

A CONTACT ZONE BETWEEN COASTAL AND INTERIOR FOX SPARROWS IN SOUTH-CENTRAL ALASKA*

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ABSTRACT: I report observations, supported by museum voucher specimens, photographs, and audio recordings, from an area of breeding contact between two divergent groups of subspecies of the Fox Sparrow (*Passerella iliaca*) in upper Cook Inlet, south-central Alaska. In this area, covering ~50 km², the interior *iliaca* group comes in contact with the Pacific coast *unalaschcensis* group in lowland mixed boreal forest. Phenotypically pure *P. i. zaboria* and *P. i. sinuosa* (subspecies representing the *iliaca* and *unalaschcensis* groups, respectively) occur in approximately equal abundances and outnumber intermediate phenotypes. These subspecies co-occur on a fine scale, males of *zaboria* and *sinuosa* often holding adjacent territories. I conclude that some form of pre- or post-zygotic isolating mechanism between these two subspecies-groups is hindering free interbreeding.

Areas of secondary contact between closely related taxa form ideal scenarios for studying myriad aspects of compatibility, isolating mechanisms, and speciation (e.g., Harrison 1993). Although intermediate phenotypes indicating regions of hybridization have been recognized since early in the biological exploration of North America (e.g., Audubon in 1843, *in* Short 1965), focused research on hybrid zones in North America started in earnest with descriptions of clines in plumage variation (e.g., Short 1965, Rising 1983). Subsequently, research on hybrid zones has expanded into more detailed studies of the associations among plumage, vocalizations, and genomic clines (e.g., Dixon 1989, Mettler and Spellman 2009, Manthey and Robbins 2016, Toews et al. 2016, Irwin et al. 2018, Billerman et al. 2019, Oswald et al. 2019). Levels of compatibility and hybridization across these secondary contact zones vary with degree of divergence and breeding isolation between contacting taxa and cover a continuum from free interbreeding with wide clines of intermediate phenotypes, as in the flickers (e.g., Short 1965), to very narrow contact or overlap zones, as in the scrub-jays (e.g., Delaney et al. 2008). The latter scenario may result in an overlap zone with a mix of phenotypes at any single site including apparently pure parental and intermediate phenotypes.

Although some contact zones are very well studied (e.g., Sibley and Short 1964, Rising 1970, Jacobsen and Ormland 2012, Baldassarre et al. 2014, Walsh et al. 2020), others remain barely described. Despite the attention contact zones have received from evolutionary and genomic research, there is still a

* I dedicate this paper to the memory of Leonard J. Peyton (1924–2010), a determined field ornithologist and a pioneer in audio recording the vocalizations of Alaska's birds. He harbored a keen interest in the variation of the Fox Sparrow's song, particularly in the contact area between subspecies groups in south-central Alaska, including upper Cook Inlet. Leonard's audio recordings were deposited at the University of Alaska Museum's Film Center, documenting his interest in the subject. I hope he would be proud to see a subject so close to his heart come into print.

need for descriptive ornithological work on under-studied areas of contact. Here I take the opportunity to describe a poorly known area of contact between two subspecies-groups of the Fox Sparrow (*Passerella iliaca*) to provide a foundation for future research.

The Fox Sparrow is “variable to an extreme degree” (Swarth 1920) and comprises 19 described subspecies, ranking it among the species with the most complex geographic variation in North America. These 19 subspecies are parsed into three (Swarth 1920) or four (Zink and Weckstein 2003) groups and have also been considered to represent four species (e.g., Gill et al. 2020), though the contact zones remain poorly studied. Two subspecies-groups occur in Alaska, the *iliaca* group, which nests across boreal North America from western Alaska to maritime Canada, and the *unalaschcensis* group, which nests along the Pacific coast from southern British Columbia to the eastern Aleutian Islands (Gibson and Withrow 2015). Within Alaska the *iliaca* group is represented by subspecies *zaboria* and the *unalaschcensis* group by the subspecies *unalaschcensis*, *insularis*, *sinuosa*, *annectens*, *townsendi*, and *chilcatensis* (Gibson and Withrow 2015).

The *iliaca* and *unalaschcensis* groups come into breeding contact in limited areas where interior and coastal faunas mix along the Pacific coast. From intermediate specimens collected in the winter range, Swarth (1920) suggested that these groups interbreed, and Zink (1994) found evidence of genetic mixing between these groups near Telegraph Creek in British Columbia. Williamson and Peyton (1962) discussed an area of confusing mixing of three subspecies on the Alaska Peninsula, where they suggested *unalaschcensis*, *sinuosa*, and *zaboria* all came into breeding contact. Of interest, Williamson and Peyton (1962) noted that intergrades between *zaboria* and *unalaschcensis* or *sinuosa* were rare and that this zone of contact was narrow, suggesting recent contact of well-differentiated forms. If contact between *zaboria* and *chilcatensis* or *townsendi* occurs in major river drainages along the Pacific coast of southeastern Alaska, such contact has not been noted in the literature. In south-central Alaska there are three known regions of contact between *sinuosa* and *zaboria*: the Copper River valley, the Tsina/Tiekel River drainage inland of Valdez, and the Cook Inlet area (Williamson and Peyton 1962, Gibson and Withrow 2015; University of Alaska Museum [UAM] specimens). Regarding the Cook Inlet contact area near Anchorage, Williamson and Peyton (1962:63) were the first to make mention of this apparently unknown contact area and noted that “hybrids are rare, even in areas where pairs of both races nest in proximity.” These areas are known for drawing interior taxa to otherwise coastal faunal regions, and vice versa (Gibson and Withrow 2015).

Here I detail observations from a contact area in upper Cook Inlet made opportunistically over four years, assess the breeding interaction between these two subspecies, and describe their variation in plumage and voice. I mean this publication to provide preliminary documentation of the poorly understood contact area in upper Cook Inlet in hopes that future research may build on this groundwork.

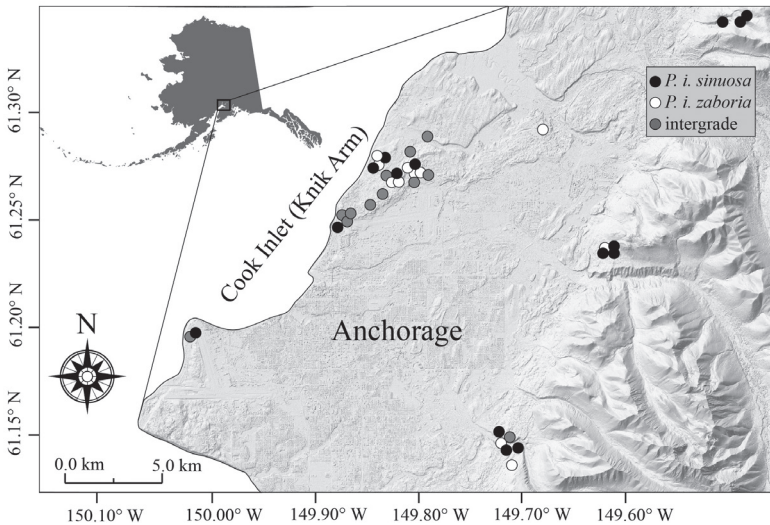


FIGURE 1. Map of the Anchorage area and foothills of the Chugach Mountains with sites of specimens of *Passerella iliaca* indicated by circles. Black fill, the coastal subspecies *sinuosa*; white fill, the interior subspecies *zaboria*; gray fill, intermediate specimens. Note the thorough spatial mixing of phenotypes in this area.

METHODS

Over four years (2013–2016), I made observations, collected specimens (deposited at the UAM, in Fairbanks), and made audio recordings (deposited at the Macaulay Library, Cornell Lab of Ornithology [ML]) of breeding Fox Sparrows around upper Cook Inlet, south-central Alaska. Most of the observations were in lowland mature mixed boreal forest ~10 km northeast of Anchorage, an area measuring $\sim 5 \times 10$ km and ranging in elevation from 0 m to 100 m above sea level (61.282° N, 149.800° W; Figure 1). These mixed boreal forests are characterized by aspen (*Populus tremuloides*), balsam poplars (*Populus balsamifera*), and paper birch (*Betula papyrifera*) interspersed with stands of white spruce (*Picea glauca*) and patches of alder (*Alnus* sp.) in natural openings or along forest edges. I also made observations in the foothills of the Chugach Mountains at elevations up to ~600 m (Figure 1). I took note of the habitat associations of territorial birds and any information I could obtain on pairing. All my observations come from late April through June (spring arrival in this area is typically mid- to late April), and most information is from territorial males. I lacked the time required to assess levels of assortative mating and the frequency of mixed pairings by identifying both individuals of a pair. Therefore, it was unusual for me to be able to observe, photograph, or collect a paired female. As my goal was to document this area of contact, my sampling focused on providing representative examples of the phenotypes and does not represent the abundance of each phenotype—intergrades are over-represented in my specimen series with respect to their observed abundance in the field.



FIGURE 2. Side view of Fox Sparrow specimens from the area of contact of *Passerella iliaca zaboria* and *sinuosa* around upper Cook Inlet, south-central Alaska. (A, UAM 34095) Subspecies *zaboria*, representing the interior *iliaca* subspecies-group; (B, UAM 41232) individual of intermediate plumage assumed to be an intergrade; and (C, UAM 36901) subspecies *sinuosa*, representing the coastal *unalaschensis* subspecies-group. Note differences in patterning and coloration of the face, flanks, and greater wing coverts.

Photos by Lucas DeCicco

RESULTS

Between 2013 and 2016, I collected 39 Fox Sparrow specimens, 15 of which have associated audio recordings (Table 1). Twenty-three of these specimens came from the 5×10 -km area of mixed lowland boreal forest described above and represent the mix of phenotypes at a single site in a contact area between the *iliaca* and *unalaschensis* subspecies-groups. Of the 45 nesting-season specimens available from upper Cook Inlet (39 collected from 2013 to 2016 and six collected in 1969), I identified 12 as *zaboria*, 24 as *sinuosa*, and nine as showing intermediate characteristics so presumably representing intergrades. Of the 23 from the 5×10 -km area of lowland mixed boreal forest, I identified eight as *zaboria*, eight as *sinuosa*, and seven as intergrades. Again, this is not an appropriate assessment of the abundance of intergrades because I targeted those phenotypes to provide adequate representation in the specimen series.

On the basis of these specimens and observations I conclude that phenotypically pure examples of *zaboria* and *sinuosa* occur at approximately equal abundances in this area, they freely intermix spatially, and phenotypically intermediate individuals occur but are less numerous than parental phenotypes (Figure 1, Table 1). At this location, it is not uncommon for males of the two taxa to hold neighboring territories, but these subspecies differ in habitat

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TABLE 1 Specimens of the Fox Sparrow from the Anchorage Area, South-Central Alaska

Specimen ^a	Sex	Date	Locality	Latitude	Longitude	Elevation (m)	Audio ^b
<i>P. i. sinuosa</i>							
4337	♂	16 June 1969	Point Woronzof	61.200	-150.022	28	—
4342	♂	16 June 1969	Point Woronzof	61.200	-150.022	28	—
4350	♂	16 June 1969	Point Woronzof	61.200	-150.022	28	—
4357	♂	16 June 1969	Point Woronzof	61.200	-150.022	28	—
4359	♂	16 June 1969	Point Woronzof	61.200	-150.022	28	—
34099	♂	26 May 2013	upper Carol Cr.	61.342	-149.506	537	118745
34100	♂	26 May 2013	upper Carol Cr.	61.342	-149.489	745	—
34101	♂	27 May 2013	S Fork Campbell Cr.	61.144	-149.704	348	118751
34102	♂	1 June 2013	Arctic Valley Rd.	61.235	-149.612	350	118759
36899	♂	17 June 2014	upper Campbell Cr.	61.147	-149.713	274	—
36900	♂	17 June 2014	upper Campbell Cr.	61.150	-149.714	273	—
36901	♂	18 May 2014	upper Campbell Cr.	61.147	-149.713	274	—
38224	♂	19 May 2015	Triangle Lake	61.272	-149.815	107	—
38225	♂	24 May 2015	Ship Creek Valley	61.237	-149.610	400	516992
38226	♂	24 May 2015	Ship Creek Valley	61.236	-149.621	290	—
38227	♂	24 May 2015	Ship Creek Valley	61.237	-149.400	615	516993
38228	♂	23 May 2015	Campbell Track	61.147	-149.712	285	—
38230	♂	19 May 2015	Triangle Lake	61.272	-149.794	89	—
40393	♂	4 June 2016	W end Dena'ina Rd.	61.247	-149.878	41	56804531
40394	♂	23 May 2015	Campbell Track	61.147	-149.713	273	—
40395	♂	15 May 2016	Green Lake	61.281	-149.840	44	—
40397	♂	5 June 2016	W end Dena'ina Rd.	61.248	-149.869	60	—
40398	♂	15 May 2016	Green Lake	61.281	-149.840	44	—
41230	♂	27 May 2017	Fish Lake	61.276	-149.806	98	—
<i>P. i. zaboria</i>							
34095	♂	7 June 2013	Hillberg Lake	61.272	-149.821	62	118767
34096	♂	27 May 2013	S Fork Campbell Cr.	61.136	-149.710	368	118748
34097	♂	1 June 2013	Arctic Valley Rd.	61.237	-149.620	304	118757
36902	♂	17 June 2014	upper Campbell Cr.	61.147	-149.715	244	—
40402	♂	20 May 2015	Sixmile Lake	61.290	-149.793	37	516708
40403	♂	29 May 2016	Triangle Lake	61.272	-149.798	90	64923281
40404	♂	13 May 2015	Green Lake	61.281	-149.838	32	516681
40405	♂	28 May 2016	Triangle Lake	61.272	-149.801	101	—
40406	♂	15 May 2016	Green Lake	61.280	-149.840	35	—
40407	♂	29 May 2016	Fish Lake	61.269	-149.817	94	64923911
40408	♂	14 May 2016	Otter Lake	61.292	-149.680	49	—
41233	♂	27 May 2017	Fish Lake	61.275	-149.809	103	—
<i>P. i. zaboria</i> × <i>sinuosa</i>							
4360	♂	16 June 1969	Point Woronzof	61.200	-150.022	28	—
34098	♂	5 June 2013	Hillberg Lake	61.272	-149.822	56	118764
36903	♂	18 May 2014	Upper Campbell Cr.	61.149	-149.712	274	—
38229	♂	13 May 2015	Sixmile Lake	61.281	-149.807	65	516680
40399	♂	4 June 2016	W end Dena'ina Rd.	61.247	-149.876	41	—
40400	♂	29 May 2016	Fish Lake	61.268	-149.805	93	—
40401	♂	15 May 2016	Triangle Lake	61.261	-149.835	93	—
41231	♂	27 May 2017	W end Dena'ina Rd.	61.248	-149.874	44	—
41232	♂	10 June 2017	Dena'ina Rd. & Fairchild Ave.	61.257	-149.847	75	—

^aAll specimens archived at the University of Alaska Museum (UAM).

^bAll recordings archived at the Macaulay Library (ML), Cornell Lab of Ornithology.

preferences, and their songs are recognizably different in the field. Due in part to this difference in habitat preference, there is also an elevational gradient, with *sinuosa* being more numerous at higher elevations where alder thickets, its preferred habitat, dominate over mixed boreal forest. Only in mixed boreal forest with natural openings with alder thickets did I find thorough spatial mixing of these subspecies.

Phenotype Descriptions and Assessment

The coastal *unalaschcensis* group differs from the interior *iliaca* group in many plumage aspects (Figures 2 and 3). In the *iliaca* group, the facial plumage is much more patterned with rusty-red auriculars contrasting with a gray crown and nape and a pale malar (Figure 2a). In *sinuosa*, the face is plain gray-brown with pale speckling in the lores and distal portion of the malar (Figure 2c). Individuals of subspecies *sinuosa* occurring near Anchorage show slight patterning with diffuse warmer brown plumage along the edge of the auriculars and upper nape into the crown (Figure 2c). The pattern of the mantle differs clearly, with *zaboria* showing a strongly patterned mantle with pale brownish gray contrasting with rich red-brown stripes (Figure 3a), *sinuosa* showing a uniform dark brown mantle (Figure 3c). Following these general patterns, the colors of the tail and upper tail coverts also differ, the tail being a rich rufous contrasting with the rump and back in *zaboria* (Figure 3a), while *sinuosa* has a dark chestnut tail and upper tail coverts barely contrasting with the upper rump and mantle (Figure 3c). Flank and breast patterning also differ: in *zaboria* the chevrons are rufous or chestnut-colored (Figure 2a), in *sinuosa* brown and denser (Figure 2c). The wing pattern, due primarily to the coloration and patterning of the wing coverts, differs with *zaboria* showing rufous-brown greater and median coverts with pale terminal spots that form a double wing bar (Figure 2a), *sinuosa* showing uniformly brown wing coverts (Figure 2c). Specimens I identified as intergrades were intermediate in these plumage characteristics (Figures 2b and 3b). My identifications in the field and of the specimens were based primarily on these characteristics, with specimens also being compared to those from areas that should not show influence from other subspecies.

Intergrades between *zaboria* and *sinuosa* were intermediate, showing a diffusely striped mantle, faint facial pattern with a paler auricular triangle, flanks with streaks intermediate between the light streaks of *zaboria* and the heavy streaks of *sinuosa*, and a faint set of wing bars. In the field, these intermediate individuals might appear to be *sinuosa*, as their overall appearance was darker than *zaboria*, but the more subtle intermediate characteristics listed above clearly separate them from phenotypically pure *sinuosa*. It is worth noting that these phenotypes may not be representative of true levels of intergradation, as may be assessed by molecular techniques. For example, Zink (1994) found mtDNA haplotypes of the *unalaschcensis* group in individuals that appeared to be pure *iliaca* group on the basis of plumage. Thus introgression is likely greater than may be assessed from the phenotype alone.



FIGURE 3. Dorsal view of Fox Sparrow specimens from the area of contact of *Passerella iliaca zaboria* and *sinuosa* around upper Cook Inlet, south-central Alaska. (A, UAM 34095) Subspecies *zaboria*, representing the interior *iliaca* subspecies-group; (B, UAM 41232) individual of intermediate plumage assumed to be an intergrade; and (C, UAM 36901) Subspecies *sinuosa*, representing the coastal *unalaschcensis* subspecies-group. Note the differences in mantle patterning and coloration and coloration and in contrast of the lower back, rump, and tail plumage.

Photos by Lucas DeCicco

Habitat Association

These two subspecies also differed in habitat association, with *zaboria* preferring deciduous boreal forest dominated by paper birch and aspen and *sinuosa* preferring thickets of alder that occurs as a successional or edge species. Within the area of mixed lowland boreal forest near Anchorage (elevation 0 to ~100 m), there are ample disturbed areas or natural openings where alders persist, constituting a natural mosaic of mature deciduous boreal forest and alder thickets (Figure 4). This intermixing of habitats facilitates close association of these two subspecies. A similar mosaic of habitat occurs at middle elevations (~200–400 m) along the foothills of the Chugach Mountains, where I also found both *sinuosa* and *zaboria* co-occurring. Above ~400 m elevation in the Chugach Mountains, however, the habitat changes into subalpine meadows and alder thickets. At this higher elevation I was able to find examples of *sinuosa* only. Although the mosaic of habitat at the lowland site on which I focused is partially a result of anthropogenic disturbance, this same mosaic of habitat occurs naturally both at middle elevations and in lowland areas.

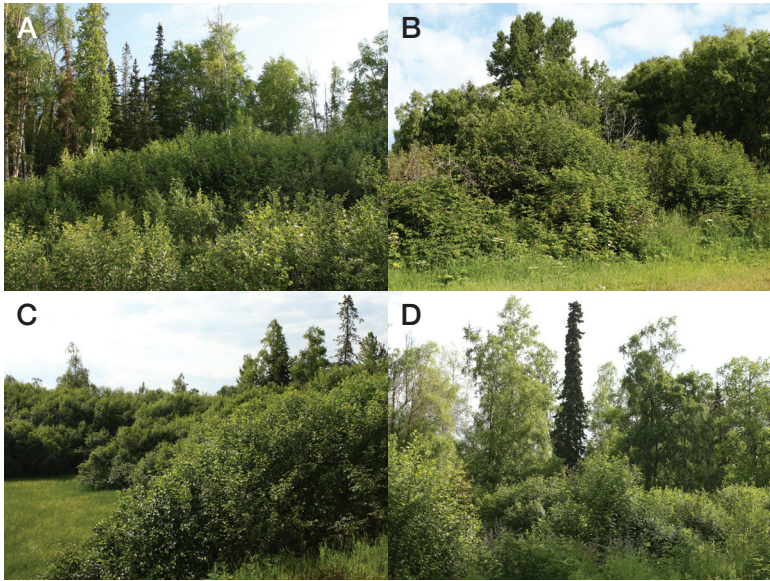


FIGURE 4. Examples of the mosaic of mixed boreal forest and alder thickets near sea level around upper Cook Inlet that hosts representatives of two subspecies-groups of the Fox Sparrow. *Passerella i. zaboria* prefers the mixed boreal forest (e.g., D, and background in rest), whereas *P. i. sinuosa* prefers alder thickets (e.g., C, and foreground in rest).

Photos by Laura McDuffie

Vocal Variation

The songs of *sinuosa* and *zaboria* differ notably in pattern, cadence, and variability. I have not assessed vocal variation between these two taxa comprehensively, but many of the specimens have archived linked audio recordings (Table 1), and here I interpret their songs' differences roughly. The songs of *zaboria* were generally very consistent, both from individual to individual and within a single individual's repertoire, to the extent that around upper Cook Inlet this subspecies appeared to sing a single song type. The songs of *zaboria* were more drawn out, languid, and had more pure-toned upswept notes than did the songs of *sinuosa* (Figure 5). In comparison, the songs of *sinuosa* were much choppier, less lyrical, and varied more, within a single individual's repertoire as well as from bird to bird. Many examples of *sinuosa* gave multiple notes between songs, a pattern that was generally absent in *zaboria*. Many examples of *sinuosa* sang songs of two alternating types. One song type included a terminal series of repeated notes that was absent in songs of *zaboria* (Figure 5). Most individual Fox Sparrows were identifiable to subspecies in the field by their song. More research on this subject is needed to quantify the amount of individual variation and degree of overlap (if any) in songs between these subspecies.

I recorded the songs of three individuals that I later identified as intergrades from specimens (Table 1). One of these (UAM 34098) sang a relatively

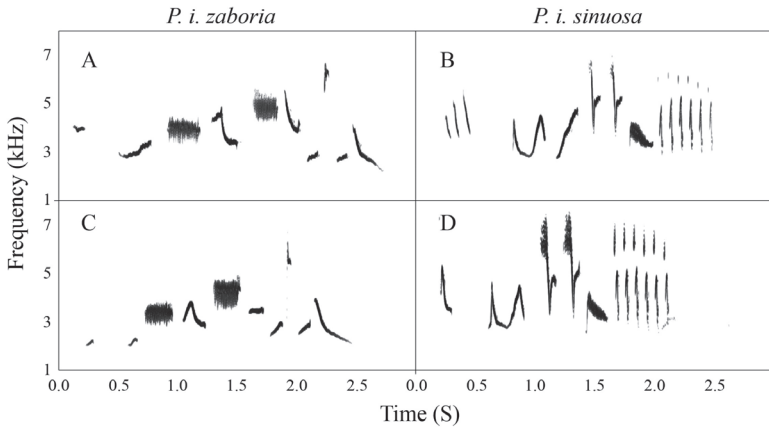


FIGURE 5. Songs of the two subspecies of the Fox Sparrow breeding around Anchorage, from recordings archived at the Macaulay Library (ML), Cornell Lab of Ornithology. Left column, *zaboria*, right column, *sinuosa*. Note the repeated notes at the end of the songs of *sinuosa*, repetitions that are missing entirely from songs of *zaboria*. These selected songs represent the extremes in differences; this topic requires additional investigation. (A), UAM 34095 and ML 118767; (B), UAM 34101 and ML 118751; (C), UAM 34096 and ML 118748; (D), UAM 38225 and ML 516992.

typical *sinuosa* song, another (UAM 40402) sang a relatively typical *zaboria* song, and the last (UAM 38229) sang a song that was intermediate but more similar to that of *zaboria*. This assessment should be taken with care, as characterizing the vocalizations in this area of contact was not my focus, and more work is needed for a thorough understanding of the vocal variation between these two subspecies-groups in areas of contact.

DISCUSSION

This is the first detailed published account of breeding contact between *Passerella iliaca zaboria* and *sinuosa*, representatives of the *iliaca* and *un- alaschensis* subspecies-groups of the Fox Sparrow. From my observations, specimens, and recordings, it is clear that near Anchorage these taxa do not meet in a homogeneous intergradation zone of phenotypically similar but intermediate individuals. The fact that in a discrete zone of contact, parental and intermediate phenotypes occur together, rather than a broad cline of intermediate individuals, suggests that evolutionary pressure is restricting free interbreeding or reducing the fitness of intergrades. There are many mechanisms that could result in this pattern, from pre-zygotic mechanisms such as positive assortative mating to post-zygotic mechanisms such as negative selection of intergrades. Another explanation is that contact between these subspecies is so recent that despite free interbreeding a continuous phenotypic gradient has not yet been established. It is unknown how long *sinuosa* and *zaboria* Fox Sparrows have been in contact in upper Cook Inlet. However, on the basis of specimens at UAM collected by Leonard Peyton in

1969, who was the first ornithologist to make note of this contact area, and the brief description in Williamson and Peyton (1962), it is apparent that these subspecies were in contact by the early 1960s and likely much earlier. Furthermore, it is difficult to exclude the possible influence of anthropogenic habitat changes that may have facilitated the recent contact of these two taxa, as Hunn and Baudette (2014) showed for subspecies of the White-crowned Sparrow (*Zonotrichia leucophrys*). However, in both mature lowland boreal forest and mid-montane transitional forest, I observed both *zaboria* and *sinuosa* in what appeared to be natural habitats unaltered by anthropogenic factors. With that said, *sinuosa* also took advantage of recent regrowth of alders in disturbed areas (e.g., overgrown gravel pits), particularly in the lowland area. I refrain from suggesting that these results provide support for recognizing these two subspecies groups as independent species. My observations lack a genetic assessment for such a conclusion and come from a single small point of contact that should not be used as a proxy for a comprehensive understanding of the interactions between these two subspecies-groups in all areas of their contact.

The pattern I observed of sympatry of *zaboria* and *sinuosa* with limited intergradation around upper Cook Inlet stands in contrast to the situation of other species whose coastal and interior forms come into contact in the same region. The best comparable example is of the Orange-crowned Warbler (*Leiothlypis celata*), of which the interior subspecies *celata* and coastal *lutescens* intergrade from the Kenai Peninsula through at least upper Cook Inlet (Gilbert and West 2015). Unlike those of the Fox Sparrow, these two warbler subspecies form a broad cline of intermediate populations. In the Anchorage area (pers. obs.) and the Kenai Peninsula (Gilbert and West 2015; UAM specimens) populations are relatively homogeneous and phenotypically intermediate (i.e., both parental phenotypes do not occur in sympatry).

There are many avenues for more research on this contact area between these two groups of Fox Sparrow subspecies. First, the spatial limits of this contact area need to be identified. Sampling to the north into the Alaska Range in the Susitna River drainage and to the northeast into the Talkeetna Mountains along the Matanuska River drainage would identify the northern (interior) extent of the influence of coastal *sinuosa*. Similarly, sampling to the south along Turnagain Arm and into the Kenai Peninsula would define the southern (coastal) limit of the influence of *zaboria*. Studies that address the degree of assortative mating between these two subspecies groups would provide information essential to our understanding of this situation. Furthermore, this contact area might lend itself well to genomic research on factors that limit intergradation between these forms or regions of the genome linked to differences in plumage or migration routes. I hope that future researchers can build on these observations and begin to answer some of the more interesting evolutionary questions that can be asked through the Fox Sparrow.

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