . . . . *M. m. mexicana*

Ecogeographic variation

Aldrich's (1984) ecogeographic analysis of the Song Sparrow addressed mensural variation on a broad scale, but according to Zink (1985) the study was weakened because the analytical design could not distinguish between ecophenotypic and genetic mechanisms for generating observed geographic variation. Oddly, Zink did not point out that Aldrich's study was limited because plumage variation, certainly the most striking feature of morphological variation in the Song Sparrow, was not considered. Indeed, geographic variation in the species follows two established ecogeographic rules, Gloger's and Bergmann's (Aldrich, 1984; Zink & Remsen, 1986).

Gloger's rule, the tendency toward more heavily pigmented colouration in more humid areas, is well established in birds: over 95% of species that Zink and Remsen (1986) studied conformed to predicted trends, with the Song Sparrow among the 'species that generally support' the rule. Applied to North America, Gloger's rule generates specific predictions, such as pale subspecies in the arid Southwest, grey subspecies in the Great Basin, and dark, heavily pigmented subspecies in the Pacific Northwest. These predictions fit geographic variation in the Song Sparrow (e.g. *M. m. fallax/M. m. rivularis*, *M. m. montana* and *M. m. morphna/*etc., respectively). The prevailing hypothesised mechanism for the resultant pattern known as Gloger's rule is one of background matching, to reduce detectability by competitors, predators and prey (Miller & Miller, 1951; Zink & Remsen, 1986). Whether this mechanism is responsible for the pattern shown by Song Sparrows awaits study.

Song Sparrows also follow Bergmann's rule, another well known biogeographical principle. This 'rule' is really the tendency for body size of homeothermic organisms to increase with decreasing temperature. In contrast to Gloger's rule, Bergmann's Rule has much weaker support among North American birds: only 44% 'clearly show the predicted relationship between body size and isophane' (Zink & Remsen, 1986). But the Song Sparrow is among the species that follows this rule (Aldrich, 1984), with the largest birds in Alaska, medium-sized birds on the cool coast of the Pacific Northwest, and small birds in the arid habitats of the southwestern United States and northwestern Mexico. The causal mechanism responsible for Bergmann's rule is debatable (Partridge & Coyne, 1997), although it is generally accepted that the correlation results from a physiological advantage of larger body size in colder climates (Kendeigh, 1969; Zink & Remsen, 1986; Ridley, 1993).

Despite our ignorance of underlying mechanisms, it is clear that there is a predictable association between the Song Sparrow's environment and both its size and plumage colouration. Even on a crude scale, the breeding ranges (Fig. 1) of many subspecies coincide with Köppen's twelve 'climate zones' (Fig. 2) of North America, which are based on annual rainfall and temperature. Specifically, the breeding range of *M. m. melodia* coincides with the humid continental zone, *M. m. atlantica* with the north-coastal humid subtropical, *M. m. montana* with semiarid, *M. m. fallax* with arid, *M. m. heermanni* with Mediterranean, *M. m. merrilli* with western highlands, *M. m. cleonensis* through *M. m. caurina* with humid oceanic, *M. m. kenaiensis* through *M. m. maxima* with southwest-coastal subarctic, and *M. m. zacapu* through *M. m. mexicana* with southern highlands (compare Figs 1 and 2).

The significance of this close association with environmental conditions is apparent when one considers that most subspecies of the Song Sparrow meet each other in broad contact zones where they interbreed extensively. It thus may be fair to conclude that 'ecological forces selecting adaptive genetic differences have a greater effect on morphological change or microevolution than do geographical separation or isolation' (Aldrich, 1984:118). After all, there is substantial morphological variation 'between populations with no apparent impediment to exchange of genes other than marked ecological differences in habitat' but little or no morphological variation 'between some populations with ecologically similar habitat . . . separated by long stretches of inhospitable environment' (Aldrich, 1984:118). With this view one might conclude that much of the differentiation among Song Sparrow subspecies has taken place despite gene flow (e.g. Chan & Arcese, 2002; cf. Pruett & Winker, 2005), which would be noteworthy given the demonstrated genetic variation in and natural selection on some geographically variable traits occurs in the species (Smith & Zach, 1979; Smith & Dhondt, 1980). Variation is not, therefore, merely an environmental effect, although imperfect but nontrivial concordance between genes and morphology (Pruett *et al.*, 2008b) implies a complex evolutionary history.

The Song Sparrow as a ring species

We suggest that three conditions must be met for a species to be considered unquestionably a ring species:

- contact must be clear between neighbouring subspecies,
- save for the terminal points, the transition between all connecting forms must be smooth, with extensive intergradation, and
- two adjoining subspecies (the terminal points) must show a sharp break in morphology/ecology/behaviour/etc., and thus behave like good biological species where they come into contact.

In reality, however, these conditions may be too stringent. In particular, requirements for clear contact and smooth intergradation between neighbouring taxa might exclude all examples, even the best ones described by Irwin *et al.* (2001a, b) and
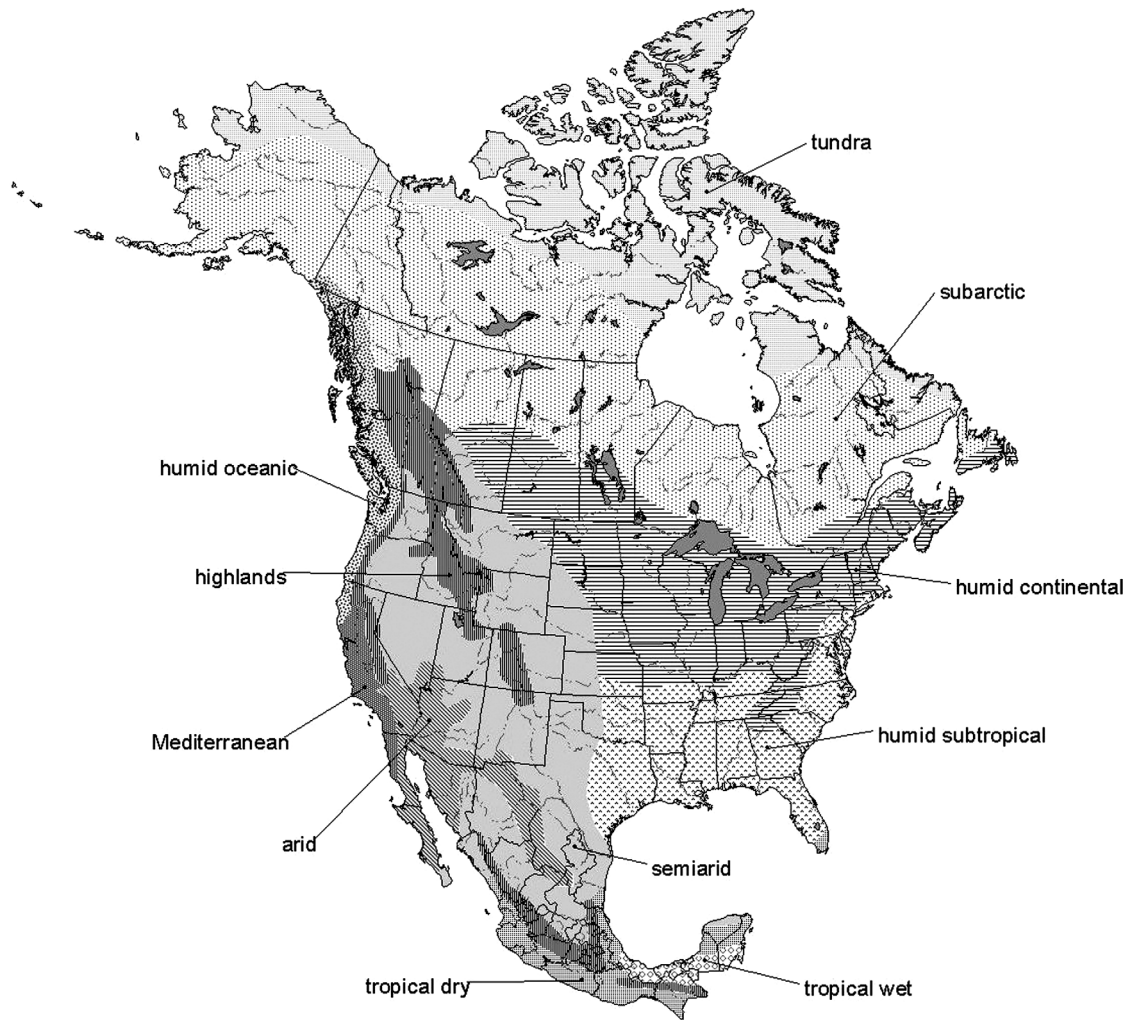
Figure 2 General Köppen climate zones in North America (after National Geographic Society, 1999).

Wake (2006). For this reason a more practical criterion might be a looser combination of the first two criteria above:

- a series of progressively intermediate forms must be arranged in a ring.

In either case, the endpoints must behave as biological species. Based on these criteria, Song Sparrows in western North America form a valid ring species, the centre of the ring being the Sierra Nevada and Mojave Desert and the endpoints being the contact zone between *M. m. heermanni* and *M. m. fallax* (Fig. 3; Patten *et al.*, 2004b). Here we outline the taxa that form the ring, discuss evidence of broad zones of intergradation between subspecies, present the sharp morphological break between endpoint taxa, and summarise how these two subspecies behave like good biological species where they meet.

Beginning with the southwesternmost taxon and working clockwise (Figs 3, 4; Patten *et al.*, 2004b), Song Sparrows ranging from northwestern Baja California north along the Pacific Coast to Santa Cruz and in central California to the Sacramento Valley and the southern fringe of the Sierra Nevada are *M. m. heermanni*, an olive-grey subspecies with

the streaking fuscous, colouration minimally reddish, and the mantle feathers generally fringes with grey. The last character varies clinally, lessening in extent from south to north; the bill also becomes slightly deeper in the north. In these two respects the morphology of *M. m. heermanni* approaches, respectively, *M. m. gouldii*, whose mantle fringes always lack grey, and *M. m. maxillaris*, whose bill is swollen basally. *Melospiza m. heermanni* meets both of these subspecies at the northern edge of its range (Fig. 3). The blend into *M. m. gouldii* is particularly smooth, with birds in the Santa Cruz region of coastal central California (formerly called *M. m.* '*santaecrusis*') exhibiting a mosaic of intermediate characters. Local differentiation around San Francisco Bay of *M. m. maxillaris*, yellow *M. m. pusillula*, and brown, short-tailed *M. m. samuelis* (Marshall, 1948; Chan & Arcese, 2002, 2003) does not disrupt the broader ring pattern.

The next subspecies to the north of *M. m. gouldii* is *M. m. cleonensis*. As noted in the above synopsis, *M. m. cleonensis* is a nearly perfectly intermediate form between highly disparate subspecies, *M. m. gouldii* and *M. m. morphna*. It is a mix of olive and rufous, with dorsal streaking fuscous and ventral streaking fuscous bordered with dark rufous-brown. This
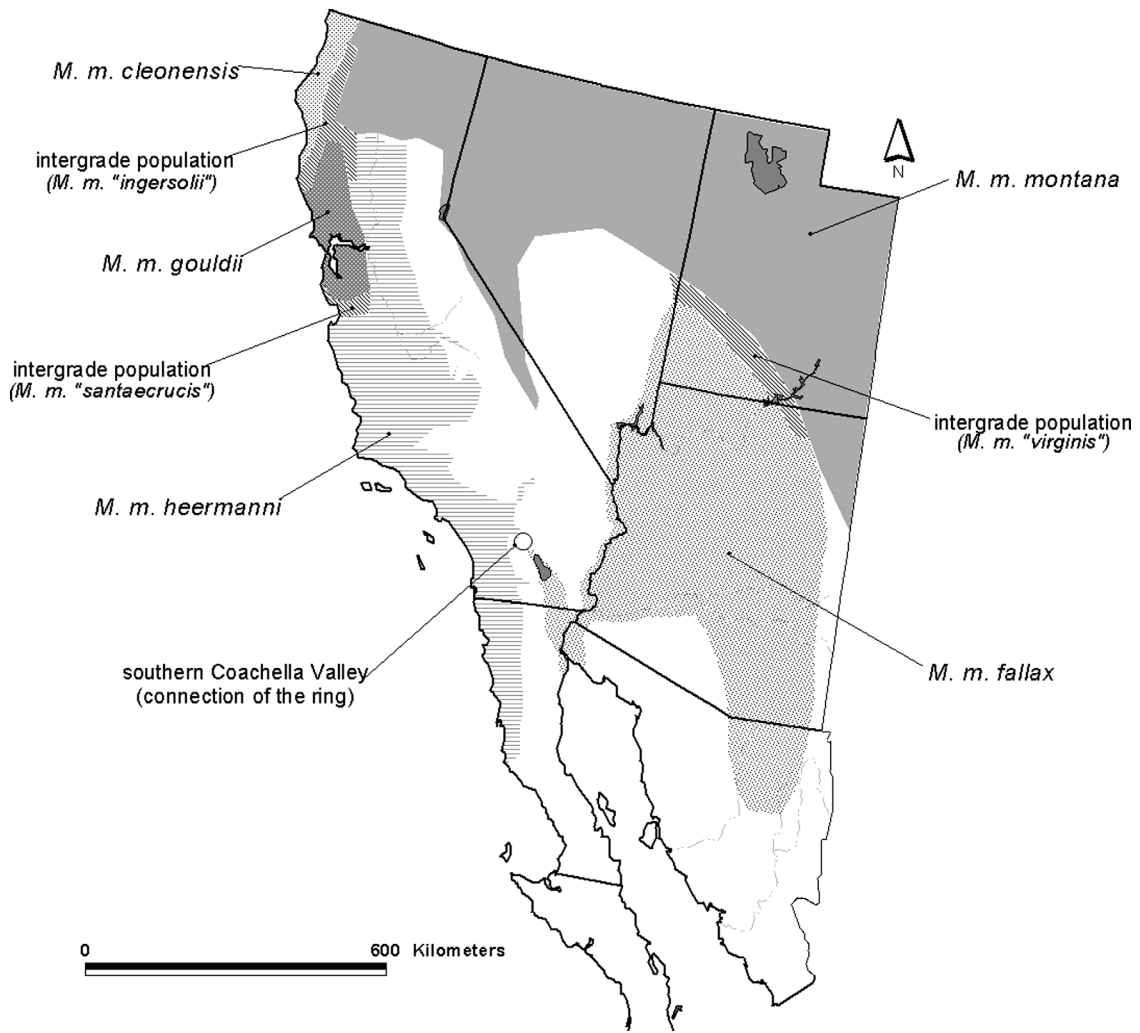
Figure 3 The Song Sparrow ring in western North America, showing the taxa involved and the zones of intergradation.
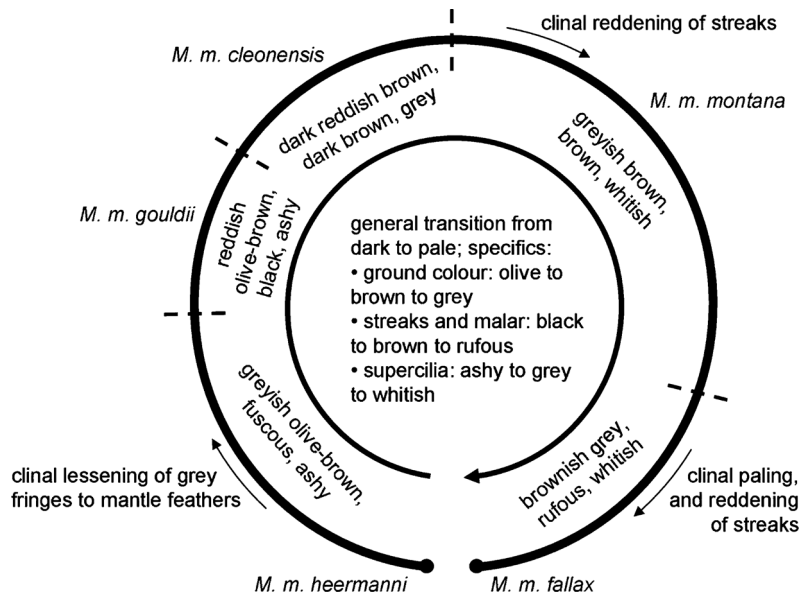

Figure 4 A stylised diagram showing morphological variation around the Song Sparrow ring in western North America. The diagram is oriented to match, roughly, the map in Fig. 3, and described general variation moves in a clockwise direction. Clinal variation displayed is for within that particular subspecies.

subspecies meets *M. m. montana* and forms a hybrid zone with it (formerly called *M. m.* 'ingersolii') on the eastern flank of the coast range and the western edge of northern Sacramento Valley (Fig. 3). This contact is actually with the redder western end (formerly called *M. m.* 'fisherella') of a cline within *M. m. montana*. This redder colour perhaps reflects introgression between *M. m. montana* with the redder *M. m. cleonensis* and *M. m. gouldii*. Regardless, the transition from both *M. m. gouldii* and *M. m. cleonensis* to *M. m. montana* is broad and smooth (Fig. 3).

The range of *M. m. montana* lies largely east of the Coast Range/Cascades axis. It is similar to *M. m. cleonensis* but has the streaking brown and overall colour much greyer. Its range extends inland through the Modoc Plateau and thence south along the eastern flank of the Sierra Nevada and eastward through the Great Basin to the Mogollon Plateau of the Four Corners region of the southwestern USA. Along the entire southwestern edge of the range of *M. m. montana* (Fig. 3), it meets and interbreeds with *M. m. fallax* (Behle, 1985), with some of these hybrids previously called *M. m.* 'virginis'. Suitable Song Sparrow habitat is more localised in the southern Great Basin and northern Mojave Desert, where these subspecies come into contact, but there is nonetheless a broad, smooth transition from the medium grey, black-streaked *M. m. montana* and the pale grey, red-streaked *M. m. fallax* (Patten *et al.*, 2004b). The range of *M. m. fallax* sweeps southward through much of Arizona and reaches westward through the western Sonoran Desert, where slight clinal variation (Fig. 4) results in the palest birds (formerly called *M. m.* 'saltonis'). *Melospiza m. fallax* is the common breeding Song Sparrow around the Salton Sea in southeastern California (Patten *et al.*, 2003). It meets *M. m. heermanni*, the beginning point of the ring, in a narrow hybrid zone (Fig. 3) that exhibits an abrupt break in plumage colouration.

Aside from the last contact zone, every transition between subspecies is smooth: plumage colouration and other morphological transitions (e.g. size) blend in a broad zone from its own population into another. Note that in each case Song Sparrows in the contact zones between subspecies forming the ring were named as novel subspecies in their own right because they exhibited intermediate characters that fit neither 'parental' form. Thus, on the basis of the ranges of the various subspecies and the clear zones of intergradation that have already been documented in the literature, our first two criteria have been satisfied for the Song Sparrow being a valid ring species.

Connecting the ring: the *M. m. heermanni*/*M. m. fallax* contact zone

Plumage divergence
The last criterion requires evidence that the two subspecies connecting the endpoints of the ring show an abrupt transition in morphology and behave as good biological species. Unlike all other links in the chain of Song Sparrow

subspecies forming the ring, the contact zone between *M. m. heermanni* and *M. m. fallax* along the Whitewater River in the southern Coachella Valley of southeastern California is abrupt, with limited evidence of hybridisation and intergradation. The sole mensural difference (cf. Aldrich, 1984) is that *M. m. fallax* has, on average, a longer tail $\bar{x}(_{fallax} = 67.0 \pm 3.0$ mm, $\bar{x}_{heermanni} = 62.7 \pm 3.0$ mm; $n = 28$ live males of each, $t = 5.34$, $P < 0.001$). Yet plumage differs strikingly: *M. m. fallax* is clay-grey with rich rufous-red streaks, ochraceous spots on the tail coverts, and is generally pale, whereas *M. m. heermanni* is olivaceous mouse-grey with fuscous-black streaks, black spots on the tail coverts, and is generally dark.

To quantify these differences, we scored 463 specimens and live birds of these two subspecies ($n = 236$ *M. m. heermanni*, 219 *M. m. fallax*, 8 putative hybrids) on nine plumage colours and patterns (Table 3). There was no overlap in colouration between these subspecies (Fig. 5; Patten *et al.*, 2004b). Mean ($\pm$SD) scores for *M. m. fallax* were 2.6 ± 1.8, whereas those for *M. m. heermanni* were 23.6 ± 2.0. Six specimens were scored as hybrids (Table 4), four from the Coachella Valley, where the subspecies come into contact, and two from the southwestern edge of the Salton Sea in winter, where some *M. m. heermanni* (and presumably their hybrids) disperse or migrate at that season (Patten *et al.*, 2003). Patten *et al.* (2004b) also assigned specimens to subspecies a priori based on collection locale and used discriminant function analysis (DFA) of the scored characters, which revealed that colour of streaking on the breast, malar and uppertail coverts were the best signs of intermediacy, although most hybrids tended to have a mix of other characters as well. With putative hybrids included, the DFA correctly classified 97.8% of 463 specimens.

Nearly all Song Sparrows around the Salton Sea show characters of typical *M. m. fallax* (Patten *et al.*, 2003, 2004b); their plumage shows no signs of intergradation with *M. m. heermanni* (contra Garrett & Dunn, 1981). Likewise, sparrows from the northern edge of the Coachella Valley (Whitewater Canyon, Palm Springs) show characters typical of *M. m. heermanni*; e.g. an historical specimen from Palm Springs (MCZ 241213, adult ♂ 24 April 1889) matches *M. m. heermanni* but has the malar perfectly intermediate. The plumage break between these two subspecies is abrupt (Patten *et al.*, 2004b). The most parsimonious conclusion from these data is that there is a narrow hybrid zone where *M. m. heermanni* meets *M. m. fallax* in the southern Coachella Valley of southeastern California.

Behavioural and ecological divergence
That *M. m. heermanni* and *M. m. fallax* hybridise little where they come into contact conceivably could be the result of rarity of encounter rather than any tendency to behave as good biological species. To test the latter hypothesis, Patten *et al.* (2004b) carried out studies of variation in habitat occupancy, song, female mate preference for song and plumage, and male song recognition between these two subspecies. We report salient findings herein; please refer to Patten *et al.* (2004b) for full details.

A. BREAST/FLANK STREAKS
  0 clear rufous (SDNHM 43139) – 2.5YR 4/8 throughout
  1 rufous with brown centre (SDNHM 9998) – 2.5YR 3/6 fringe, 5YR 2.5/1 centre
  2 brown with rusty edges (SDNHM 38933) – 5YR 4/4 fringe, 5YR 2.5/1 centre
  3 mostly solid fuscous (SDNHM 49574) – 7.5YR 2/0 x̄throughout

B. BACK STREAKS
  0 clear rufous (SDNHM 46507) – 5YR 4/6 throughout
  1 rufous with thin brown centres (SDNHM 42847) – 5YR 3/4 nearly throughout, with blacker centre
  2 rufous with wide brown centres (SDNHM 49109) – 5YR 3/4 fringe, 5YR 2.1/1 centre
  3 brown with wide rusty edges (SDNHM 3379) – 5YR 3/3 fringe, 5YR 2.5/1 centre
  4 fuscous with narrow rusty borders (SDNHM 49883) – 7.5YR 3/4 fringe, 7.5YR 2/0 centre
  5 fuscous with no appreciable rusty borders (SDNHM 49617) – 7.5YR 2/0 x̄throughout

C. UNDERTAIL COVERTS
  0 mostly uniform dull ochre, perhaps with faint rusty-clay streaks of minimal contrast (SDNHM 43139) – 7.5YR 8/4 throughout
  1 dull ochre with dull, contrasting rust streaks (SDNHM 15636) – 7.5YR 8/4 fringe, 2.5 YR 4/8 centre
  2 buff-whitish with fuscous-brown streaks (SDNHM 42928) – 10YR 7/2 fringe, 5YR 2.5/1 centre

D. MALAR STREAKS
  0 clear rufous, perhaps with a hint of a dark centre (SDNHM 43139) – 2.5YR 4/9 throughout
  1 mixed rufous/fuscous, x̄50:50 (SDNHM 47781) – 5YR 2.5/1 for fuscous, 5YR 3/3 for rufous
  2 fuscous, perhaps with slight rufous fringes (SDNHM 49894) – 7.5YR 2/0 x̄throughout

E. SIDES OF NECK/NAPE
  0 dull clay-grey without streaks (SDNHM 48785) – 10YR 5/2 x̄throughout
  1 pale/dull clay-grey with rusty spots/streaks (SDNHM 46507) – 10YR 5/2 with 2.5YR 4/6 streaks
  2 grey with rusty-brown streaks (SDNHM 49644) – 10YR 5/1 with 7.5YR 4/4 streaks
  3 dark brown-grey with fuscous streaks (SDNHM 48941) – 10YR 5/1 with 10YR 2/2 streaks

F. UPPERTAIL COVERTS
  0 mostly clear rufous, perhaps with a faint dark centre (SDNHM 45510) – 5YR 4/6 x̄throughout
  1 rufous with thin to mid-width fuscous centre (SDNHM 43255) – 5YR 4/6 with 5YR 2.5/2 streaks
  2 warm grey-brown (with a hint of rufous) with mid-width fuscous centre (SDNHM 47781) – 10YR 4/3 with thin 5YR 2.5/1 streaks
  3 warm grey-brown with a wide fuscous centre (SDNHM 49894) – 10YR 4/3 with 7.5YR 2/0 streaks

G. CROWN COLOUR
  0 mostly clear rufous (SDNHM 49109) – 2.5YR 3/6 x̄throughout
  1 rufous with dark centres (SDNHM 44608) – 2.5YR 3/6 with 2.5YR 2.5/2 streaks
  2 rufous-grey with dark centres (SDNHM 38933) – 2.5YR 3/4 with 5YR 2.5/1 streaks
  3 streaked with rufous and fuscous with grey intermixed (SDNHM 43712) – 2.5YR 3/4 with wide 7.5YR 2/0 streaks

H. TIP OF 'TERTIAL' [= INNERMOST SECONDARY] CENTRE
  0 sharply pointed (SDNHM 48709)
  1 softly pointed (SDNHM 42847)
  2 rounded with angled tip (SDNHM 47781)
  3 smoothly rounded (SDNHM 49884)

I. SUBTERMINAL FRINGE OF 'TERTIAL'
  0 dull brown centre with width of rufous subterminal fringe . whitish fringe (SDNHM 46507) – 7.5YR 4/3 centre, 5YR 5/8 subterminal, 10YR 8/2 fringe
  1 fuscous-brown centre with rufous subterminal fringe wide but < outer fringe (SDNHM 48709) – 5YR 2.5/2 centre, 5YR 3/4 subterminal, 10YR 8/2 fringe
  2 narrow (but obvious) rufous subterminal fringe (SDNHM 49644) – 5YR 2.5/1 centre, 5YR 3/3 subterminal, 10 YR 8/1 fringe
  3 faint to absent rufous subterminal fringe (SDNHM 49618) – 7.5YR 2/0 centre, 10YR 8/1 fringe

Table 3 Scoring schemes and standard specimens used for quantifying plumage variation in *Melospiza melodia heermanni*, *M. m. fallax*, and their hybrids. Colour standards are provided following the 1990 version of the Munsell soil colour chart.

SPECIMEN	year	location	Character (see Table 3)									
			A	B	C	D	E	F	G	H	I	total
MVZ 907	1908	Coachella Valley; Mecca	1	3	1	1	1	1	1	1	2	12
SDNHM 48708	1993	Salton Sea; southwest shore	1	2	1	1	0	1	1	1	1	9
SDNHM 3379	1993	Salton Sea; south shore	1	3	1	2	2	1	1	1	1	13
SDNHM 48870	1994	Coachella Valley; Thermal	1	4	1	1	2	1	1	1	0	12
SDNHM 48869	1994	Coachella Valley; Thermal	1	3	1	1	2	0	1	0	1	10
USFWS 23036	2000	Coachella Valley; Indio	1	3	1	1	1	1	0	2	1	11

Table 4 Documented hybrids between *M. m. heermanni* and *M. m. fallax*. The scoring scheme is from Table 3. Aside from an anomalous series of *M. m. heermanni* from El Rosario and vicinity, Baja California (see the text), none of the other 435 specimens or live birds that we scored of these taxa had intermediate plumage.
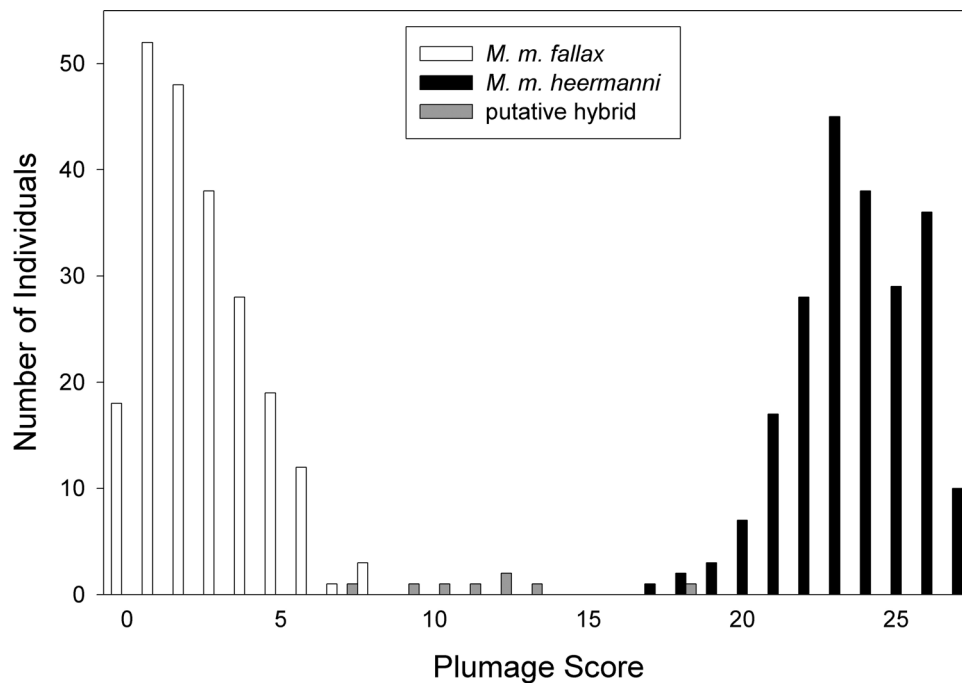
Figure 5 Histogram of plumage scores showing the sharp break between *M. m. heermanni* and *M. m. fallax* in plumage colour and pattern. The limited number of hybrids fall toward the centre of the plumage range (see Tables 3 and 4).

Both subspecies occupy riparian habitats, but habitat structure differs greatly between them. *Melospiza m. heermanni*, a coastal-slope taxon, generally occupies gallery riparian forests dominated by *Populus fremontii*, *Salix* spp., and *Baccharis salicifolius* ('mesoriparian' *sensu* Johnson *et al.*, 1984). Although this subspecies will use riparian scrub, it tends to avoid this habitat if riparian forest is available. These mesoriparian forests show a great deal of vertical heterogeneity, with trees and shrubs spaced widely, ground cover dense, and trees tall. *Melospiza m. fallax*, a Sonoran Desert taxon, generally occupies riparian scrub dominated by non-native *Tamarix ramosissima* and intermixed *Salix gooddingii*, *Allenrolfea occidentalis*, *Pluchea sericea* and *Phragmites australis* ('xeroriparian' *sensu* Johnson *et al.*, 1984). Only in certain locales in the Colorado River drainage (e.g. the Bill Williams River) does this subspecies occupy riparian forest. *Melospiza m. fallax* often reaches peak abundance in dense thickets of *Tamarix*. This xeroriparian habitat is fairly uniform vertically, with trees and shrubs packed tightly, ground cover sparse (i.e. more open ground or water between clumps of vegetation), and trees short.

Despite much inter- and intra-individual variation, Song Sparrow songs can be described as a series of short introductory notes, a central trill, and a closing flourish of 'two-note phrases' (Saunders, 1951). Both *M. m. heermanni* and *M. m. fallax* fit this general description. Yet they differ consistently from each other in a few parameters related to differences in habitat structure, in ways matching predictions of the acoustic adaptation hypothesis (Morton, 1975). The song of *M. m. fallax* has higher-pitched introductory notes and more tightly spaced individual notes within trills and buzzes, apparently stemming from the lesser vertical heterogeneity (males perching atop a shrub will have their song carry farther and experience less attenuation in the riparian scrub of the Sonoran Desert

relative to gallery riparian forest). By corollary, the lower-pitched, more widely spaced song of *M. m. heermanni* is related to the greater attenuation in riparian habitats with substantial vertical heterogeneity. Not only do the subspecies differ on average in the directions predicted by the acoustic adaptation hypothesis, but individual males within each subspecies tend to match predictions as well (Patten *et al.*, 2004b).

Both females and males respond to these differences in song. Females of either subspecies exhibit the strongest preferences for males with homotypic song and plumage. They show equally weak preference for the heterotypic song, regardless of plumage. Males exhibit stronger song recognition, and thus territorial defence, toward homotypic song. Experimental results show that the subspecies mate assortatively and exhibit differential recognition of songs and, at least with females, plumage (Patten *et al.*, 2004b). The evidence thus supports the hypothesis that *M. m. heermanni* and *M. m. fallax* act as good biological species where their ranges meet, satisfying the last criterion for the Song Sparrows of western North America being a ring species.

Genetic divergence

Previous studies of genetic variation across the range of the Song Sparrow (Zink, 1991; Zink & Dittmann, 1993; Fry & Zink, 1998) detected no concordance between mtDNA and morphology and no geographic substructure in mtDNA. Instead there were common mtDNA haplotypes throughout the species' range with, for example, some shared between birds on the Mexican Plateau and Alaska. As a result, subspecies could not be diagnosed, leading Zink and Dittmann (1993) to question the utility of the Song Sparrow in studies of speciation. Their data suggest rapid range expansion following Pleistocene glaciation, effectively 'scattering' mtDNA haplotypes across the continent (Zink & Dittmann, 1993), perhaps from multiple refugia (Fry & Zink, 1998).

As discussed above, using mtDNA to deduce evolutionary relationships and population substructure among subspecies is problematic. Subspecies are defined by continuing gene flow between populations, with adaptation to local environments likely playing a substantial role in geographic variation (e.g. Gloger's and Bergmann's rules). Rapid range expansion (Fry & Zink, 1998) coupled with local adaptation (Aldrich, 1984) would result in strong population structure in morphology but virtually none in mtDNA or other slowly evolving genes shielded from natural selection on the organism. We feel that the conflicting patterns of geographic variation in morphology and genes in the Song Sparrow implies just such a process; indeed, rapidly evolving microsatellites show genetic substructure among various subspecies of the Song Sparrow (Chan & Arcese, 2002; Patten *et al.*, 2004b; Pruett & Winker, 2005; Pruett *et al.*, 2008a,b).

Our study of microsatellite variation (Patten *et al.*, 2004b) found limited gene flow between *M. m. heermanni* and *M. m. fallax* and concordance between genetic and morphological variation, yet there is limited microsatellite data for populations around the ring. Plumage variation was not examined in a study of the four subspecies around San Francisco Bay (*M. m. gouldii*, *M. m. samuelis*, *M. m. maxillaris* and *M. m. pusillula*), but there was no association between mensural and microsatellite variation (Chan & Arcese, 2002, 2003), implying more extensive gene flow among those populations. By contrast, our recent analysis across a vastly broader spatial scale (Pruett *et al.*, 2008b) did find an association between morphology and microsatellites for at least some of the western North American subspecies, including several around San Francisco Bay.

Patten *et al*. (2004b) reported predominantly negative values of F_{IS}, implying sex-biased dispersal (Hartl & Clark, 1989:300), and in most passerines females are the dispersing sex (Clarke *et al*., 1997). The high philopatry of individual Song Sparrows, with dispersal distances estimated at 300 m from demographic data (Nice, 1943) and 6.1 km from mtDNA data (Zink & Dittmann, 1993), likely means that the *M. m. heermanni* × *M. m. fallax* hybrid zone is stable. On the basis of our field observations, we feel it likely that the hybrid zone will prove to be a 'tension zone' (Barton & Hewitt, 1989) maintained by small numbers of *M. m. heermanni* dispersing regularly south into areas occupied by the sedentary *M. m. fallax*. Alternatively, it may be a 'bimodal hybrid zone' (Jiggins & Mallet, 2000), in which hybrids are rare and parental forms predominate because ecology and assortative mating are keys to reproductive isolation. Detailed demographic studies are needed to determine the nature of the hybrid zone.

Concluding remarks

A principal question in evolutionary biology is whether populations can diverge when there is extensive gene flow between them. The position emerging from the evolutionary synthesis was that divergence was impossible unless gene flow was negligible (Dobzhansky, 1937; Mayr, 1942). Conventional Mayrian speciation models imply that genetic incompatibilities (most forms of postzygotic isolation) preceded acquisition of sexual isolation, habitat differentiation, or other forms of prezygotic isolation. This idea stems from the notion that reproductive isolation evolves in allopatry as a genetic byproduct of drift or local selection. Recent reviews have challenged this position (Coyne & Orr, 1989; Grant & Grant, 1997; Schluter, 1998; Doebeli *et al.*, 2005), and population genetics theory makes it clear that divergence can occur in the face of gene flow either because selection overcomes it (Endler, 1973, 1977; Fry, 2003) or because isolation by distance can be as effective as a simple physical barrier, making parapatric divergence as likely as allopatric (Barton, 1988). Hybrid zones and ecotones are ideal for studying processes of speciation (Barton & Hewitt, 1989) and make the study of speciation explicitly ecological. Such studies have aided in the development of two classes of alternatives to conventional models, one incorporating sexual selection, the other habitat selection.

Theory suggests that species divergence can occur through sexually selected traits or if sexual selection accompanies natural selection on these traits (Lande, 1981, 1982; Turner & Burrows, 1995). In birds, sexual isolation between taxa may be related to morphology, which is classically

inherited, and to song, which is (partly) culturally inherited in oscines. Although much song is inherited culturally, female choice on song plays an important role in reproductive isolation (Searcy & Andersson, 1986; Remsen, 2005), and song learning may enhance the speciation process (Lachlan & Servedio, 2004). A growing body of theoretical and empirical evidence suggests that speciation can also occur via disruptive selection on habitat differences (Tauber & Tauber, 1977; Rice, 1984; Rice & Salt, 1988; McKinnon *et al.*, 2004). Competitive exclusion predicts that before divergent forms can coexist they must use resources differently, either via different habitats or character displacement (Patten, 2008). It would be of particular interest if divergence in both sexual isolation and habitat use is discovered, as this coupling is critical if sympatric divergence is to occur (Johnson *et al.*, 1996; Fry, 2003); further, if there were no postzygotic isolation, it would be strong evidence against conventional speciation models (Jiggins & Mallet, 2000).

An ideal system for studying alternative modes of speciation would be a hybrid zone across a clearly defined ecotone and involving distinct taxa whose hybrids can be diagnosed readily and whose postzygotic isolation, habitat selection, and mate choice on both genetically and culturally inherited characters could be examined. The best system would be one wherein taxa are known to be conspecific regardless of the species concept used. The hybrid zone between *M. m. heermanni* and *M. m. fallax* Song Sparrows provides such an ideal. The ecotone through San Gorgonio Pass (the geographic feature connecting the subspecies) is dramatic and sharp, with an elevational change of nearly 1000 m in < 50 km and a concomitant change from a Mediterranean to a desert climate. Morphologies are highly divergent, the taxa occupy distinctly different riparian habitats, females exhibit consubspecific mate preference on song and plumage, and males exhibit consubspecific song recognition, with its associated agonistic behaviour. Lastly, because this hybrid zone is across the end points of a ring species, the taxa must (by definition) be conspecific. The extent of postzygotic isolation remains to be determined, but there is no evidence that hybrids are infertile, and it is possible that the hybrid zone is maintained by repeated dispersal into it by pure individuals – i.e. it is a tension zone, *sensu* Barton and Hewitt (1989).

The remainder of the Song Sparrow ring needs to be studied in similar detail. In particular, data are needed on behavioural ecology in each zone of intergradation (Fig. 3) and genetic variation of all core and hybrid zone populations. Not only can we better characterise the Song Sparrow ring, but we can shed light on its origins. There exist three possibilities: (1) the ring formed by southward expansion of populations, with each fork diverging sufficiently that populations coming into contact at the southern pole no longer interbred (this is the standard model of ring formation); (2) the ring formed by northward expansion, with populations at the southern pole diverging in parapatry while those on each fork diverged insufficiently (e.g. there was less time) to prevent interbreeding when they merged at the north, or (3) the ring has evolved *in situ*, with a sharper boundary at the south pole because it is at the steepest ecotone. Postulated Pleistocene refugia for

the Song Sparrow are the mid-Atlantic coast, Queen Charlotte Islands and probably southern California (Fry & Zink, 1998). This last refugium would have been a source for northward expansion, and both the second and third scenarios are plausible given that only the centre of the ring (e.g. the Sierra Nevada) was glaciated during the Last Glacial Maximum (Ehlers & Gibbard, 2004). That the basilar mtDNA haplotype occurs at the Salton Sea (Fry & Zink, 1998) lends support to a northward expansion model, and the high degree of concordance between plumage and genetics of *M. m. fallax* (Pruett *et al.*, 2008b) may lend further support. This model stands in opposition to the standard model for the evolution of a ring species, but, at the least, our data suggest its plausibility and thus shed light onto the process of speciation. Patterns of song and plumage differentiation are of the same kind as microevolutionary differences frequently documented (and expected) in different populations. That song and plumage differences are associated with assortative mating leads to the important conclusion that speciation can result from microevolution, provided only that selection can overcome gene flow, a likely prospect across an ecocline (Endler, 1973; Barton, 1988; Smith *et al.*, 1997). In many instances, speciation may be little more than the accumulated end product of microevolutionary processes.

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