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.
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 conspecific song and plumage, and males have stronger reactions to conspecific 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 synonyms. 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 (Eremophila 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. keniensis, 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. rivalaris, M. m. goldmani*).

5. Mexican Plateau – small to medium; breast spotted; throat clean white (*M. m. zacapa, 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 (A madon, 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 juvenile 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...
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


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


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


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

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

**Passerella melodia juddi linsdalei** 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


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

**Melospiza melodia melanacha** 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 (♂ 18.0–25.3 g, ¯x = 21.8 g, n = 28; ♀ 18.8–24.0 g, ¯x = 21.1 g, n = 27); wing length moderate (♂ 63–72.5 mm, ¯x = 66.5 mm, n = 171; ♀ 59–71.5 mm, ¯x = 64.1 mm, n = 88); tail length moderate (♂ 62–74 mm, ¯x = 67.7 mm, n = 49; ♀ 55–72 mm, ¯x = 64.4 mm, n = 44); bill length moderate (8.5–10.3 mm, ¯x = 9.3 mm, n = 52); bill deep (7.4–8.4 mm, ¯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; supercilium 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*
The Song Sparrow, *Melospiza melodia*, as a ring species

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 (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.

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 inconsistent 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 conclude that recognition of subspecies through much of eastern North America ‘extends[] 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


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


**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, ♂ 22.2 g, n = 3; ♀ 19.8–21.2 g, ♂ 20.5 g, n = 2); wing length moderate (♂ 67–73 mm, ♂ 67.3 mm, n = 17; ♀ 63–71 mm, ♂ 64.8 mm, n = 15); tail length moderate (♂ 65–73 mm, ♂ 66.4 mm, n = 17; ♀ 66–72 mm, ♂ 64.8 mm, n = 15); bill length moderate (♂ 9.5 mm, n = 25); bill deep (♀ 8.3 mm, n = 25); plumage like *M. m. melanchra* 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 coastaly from Maryland to Georgia.

REMARKS: Remarkably, the type locality of *M. m. fallax* (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 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).

**Melospiza melodia montana** Henshaw

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


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


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

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


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


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


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


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, 8 = 21.3 g, n = 262; ♀ 16.0–26.7 g, 8 = 20.6 g, n = 162), though wings average longer; wing relatively long (♂ 65.5–74 mm, 8 = 69.3 mm, n = 43; ♀ 62.5–71 mm, 8 = 66.2 mm, n = 34); tail relatively long (♂ 63.5–77 mm, 8 = 69.7 mm, n = 43; ♀ 62.5–73 mm, 8 = 67.0 mm, n = 33); bill length moderate (8–11.1, 8 = 9.2 mm, n = 70); bill depth moderate (6.8–8.1, 8 = 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.
Melospiza melodia semidiensis Paynter, 1970, Gabrielson & Lincoln, 1951, Passerella melodia sanaka

Melospiza cinerea cinerea

Melospiza melodia cinerea

Melospiza melodia

Melospiza insignis

n deep (7.6–9.1 mm, \( \bar{x} \))

\boldsymbol{\text{DIAGNOSIS: Size of }} M. \text{ m. maxima} (\sigma \text{’} 44.5–52.7 \, \text{g}, \bar{x} = 47.8 \, \text{g}, n = 9); \sigma \text{’} 45.1–44.1 \, \text{g}, \bar{x} = 42.7 \, \text{g}, n = 4); wing extremely long (\sigma \text{’} 82–86.5 \, \text{mm}, \bar{x} = 83.6 \, \text{mm}, n = 33; \varphi 77–84 \, \text{mm}, \bar{x} = 80.2 \, \text{mm}, n = 18); tail extremely long (\sigma \text{’} 76–86 \, \text{mm}, \bar{x} = 80.8 \, \text{mm}, n = 33; \varphi 75–81 \, \text{mm}, \bar{x} = 77.3 \, \text{mm}, n = 18); bill long (10.9–14.0 \, \text{mm}, \bar{x} = 12.8 \, \text{mm}, n = 28); bill deep (7.6–9.1 \, \text{mm}, \bar{x} = 7.8 \, \text{mm}, n = 44); plumage like \text{ M. m. maxima} but greyer overall. Also note shorter bill (\text{M. m. sanaka} generally \( < 13.0 \, \text{mm}, \text{ M. m. maxima} \) generally \( > 13.5 \, \text{mm})).

\boldsymbol{\text{BIRDS ON THE SEMIDI ISLANDS AVERAGE SLIGHTLY GREYER. A WEAKLY DEFINED SUBSPECIES.}}

\boldsymbol{\text{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).}}

\text{Melospiza melodia sanaka McGregor}

\text{Melospiza sanaka McGregor, 1901, Condor 3:8}

\text{Fringilla cinerea Gmelin, 1788, Syst. Nat. 1(2):922}

[preoccupied; \( \text{Auk} 25:380, 1908)]

\text{?Emberiza unalaschensis (\text{not of Gmelin}) Brandt, 1836, Descr. Anim. Ross., pl. 2, fig. 4}

\text{Zonotrichia cinerea Gray, 1849, Gen. Birds 2:373}


\text{Melospiza insignis (\text{not of Baird}) Dall, 1873, Proc. Calif. Acad. Sci. 5:27, part}

\text{Melospiza melodia var. insignis Baird, Brewer, & Ridgway, 1874, Hist. N. Am. Bird 2:30, part}

\text{Melospiza melodia cinerea Grinnell, 1901, Condor 3:20}

\text{Melospiza cinerea Ridgway, 1901, Bull. U. S. Natl. Mus. 50(1):377}


\text{Melospiza melodia sanaka American Ornithologists’ Union, 1908, Auk 25:379}

\text{Passerella melodia sanaka Linsdale, 1928, Condor 30:350}

\text{Passerella melodia semidiensis Linsdale, 1928, Condor 30:350}

\text{Melospiza melodia amaka Gabrielson & Lincoln, 1951, Condor 53:253}

\text{Zonotrichia melodia amaka Paynter, 1970, Check-list Birds World 13:49}

\text{Zonotrichia melodia insignis Paynter, 1970, Check-list Birds World 13:49}

\text{HOLOTYPE: USNM 52476; adult \( \varphi \text{’} \), 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 \( \sigma \text{’} \), 24 May), USNM 52478 (lost), USNM 52479 (adult \( \sigma \text{’} \), 10 June), USNM 54536 (adult, 25 September), and USNM 54537 (adult, 12 August).

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

\text{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.}}

\text{Melospiza melodia insignis Baird}

\text{Melospiza insignis Baird, 1869, Trans. Chicago Acad. Sci. 1:319, pl. 29, fig. 2}

\text{Zonotrichia insignis Gray, 1870, Hand-list 2:94}

\text{Melospiza melodia var. insignis Coues, 1872, Key N. Am. Birds, p. 140}

\text{Melospiza cinerea (not Fringilla cinerea) Ridgway, 1880, Proc. U. S. Natl. Mus. 3:3}

\text{Melospiza melodia insignis Goode, 1883, Bull. U. S. Natl. Mus. 25:328}


\text{Melospiza cinerea insignis Ridgway, 1901, Bull. U. S. Natl. Mus. 50(1):376}

\text{Passerella melodia insignis Linsdale, 1928, Condor 30:350}

\text{Zonotrichia melodia insignis Paynter, 1970, Check-list Birds World 13:49}
**Melospiza melodia kenaiensis** Ridgway

Melospiza melodia kenaiensis Ridgway, 1900, Auk 17:29


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


**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, \( \bar{x} = 29.7 \) g, 9; ♂️ 29.6 g, 1; wing long (♂️ 76.5–80 mm, \( \bar{x} = 78.2 \) mm, 8; ♂️ 78.2 mm, 11); tail long (72–73 mm, \( \bar{x} = 72.5 \) mm, 9; 75.4 mm, 1); bill long (10.5–11.3 mm, \( \bar{x} = 10.9 \) mm, 3); bill depth moderate (7.1–7.6 mm, \( \bar{x} = 7.4 \) mm, 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 coastaly south to British Columbia.

**Melospiza melodia caurina** Ridgway

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


Melospiza fasciata rufina (not *Passerella rufina* Bonaparte)


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


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


**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, \( \bar{x} = 28.7 \) g, 9; ♂️ 25.5–30.0 g, \( \bar{x} = 27.0 \) g, 6); wing long (♂️ 69–80 mm, \( \bar{x} = 72.6 \) mm, 23; ♂️ 67–71 mm, \( \bar{x} = 68.8 \) mm, 5); tail long (♂️ 63.5–73 mm, \( \bar{x} = 68.0 \) mm, 23; ♂️ 62.5–67 mm, \( \bar{x} = 64.8 \) mm, 5); bill length moderate (9.1–11.3 mm, \( \bar{x} = 10.0 \) mm, 11); bill depth moderate (6.2–7.6 mm, \( \bar{x} = 6.8 \) mm, 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


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


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


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

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


**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, \( \bar{x} = 71.6 \) mm, 42; ♂️ 64–70.5 mm, \( \bar{x} = 67.2 \) mm, 18); tail long (♂️ 60–76 mm, \( \bar{x} = 68.6 \) mm, 42; ♂️ 58–70.5 mm, \( \bar{x} = 63.6 \) mm, 29); bill length moderate (9.1–11.9 mm, \( \bar{x} = 10.4 \) mm, 26); bill depth moderate (6.2–7.8 mm, \( \bar{x} = 6.9 \) mm, 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

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 meloida guttata Henshaw, 1879, Ornithol. Rep. Wheeler’s Surv., p. 299, part
Melospiza fasciata rufina Fisher, 1893, N. Am. Fauna 7:100, part
Melospiza cinerea phaea Fisher, 1902, Condor 4:36, part
Melospiza melodia phaea Grinnell, 1915, Pac. Coast Avifauna 11:123
Passerella melodia morpha Linsdale, 1928, Condor 30:350

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. phaea (Deignan, 1961:664). A cotype of F. guttata Nuttall [=M. m. morpha] is a . . . 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, ♂ 23.6 g, n = 27; ♀ 16.5–29.9 g, ♀ 22.1 g, n = 30); wing length moderate (♂ 61.5–71.5 mm, ♂ 67.1 mm, n = 96; ♀ 62–69 mm, ♂ 65.0 mm, n = 26); tail length moderate (♂ 58–73 mm, ♂ 65.2 mm, n = 96; ♀ 57.5–68 mm, ♂ 63.0 mm, n = 26); bill length moderate (8.1–10.9 mm, ♂ 9.4 mm, n = 89); bill shallow (6.0–7.0 mm, ♂ 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. Distinquished 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. morpha was not applied until 1899. This confusion led to questions about designation of the type. Subspecific limits between M. m. morpha, M. m. inexpectata, 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. morpha and M. m. rufina, but merged M. m. inexpectata 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 Umqua River, Oregon, USA; 1 December 1901; Edmund Heller) was nothing more than a name for a narrow hybrid zone between M. m. morpha 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 fasciata ingersolli McGregor, 1899, Bull. Cooper Ornithol. Club 1:35
Melospiza melodia merrilli American Ornithologists’ Union, 1908, Auk 25:379
Melospiza melodia inexpectata [sic] Stone, 1912, Auk 29:117
Passerella melodia inexpectata Linsdale, 1928, Condor 30:350
Passerella melodia merrilli Linsdale, 1928, Condor 30:350

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

DIAGNOSIS: Size of M. m. morpha (♂ 17.8–30.5 g, $\bar{x}$ = 23.4 g, n = 59; ♀ 17.7–28.0 g, $\bar{x}$ = 21.8 g, n = 41), though tail averages longer; wing length moderate ($\bar{x}$ 63–72 mm, $\bar{x}$ = 67.4 mm, n = 36; ♀ 61–68.5 mm, $\bar{x}$ = 66.1 mm, n = 30); tail length moderate ($\bar{x}$ 63–74 mm, $\bar{x}$ = 68.2 mm, n = 36; 60–71 mm, $\bar{x}$ = 64.8 mm, n = 30); bill short (8.0–9.3 mm, $\bar{x}$ = 8.5 mm, n = 43); bill shallow (5.5–6.8 mm, $\bar{x}$ = 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 ash brown, with feathers moderately edged grey; dorsal streaks dark brown, relatively crisp; supercilia grey; malar brown. Distinguished from M. m. morpha by ashier (less reddish) colouration overall and darker, more contrasting streaking. The plumage of M. m. merrilli is intermediate between M. m. morpha 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.] morpha.’ The intermediacy of M. m. merrilli, however, is consistent and definable. M. m. ingersollii (holotype: AMNH 405733; adult ♂; Battle Creek, Tehama County, California, USA; 19 October 1898; Richard C. McGregor 2222) is a synonym of M. m. merrilli (Ridgway, 1901:362; Grinnell, 1932). It was collected between M. m. inexspectata and M. m. merrilli.

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. morpha, 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. morpha, 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. morpha (Prueet 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 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; 25 May 1889; Richard C. McGregor 288.

DIAGNOSIS: Smaller than M. m. morpha ($\bar{x}$ 18.1–23.5 g, $\bar{x}$ = 21.0 g, n = 17; ♀ 17.2–21.4 g, $\bar{x}$ = 19.0 g, n = 19); wing short ($\bar{x}$ 58.5–68 mm, $\bar{x}$ = 62.3 mm, n = 38; ♀ 54.5–65 mm, $\bar{x}$ = 60.0 mm, n = 23); tail short ($\bar{x}$ 56–65 mm, $\bar{x}$ = 60.4 mm, n = 38; ♀ 52.5–63 mm, $\bar{x}$ = 58.4 mm, n = 23); bill short (7.7–9.2 mm, $\bar{x}$ = 8.6 mm, n = 24); bill somewhat shallow (5.6–7.4 mm, $\bar{x}$ = 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. morpha by smaller size and crisper, darker streaking, from M. m. merrilli by smaller size and redder colouration overall. Generally intermediate between M. m. morpha and M. m. Gouldi.

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

REMARKS: Regarding M. m. phaea, see remarks under M. m. morpha.

California Group

Melospiza melodia Gouldii Baird


Melospiza melodia santaecruicis Grinnell, 1901, Condor 3:92


Passerella melodia Gouldii Lindsdale, 1928, Condor 30:350

Passerella melodia santaecruicis Lindsdale, 1928, Condor 30:350

Melospiza melodia gouldii McGregor, 1899, Bull. Cooper Ornithol. Club 1:87
Passerella melodia samuelis Linsdale, 1928, Condor 30:350

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, \( \bar{x} = 19.8 \) g, \( n = 331 \); ♀ 15.1–25.0 g, \( \bar{x} = 18.3 \) g, \( n = 182 \)), though tail much longer; wing short (♂ 58–64 mm, \( \bar{x} = 61.2 \) mm, \( n = 99 \); 55.5–59 mm, \( \bar{x} = 58.4 \) mm, \( n = 12 \)); tail length moderate (♂ 63.5–69 mm, \( \bar{x} = 67.4 \) mm, \( n = 18 \); ♀ 56–67 mm, \( \bar{x} = 64.7 \) mm, \( n = 12 \)); bill short (7.8–9.4 mm, \( \bar{x} = 8.6 \) mm, \( n = 267 \); Marshall, 1948); bill somewhat shallow (6.1–7.1 mm, \( \bar{x} = 6.6 \) 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. sántaeacruceans (holotype: MVZ 35969); adult ♀; San Franciscoquito 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. *sántaeacruceans* 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. sántaeacruceans in the same manner.

**Melospiza melodia samuelis** (Baird)

*Zonotrichia gouldii* Gray, 1870, Hand-list 2:64
*Melospiza melodia var. gouldii* Coues, 1872, Key N. Am. Birds, p. 139
*Melospiza samuelis* Baird, Brewer, & Ridgway, 1874, *Hist. N. Am. Birds* 2, pl. 27, fig. 7

*Grinnell*

*Melospiza melodia maxillaris* Grinnell

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, \( \bar{x} = 20.3 \) g, \( n = 73 \); ♀ 17.0–22.3 g, \( \bar{x} = 18.8 \) g, \( n = 43 \)), though with bill longer and deeper, tail shorter; wing short (59–66 mm, \( \bar{x} = 62.5 \) mm, \( n = 36 \); Marshall, 1948); tail short (62 mm, \( n = 1 \)); bill length moderate (8.6–10.1 mm, \( \bar{x} = 9.4 \) mm, \( n = 178 \); Marshall, 1948); bill deep (7.2–8.4 mm, \( \bar{x} = 7.8 \) 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; supercilium ashy; malar reddish fuscous. Also note the distinctive swollen base of the bill, recalling McCown’s Longspur (Calcarius meccornii).

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. heermannii, 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
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, \(\bar{x} = 18.7 \, g\), \(n = 66\); ♀ 15.3–18.5 g, \(\bar{x} = 16.9 \, g\), \(n = 49\)), but smallest subspecies in overall dimensions; wing extremely short (♂ 54.5–63 mm, \(\bar{x} = 58.7 \, mm\), \(n = 81\); ♀ 53.5–61.5 mm, \(\bar{x} = 59.9 \, mm\), \(n = 26\)); tail short (♂ 50–63 mm, \(\bar{x} = 59.8 \, mm\), \(n = 32\); ♀ 52–61 mm, \(\bar{x} = 57.4 \, mm\), \(n = 26\)); bill short (7.6–9.0 mm, \(\bar{x} = 8.3 \, mm\), \(n = 206\); Marshall, 1948); bill shallow (5.5–6.8 mm, \(\bar{x} = 6.2 \, mm\), \(n = 226\); 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 skirtling 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 heermannii Baird


Melospiza melodia var. heermannii [sic] Coues, 1872, Key N. Am. Birds, p. 139
Melospiza melodia var. heermannii Coues, 1873, Check List, no. 169d
Melospiza melodia heermannii Ridgway, 1874, Bull. Essex Inst. (Oct.), p. 171
Melospiza fasciata var. heermannii Ridgway, 1877, Ornithol. 40th Parallel, p. 481
Melospiza fasciata samuelis (not Ammodramus samuelis Baird) Belding, 1883, Proc. U. S. Natl. Mus. 5:528, part
Melospiza fasciata fasciata (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 melodia mailliardi Grinnell, 1911, Univ. Calif. Publ. Zool. 7:197
Passerella melodia cooperi Linsdale, 1928, Condor 30:350
Passerella melodia heermannii Linsdale, 1928, Condor 30:350
Passerella melodia mailliardi Linsdale, 1928, Condor 30:350

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, \(\bar{x} = 20.3 \, g\), \(n = 126\); ♀ 17.0–26.0 g, \(\bar{x} = 19.3 \, g\), \(n = 89\)), though tail shorter; wing short (♂ 57.5–71.5 mm, \(\bar{x} = 63.1 \, mm\), \(n = 124\); ♀ 57–64 mm, \(\bar{x} = 59.7 \, mm\), \(n = 26\)); tail length moderate (♂ 55.5–74.5 mm, \(\bar{x} = 64.8 \, mm\), \(n = 121\); ♀ 57–65.5 mm, \(\bar{x} = 64.8 \, mm\), \(n = 14\)); bill length moderate (8.5–10.6 mm, \(\bar{x} = 9.6 \, mm\), \(n = 22\)); bill depth moderate (6.1–7.4 mm, \(\bar{x} = 6.9 \, mm\), \(n = 35\)); 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. heermannii generally < 7.2 mm, M. m. maxillaris generally > 7.5 mm), from M. m. montana by darker colouration overall, olive

The Song Sparrow, Melospiza melodia, as a ring species | 45
Melospiza melodia clementae


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


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

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

Zonotrichia melodia coronatorum 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, ℋ 22.2 g, n = 21; ♀ 19.0–25.0 g, ℋ 21.5 g, n = 18), though tail and bill shorter; wing short (♂ 57–66.5 mm, ℋ 63.0 mm, n = 145; ♀ 58–63.5 mm, ℋ 60.9 mm, n = 39); tail short (♂ 53–68.5 mm, ℋ 61.8 mm, n = 108; ♀ 55.5–69.5 mm, ℋ 61.2 mm, n = 23); bill somewhat short (♂ 8–8.7 mm, ℋ 8.3 mm, n = 12); bill depth moderate (6.4–7.6 mm, ℋ 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.
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 ♂); 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 51353; adult ♂; San Miguel Island, California, U.S.A.; 21 September 1927; Chester C. Lamb 7930) and M. m. clementae (holotype: USNM 117620; adult ♂; 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.

<table>
<thead>
<tr>
<th></th>
<th>Culmen length (mm)</th>
<th>Tarsus length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>San Clemente Island (♂, n = 10)</td>
<td>10.77 ± 0.48 (10.1–11.7)</td>
<td>20.64 ± 0.62 (19.8–21.7)</td>
</tr>
<tr>
<td>Islas Los Coronados (♂, n = 10)</td>
<td>10.61 ± 0.46 (9.7–11.2)</td>
<td>19.50 ± 0.75 (18.3–20.8)</td>
</tr>
<tr>
<td>San Clemente Island (♀, n = 3)</td>
<td>10.77 ± 0.38 (10.4–11.3)</td>
<td>19.97 ± 0.12 (19.8–20.1)</td>
</tr>
<tr>
<td>Islas Los Coronados (♀ n = 10)</td>
<td>10.22 ± 0.47 (9.4–11.0)</td>
<td>18.51 ± 0.82 (17.4–19.8)</td>
</tr>
</tbody>
</table>

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

**Melospiza melodia fallax** (Baird)


*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


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

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


**Holotype:** USNM 10281; adult, sex?; Pueblo Creek, n. of Prescott, Yavapai County, Arizona, USA; 22 January 1854; Caleb B. R. Kennerly 51.

**Diagnosis:** Smaller than *M. m. montana* (♂ 16.0–23.0 g, ♀ 18.6 g, n = 52; ♀ 13.5–20.5 g, x = 17.0 g, n = 30), though wings shorter; wing length moderate (♂ 58.5–71.5 mm, x = 67.2 mm, n = 61; ♀ 60–69.5 mm, x = 63.9 mm, n = 25); tail length moderate (♂ 65.5–73.5 mm, x = 69.8 mm, n = 26; ♀ 60.5–71.5 mm, x = 66.4 mm, n = 26); bill length moderate (8.0–9.0 mm, x = 8.6 mm, n = 12); bill depth moderate (6.5–7.4 mm, 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. Yager), 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 melodia rivularis* Oberholser, 1899, *Auk* 16:183


*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 cootypes and a series of toptotypes of *M. m. rivularis* (Grinnell 1928b:177). Various toptotypes 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, ñ = 23.9 g, n = 23; ♀ 19.9–27.1 g, ñ = 22.7 g, n = 15); wing relatively long (♂ 68.5–73 mm, ñ = 71.1 mm, n = 10; ♀ 64–69 mm, ñ = 66.6 mm, n = 7); tail relatively long (♂ 70.5–75 mm, ñ = 72.9 mm, n = 9; ♀ 66–73 mm, ñ = 68.8 mm, n = 7); bill relatively long (9.5–10 mm, ñ = 9.7 mm, n = 13); bill depth moderate (6.9–7.4 mm, ñ = 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. heermannii*).

**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 higher-latitude populations. However, only that the Song Sparrow conforms to Gloger’s rule, the tendency for colouration to be more heavily pigmented in higher-latitude populations. Moreover, it is likely that the plumage of *Z. m. rivularis* is not as heavily pigmented as that of *M. m. fallax* (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


**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, ñ = 67.1 mm, n = 24; ♀ 61–67 mm, ñ = 63.3 mm, n = 31); tail short (♂ 56–68 mm, ñ = 63.1 mm, n = 22; ♀ 56–63 mm, ñ = 60.0 mm, n = 29); bill length moderate (8.3–9.9 mm, ñ = 9.1 mm, n = 55); bill shallow (5.7–6.7 mm, ñ = 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 Panindicuario; also, perhaps, at Laguna Chapala, Jalisco.

**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 ♀ 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.

**Melospiza melodia goldmani** Nelson

*Melospiza melodia goldmani* Nelson, 1899, Auk 16:29

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


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, ñ = 71.7 mm, n = 13; ♀ 65–71 mm, ñ = 67.3 mm, n = 7); tail relatively long (♂ 67–78 mm, ñ = 72.1 mm, n = 12; ♀ 64–69 mm, ñ = 66.6 mm, n = 7); bill relatively long (9–10.6 mm, ñ = 9.6 mm, n = 17); bill shallow (5.9–6.6 mm, ñ = 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. morpha* 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 ♀ 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.

**Melospiza melodia adusta** Nelson

*Melospiza adusta* Nelson, 1899, Auk 16:28

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


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, ♂ 67.8 mm, n = 24; ♀ 61–68 mm, ♂ 64.9 mm, n = 33); tail length moderate (♂ 60–70 mm, ♂ 65.1 mm, n = 63; ♀ 58–66 mm, ♂ 62.1 mm, n = 33); bill length moderate (♂ 8.4–10.3 mm, ♂ 9.1 mm, n = 105; Dickerman, 1963); bill shallow (5.6–6.9 mm, ♂ 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 from near Toluca, Edo. México, north and west to Tarandacuao, Guanajuato, 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 villai Phillips & Dickerman

Melospiza melodia villai Phillips & Dickerman, 1957, Auk 74:380
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 Río [=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, ♂ 71.4 mm, n = 78; ♀ 61–72 mm, ♂ 67.5 mm, n = 35); tail relatively long (♂ 65–75 mm, ♂ 68.8 mm, n = 75; ♀ 60–72 mm, ♂ 66.0 mm, n = 30); bill length moderate (♂ 8.3–10.1 mm, ♂ 9.2 mm, n = 115; Dickerman, 1963); bill shallow (5.7–6.8 mm, ♂ 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, Guanajuato, and west to San Cayento, México.

REMARKS: Dickerman (1963:43) 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 Patzcuaro to determine the extent of character variation in the region.

Melospiza melodia mexicana Ridgway

Melospiza melodia var. mexicana Ridgway, 1874 in Baird, Brewer, & Ridgway, Hist. N. Am. Birds 2:18
?Melospiza pectoralis Müller, 1865, Reise Mex. 3:583
Melospiza fasciata mexicana Ferrari-Pérez & Ridgway, 1886, Proc. U. S. Natl. Mus. 9:144
Melospiza heermannii (not of Baird) Salvin & Godman, 1873, Nomen. Avifauna Neotrop., p. 32, part
Melospiza heermannii Salvin & Godman, 1886, Biol. Centr.-Am., Aves 1:388, part
Melospiza melodia mexicana Oberholser, 1899, Auk 16:183
Passerella mexicana Linsdale, 1928, Condor 30:350
Passerella melodia pectoralis Miller, 1956, Evolution 10:264
Zonotrichia melodia nicaeae Paynter, 1970, Check-list Birds World 13:52
Zonotrichia melodia mexicana Paynter, 1970, Check-list Birds World 13:52

RANGE: Resident. México in upper Río Lerma drainage from near Toluca, Edo. México, north and west to Tarandacuao, Guanajuato, and west to San Cayento, México.
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.
   B. Streaks brown.
   1. Dorsum grey; size large (±40 g).
      a. Paler; greyer .............. M. m. maxima
      b. Darker; browner; smaller (±35 g) ......................... M. m. sanaka
   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) Soofter ................. M. m. rufina
            (b) Redder .................. M. m. morpha
         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. heermannii
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. morphina/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. kenaensis 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
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. ’santaecrasis’*) exhibiting a mosaic of intermediate characters. Local differentiation around San Francisco Bay of *M. m. maxillaris*, yellow *M. m. pusillus*, 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 $\bar{x}_{\text{fallax}} = 67.0 \pm 3.0$ mm, $\bar{x}_{\text{heermanni}} = 62.7 \pm 3.0$ 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 (±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 (White-water 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 throughout

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 2.5/1 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 throughout

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, 50:50 (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 throughout

E. Sides of Neck/Nape
0 dull clay-grey without streaks (SDNHM 48785) – 10YR 5/2 throughout
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 throughout
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 throughout
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.
The Song Sparrow, *Melospiza melodia*, as a ring species

<table>
<thead>
<tr>
<th>SPECIMEN</th>
<th>year</th>
<th>location</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
<th>I</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>MVZ 907</td>
<td>1908</td>
<td>Coachella Valley; Mecca</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>SDNHM 48708</td>
<td>1993</td>
<td>Salton Sea; southwest shore</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>SDNHM 3379</td>
<td>1993</td>
<td>Salton Sea; south shore</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>SDNHM 48870</td>
<td>1994</td>
<td>Coachella Valley; Thermal</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>SDNHM 48869</td>
<td>1994</td>
<td>Coachella Valley; Thermal</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>USFWS 23036</td>
<td>2000</td>
<td>Coachella Valley; Indio</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>11</td>
</tr>
</tbody>
</table>

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 structure 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. Plume 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. pusillum*), 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 (Hart & 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) precede 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. h. heermannini 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 interbreed (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. falax (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.

Acknowledgements

We thank Peter Arcese and Yvonne L. Chan at the University of British Columbia for microsatellite screening. The following individuals kindly allowed access to and/or provided data about specimens in their care: George F. Barrowclough and Christine Blake (American Museum of Natural History), Carla Cicero and Ned K. Johnson (Museum of Vertebrate Zoology), René Corado (Western Foundation of Vertebrate Zoology), James P. Dean (National Museum of Natural History), Kimball L. Garrett (Natural History Museum of Los Angeles County), Michael McNall (Royal British Columbia Museum), James R. Northern (Moore Laboratory of Zoology), Eric Pasquet (Muséum National d’Histoire Naturelle), Alison Pirie and Douglas Siegel-Causey (Muséum of Comparative Zoology), and David Willard (Field Museum of Natural History). Richard A. Erickson and Thomas E. Wurster supplied notes on sparrows in central Baja California. MAP’s work was partly funded by GAANN and Block Grant Fellowships from the Department of Biology at the University of California–Riverside and a collection study grant from the American Museum of Natural History. A nascent version of this manuscript benefited from comments by Leonard Nunney, John T. Rotenberry, Philip Unitt and Marlene Zuk, and Barry Clarke, Darren E. Irwin, Shawn R. Kuchta, and Pamela C. Rasmussen greatly improved the submitted version.

References


GOLDMAN, E.W. 1951. Biological investigations of Mexico. Smithsonian Miscellaneous Collections 115.


Michael A. Patten and Christin L. Pruett


