Unraveling **Western Flycatchers:** A Case Against the Split

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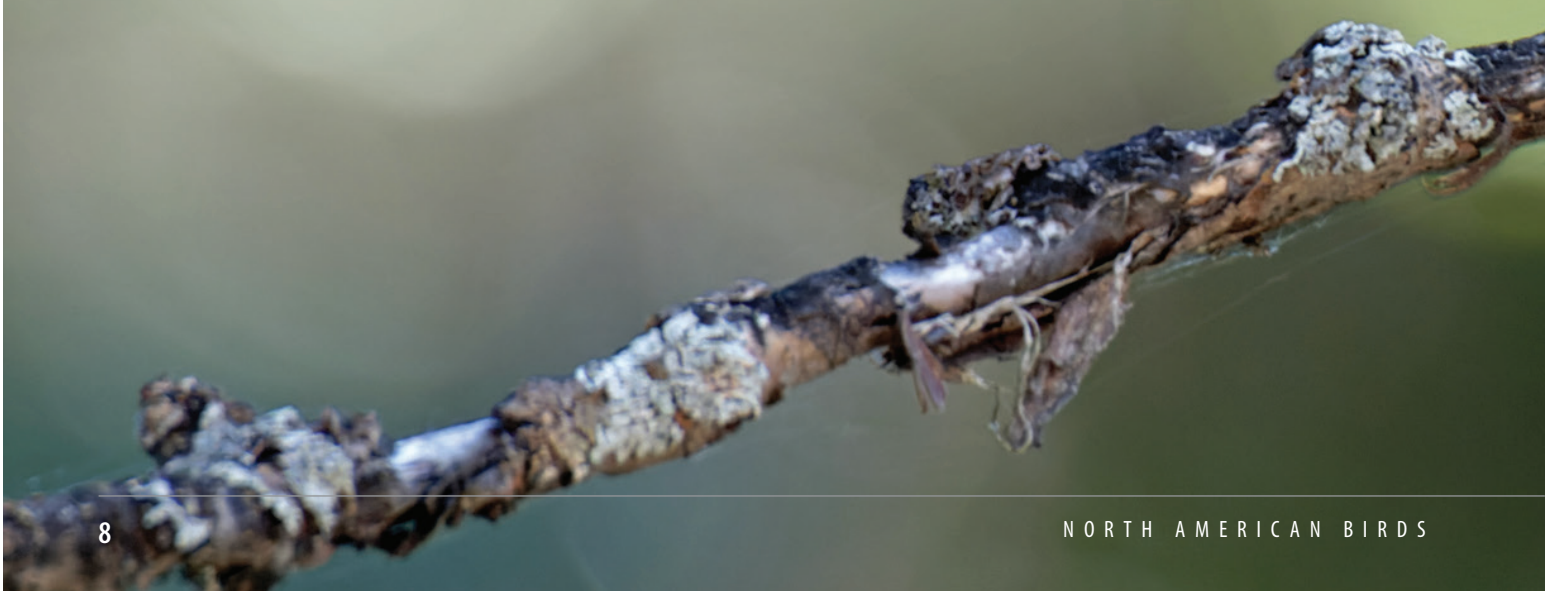
Introduction

Of all North American bird species currently recognized by the American Ornithological Society (AOS), Cordilleran Flycatcher (*Empidonax occidentalis*) and Pacific-slope Flycatcher (*Empidonax difficilis*, *sensu stricto)* are perhaps the most cryptic. Together known as the "Western Flycatcher complex", these two taxa are currently thought to be visually indistinguishable in the field, and even their vocalizations, oft-considered the best way to identify them, can be confusingly variable. Their breeding distributions are ambiguous and artificial: neighboring states and provinces generally include only one or the other, not both, even when connected by contiguous habitat. Recent genetic sampling has revealed a broad introgression zone in the northern Rockies, where the complex had previously been under-researched, and no decisive biogeographic barrier separates their populations. So, what's the deal with Western Flycatchers?

Western Flycatcher (*Empidonax difficilis*, *sensu lato*) was split into Cordilleran Flycatcher and Pacific-slope Flycatcher by the (former) American Ornithologists' Union in 1989 (Monroe et al. 1989), based primarily on the conclusions drawn by Ned K. Johnson and Jill A. Marten (1988), as well as Johnson's extensive 1980 monograph concerning the *Empidonax difficilis–flavescens* complex. The justification for the split was that the two forms "differ in vocalizations and allozyme frequencies and are sympatric in the Siskiyou region of northern California" (Monroe et al. 1989), where Johnson & Marten (1988) described evidence of assortative mating, noting that interbreeding had not yet been demonstrated conclusively. Modern research, however, paints a conflicting picture. In this paper, I summarize the original evidence presented in the 1980s by Johnson and Marten; compare it with more recent findings on Western Flycatcher's biogeography, genetics, morphology, and vocalizations; and consider how this information fits into mainstream taxonomic categories. Additionally, I briefly discuss Mexican populations in need of further research.



Presumed Cordilleran Flycatcher. Lyons, Boulder Co, Colorado. 17 Jun 2017. *Photo © Philip Stollsteimer.*

Biogeography

At the time of the split, Monroe et al. (1989) described the breeding distribution of Pacific-slope Flycatcher as stretching from southeastern Alaska and northwestern-central British Columbia south to Baja California, generally west of the Cascades and the Sierra Nevada. Cordilleran Flycatcher was described as breeding from southeastern Washington, southwestern Alberta, and northern Idaho through Montana, Wyoming, and western South Dakota, generally occurring east of the Cascades and the Sierra Nevada through northern California, Nevada, Utah, Colorado, Arizona, and New Mexico, south to the highlands of southern Oaxaca and west-central Veracruz.

At the state and provincial level, this definition varies slightly. The bird records committees of Idaho (Idaho Bird Records Committee 2020) and Montana (Montana Bird Records Committee 2022) include only Cordilleran Flycatcher on their state lists, while adjacent British Columbia and Washington include only Pacific-slope Flycatcher (British Columbia Bird Records Committee 2018, Washington Bird Records Committee 2021). Meanwhile, Alberta simply lists "Western Flycatcher" (Alberta Bird Records Committee 2022). Consistent with these records committee positions, a quick glance at the eBird observation maps of the two taxa shows range limits primarily defined not by geographical features, but political ones (Fig. 1). In these examples, the default taxon for entire states and provinces is always the one expected in the region's largest human population center (e.g., Seattle, Washington; Vancouver, British Columbia; Boise, Idaho).

At a basic level, the biogeography described in the original split and supporting research (Johnson 1980, Johnson & Marten 1988, Monroe et al. 1989) just doesn't make sense. Western Montana and northern Idaho are connected to central British Columbia by mid-elevation woodlands that extend northwest to the Pacific coast, and Western Flycatchers are consistently present throughout that region. No other western species pair follows this supposed distribution, including congeneric pairings with broadly comparable combined distributions and ecotype preferences. Examples include "Calaveras" Nashville Warbler (*Leiothlypis ruficapilla ridgwayi*), and Virginia's Warbler; and Cassin's and

Presumed Pacific-slope Flycatcher. Victoria, Vancouver Island, British Columbia. 28 Apr 2020. *Photo © Liam Singh.*

Plumbeous vireos. Unlike the status quo distribution of Western Flycatcher taxa, these taxa are separated by significant biogeographic features.

Johnson (1980) acknowledged that the distributional picture of Western Flycatcher in eastern Washington was more complex than indicated in the literature. The demonstrated presence of coastal-type birds on the eastern slope of the Cascades proved that the boreal habitats of the northern Cascades were not serving as a range limit. Johnson suggested that the birds in this region may have arrived from the Okanagan Valley of British Columbia to the north, rather than the coastal populations to the west, but he did not suggest what if anything would prevent them from expanding eastward towards Montana if this were the case. Johnson notes that Pacific-slope Flycatcher would not be expected to summer near the British Columbia–Alberta border, but his justification for this statement is unclear, given that other emblematic breeding species of the Pacific Northwest (e.g., Varied Thrush, Chestnut-backed Chickadee, Townsend's Warbler, Barred Owl, Pacific Wren) all breed in northwestern Montana (Marks et al. 2016). Johnson states that the preferred habitats of Cordilleran Flycatcher "shift dramatically from that described for the coastal forms", occurring in drier habitats and at higher elevations, from 4,500 to 9,000 feet, while Pacific-slope Flycatcher breeds in "shady forests from sea level to mid-elevations" (Johnson 1980). These habitat descriptions, however, are essentially just descriptions of the difference in forest types between the interior west and the Pacific slope, and I contend that they say little about the preferences of the birds, because these forest types are effectively non-overlapping in the areas to which Johnson refers.

Although he surveyed extensively in much of the western U.S., Johnson (1980) made no mention of the primary overlap

TOP: Presumed Pacific-slope Flycatcher. Libbey Park, Ventura Co, California. 3 Jan 2021. *Photo © Spencer Seale.*

BOTTOM: Presumed Cordilleran Flycatcher. Arizona. May 2013. *Photo © Glenn Bartley.*

A "tweener" in hand. This Western Flycatcher's measurements were intermediate between Pacific-slope and Cordilleran. Intermountain Bird Observatory, Boise, Ada Co, Idaho. 10 June 2020. *Photo © Heidi Ware Carlisle/Intermountain Bird Observatory.*

zone between the two forms. This overlap zone encompasses the "greater Kootenays" region—primarily Ferry, Stevens, Pend Oreille, Spokane, and eastern Okanagan counties in Washington; Kootenai, Bonner, Boundary, and Shoshone counties in Idaho; Lincoln, Sanders, and Flathead counties in Montana; and the regional districts of Kootenay Boundary, Central Kootenay, and East Kootenay in British Columbia. In the range maps featured in both Johnson (1980) and Johnson and Marten (1988), this entire region is left as a gap between the two forms, though Johnson did suggest that Cordilleran Flycatcher (then *E. difficilis hellmayri*) "probably" bred in southeastern British Columbia, at least locally. Johnson (1980) rejected previous evidence of Western Flycatcher breeding in eastern Washington (Dice 1918, Jewett et al. 1953), based on records from Yakima County and the Blue Mountains, where it is now known to occur (Lowther et al. 2020).

While there is some evidence that Western Flycatcher occurrence may have increased in the region in recent decades (Campbell et al. 1997), it seems unlikely that Johnson ever went to the Kootenays, because he made no mention of personal field work conducted there in any of his papers published on the topic (Johnson 1980, Johnson & Marten 1988, Johnson 1994). Western Flycatcher is not just present in the Kootenays, it's fairly common (Campbell et al. 1997), and even if it is a recent arrival there, the frequent, unrestricted intergradation documented in southeastern British Columbia by Rush et al. (2009) only weakens the case for the split. Western Flycatchers in the Kootenays may have been missed because of the region's relative remoteness, or because their preferred habitat in the area includes steep gullies that can be difficult to access. Whatever the reason, this oversight resulted in a fundamentally flawed understanding of the bird's distribution at the time of the split. Consequently, Johnson (1980) and Johnson & Marten (1988) focused their analysis of overlap between the two forms entirely on the comparatively tiny and disjunct Siskiyou region of northern California.

Genetic Variation and Assortative Mating

At the time of the original split, the Siskiyou region of northern California was the only known region of sympatry between the two forms, and interbreeding had not yet been demonstrated (Johnson & Marten 1988, Monroe et al. 1989). However, more recent genetic analysis has revealed a broad area of intergradation where the two forms occur in sympatry in interior British Columbia and southwestern Alberta (Rush et al. 2009), and continental-scale sampling has uncovered considerable evidence of genetic introgression as far east as the Black Hills of South Dakota (Linck et al. 2019). This lack of isolated, discrete, population-level genetic structure where Canadian- and U.S.-breeding populations of Pacific-slope Flycatcher and Cordilleran Flycatcher come into contact does not fit our rigid taxonomic categories; it is instead more consistent with a cline and/or ring species, in which populations that were once isolated hybridize freely and extensively when they come back into contact (Martins et al. 2013). Several other western species have population-level genetic structures that share this pattern, including Black-headed Grosbeak (Van Els et al.

2014) and Mountain Chickadee (Manthey et al. 2012); furthermore, ecological niche models applied to the latter species also identified Siskiyou County, California as an overlap zone between lineages. Like Western Flycatcher, both of these species show stronger genetic structuring in the southern parts of their breeding range than in the north, most likely the result of Pleistocene glaciation cycles (Manthey et al. 2012, Van Els et al. 2014, Linck et al. 2019).

Johnson and Marten (1988) reported that geographic trends in allozyme frequencies were clinal: the two alleles at the EST-2 locus were described as "widespread" and showed "weak clines in their geographic frequency", and the glutathione reductase (GR) locus showed a "clear clinal pattern of allelic frequencies". They go on to say that the "most striking pattern" of geographic trends in allozyme frequency, exhibited by the malic enzyme (ME) locus, also showed clinal variation, with neither fixation nor disappearance of the two most common alleles occurring in either the furthest interior or coastal populations. Notably, this consistent clinal variation was visible in Johnson and Marten's 1988 publication, even though their study contained no samples from Washington, British Columbia, Alberta, Idaho, or Montana—the primary contact zone for the two forms.

The suggestion of assortative mating in sympatry described by Johnson & Marten (1988)—and used as a core argument for the split (Monroe et al. 1989)—was based on a small sample of four mated pairs. Three of these pairs were described as representing "pure parental types" of Pacific-slope Flycatcher, and the other one of Cordilleran Flycatcher (Johnson & Marten 1988). Not only do these four pairs constitute a small sample size, they also all came from the Siskiyou region, a disjunct zone of secondary contact, rather than the primary overlap between the two forms. Assortative mating is not a necessarily effective driver of speciation, anyway (Irwin 2020), particularly when intergradation is frequent in areas of overlap and mixed genotypes are widespread. This is indeed the pattern that Rush et al. (2009) and Linck et al. (2019) have documented in the Western Flycatcher complex.

Morphology and Vocalizations

Birds in interior populations average slightly larger than coastal breeders, with longer primaries and tails, greater body mass, and brighter breast coloration (Johnson 1980). Johnson (1994) notes that these features are only consistently non-overlapping when birds are properly differentiated by age and sex. Even in the hand, many individuals must be left unidentified, and the conventional wisdom states that visual identification of the two types is not possible (Lowther et al. 2020).

In the absence of visual field marks, two vocalization types are used as the basis for field identification of Western Flycatchers: the dawn song, and the "male position note" (Johnson 1980, Pieplow 2011). Johnson (1980) states that dawn songs "differ profoundly when relatively remote populations are compared", and where their ranges meet in the Siskiyou region of northern California and adjacent southern Oregon, their songs "approach in structure but do not overlap", with differences that allegedly remain audible in the field (Johnson 1994). However, recent analysis of dawn song recordings in eastern Washington and the Idaho panhandle by Isacoff (2021) found that 28 of 29 available recordings featured mixed characteristics, meaning that field-identifiable individuals in the broad overlap zone were "very rare, or perhaps non-existent", and that "even the seemingly reliable dawn song is likely not as reliable as was thought".

The male position note is also less conclusive than originally appreciated. Even calls given by a single individual can be highly variable (Pieplow 2011). Spectrograms of typical Cordilleran Flycatcher calls look like two notes, featuring a break,

A Western Flycatcher from the "central Mexican" clade. Reserva de la Chara Pinta. Sinaloa, Mexico. 15 Jan 2020. *Photo © Eric VanderWerf.*

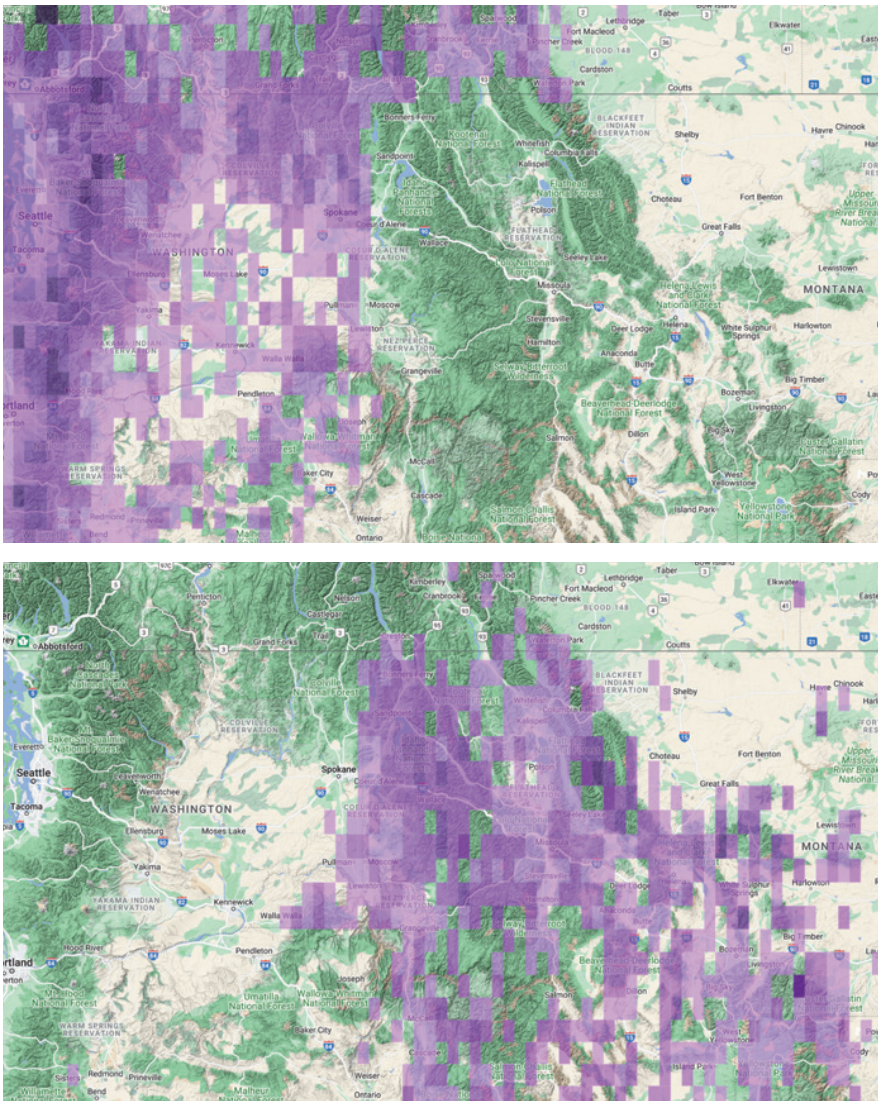


Figure 1. Maps of reporting frequency for Pacific-slope (top) and Cordilleran (bottom) flycatchers seem unlikely to represent legitimate biogeographic features. *Map images provided by eBird and created 12 Oct 2022.*

while Pacific-slope calls are connected, with a distinct "kink" near the halfway point of the note (Pieplow 2011). The single-note call typical of Pacific-slope types can be given by either form, while the two-parted call is only known from Cordilleran types (Lowther et al. 2020). The analysis of male position notes conducted by Johnson (1980) included recordings from 68 individual birds, distributed geographically in "broad regions of uniformity", separated by "narrow belts where the character changes abruptly, or where a mixture of note types is seen".

Analysis of recordings from the Macaulay Library shows that geographic transitions between call types are far broader than suggested by Johnson (1980), however (Fig. 2). In Montana, for example, only three of 25 male position notes uploaded to eBird match the two-note shape of typical Cordilleran Flycatchers, despite Montana supposedly being part of Cordilleran's range; this includes birds from well east of the continental divide, in Hill, Blaine, and Fergus counties (Table 1). Dawn songs of Western Flycatchers recorded in Montana are also inconsistent with pure Cordilleran types; instead, they more closely mirror the songs of birds in eastern Washington, which are presumably intergrades (Isacoff 2021).

Additionally, there is evidence that morphological and vocal characteristics are not always paired. Johnson (1980) reported that birds taken from Rogue River (Jackson County, Oregon), were "perfectly typical of [Pacific-slope] in song while being intermediate between [Pacific-slope] and [Cordilleran] in size and color". Birds from Siskiyou (CA) were "perfectly intermediate" in terms of song syllables, but they exhibited "enormously expanded variability" in size and color, which Johnson (1980) suggests are likely representative of either a hybrid swarm or a situation of complex secondary contact. The two forms do have slightly different vocalizations at extremes, but given their broad transition zone, lukewarm genetic differentiation, and high level of individual variation, this is more likely the result of simple geographic variation than full speciation.

Conclusions

Although taxonomic criteria can be objective, at least in theory, deciding the limits of those criteria (e.g., deciding exactly how much genetic differentiation is too much or not enough, deciding which species concept to use) will always involve some degree of subjectivity. In North American ornithology, the two most commonly recognized species concepts are the Biological Species Concept (BSC), and the Phylogenetic Species Concept (PSC) (Howell 2021). The BSC (Mayr 1942) relies on biological criteria, namely reproductive isolation of species, while the PSC (Cracraft 1981) is based on groups that share a common ancestor and have diagnosable characteristics, usually genetic or morphological.

The split of Pacific-slope and Cordilleran flycatchers fulfills the criteria of neither species concept. The two forms lack evidence of discrete population genetic structure that maps onto our taxonomic categories, owing to the apparent absence of significant reproductive isolation between them (Linck et al. 2019). Furthermore, they are not separated by decisive biogeographic features, and they do not exhibit fixed phenotypic differences in morphol-

ogy or vocalizations, instead displaying a gradual blend of features that are more consistent with a cline or ring species.

In the ABA Area, the distribution of Cordilleran and Pacific-slope flycatchers resembles the distribution of Black-headed Grosbeak (Van Els et al. 2014) and Mountain Chickadee (Manthey et al. 2012) clades. Each of these species has a subspecific introgression zone in the Siskiyou region of California. Similarly, both exhibit stronger genetic differentiation in the southern parts of their range than in the north, as do Western Flycatchers. This is likely due to the contiguous nature of suitable forest habitat from Montana to the Pacific coast, through British Columbia, which enabled unrestricted recombination of temporarily isolated populations when the Pleistocene glaciers receded (Manthey et al. 2012, Van Els et al. 2014, Linck et al. 2019). Because the research of Johnson (1980) and Johnson & Marten (1988) overlooked the broad primary overlap zone between the two forms in the northern Rockies, their data were weighted disproportionately towards the more differentiated southern populations.

It should be noted that Western Flycatchers in the Channel Islands of California are currently recognized by AOS as a subspecies of Pacific-slope Flycatcher, *E. d. insulicola*. Johnson (1980) conducted genetic analysis on these birds and did not feel that they warranted full species status, and no further research has challenged this treatment, though more modern genetic sampling of this population may be of interest.

Mexican Taxa

The isolated population of Western Flycatchers in Baja California Sur is currently treated by AOS as subspecies *cineritius*. The population is broadly consistent with mainland "Pacific-slope" types in terms of morphology (Johnson 1980) and genetics (Linck et al. 2019), and their songs are lower-pitched but otherwise similar (Howell and Cannings 1992).

While the future of Pacific-slope and Cordilleran flycatchers as separate species may be uncertain in the U.S. and Canada, there is evidence that at least one population of Western Flycatcher may warrant full species status. The genetic analysis conducted by Linck et al. (2019) found two distinct clades of Western Flycatcher in Mexico that had been previously overlooked: a "central Mexican" one in the Sierra Madre Occidental, Sierra Madre Oriental, and Transvolcanic Belt; and a "southern Mexican" one in the Sierra Madre del Sur of Guerrero and Oaxaca. A cline analysis conducted by Linck et al. (2019) found that central Mexican birds displayed more evidence of reproductive isolation from both of the northerly Pacific-slope and Cordilleran forms than those two forms did from each other. This is problematic, as the central Mexican birds are not even a recognized subspecies, in contrast to the two recognized "species" to the north that are likely subspecies at best. The southern Mexican clade was even more differentiated, which is both notable and unsurprising as the Sierra Madre del Sur is a well-established hotspot for avian endemism (Rocha-Méndez et al. 2019).

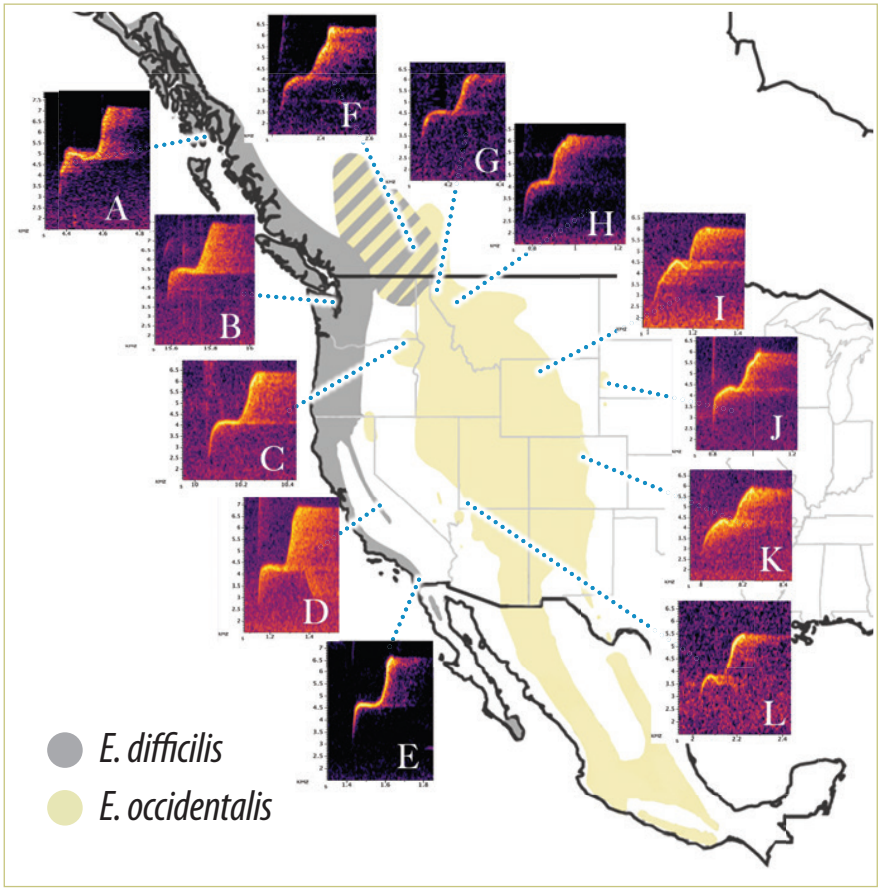
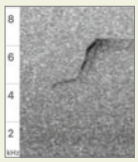
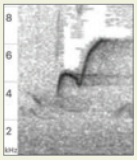
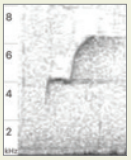
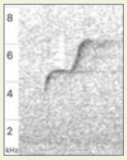
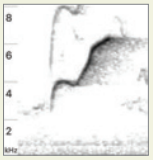
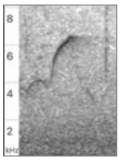
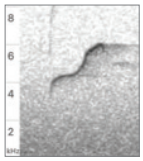
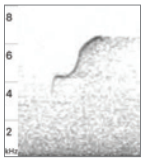
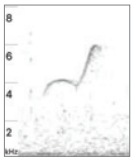
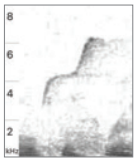
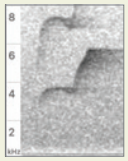
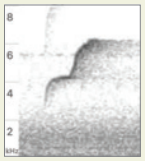
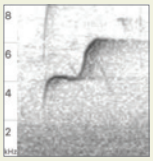
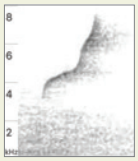
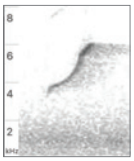
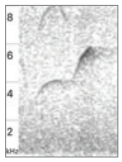
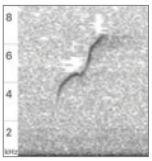
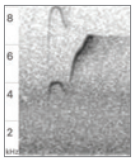
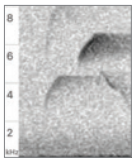
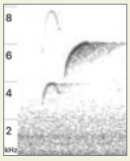
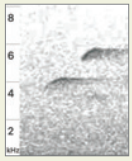
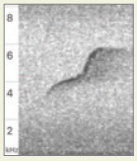
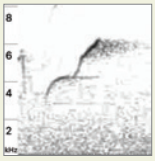
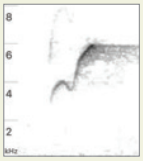


Figure 2. Male position notes across the breeding range of Western Flycatcher show a gradual transition: a pattern more consistent with clinal variation than a clear species divide. Recordings courtesy of the Macaulay Library at the Cornell Lab of Ornithology and xeno-canto.com. *A: ML194611891 (Ketchikan., AK); B: ML166940481 (King, WA); C: ML63123 (Umatilla., OR); D: ML528048 (Mariposa, CA); E: ML63699541 (San Diego, CA); F: ML165104231 (Central Kootenay, BC); G: ML184168921 (Lincoln, MT); H: ML108560051 (Missoula, MT); I: ML214994 (Washakie, WY); J: XC104534 (Custer, SD); K: ML166286601 (Boulder, CO); L: ML103403161 (Washington, UT). Range map modified from Linck et al. (2019).*

Both interior Mexican populations are worthy of further study. Of particular interest is the possibility that one or both Mexican taxa may feature diagnostic phenotypic characteristics, such as vocalizations or morphology, that could be used to consistently differentiate them from other Western Flycatcher types in the field.

Table 1. Variation in male position notes of Western Flycatchers in Montana. Two-note calls, commonly used to confirm "Cordilleran" Flycatchers, are rare in Montana, despite "Cordilleran" Flycatcher being recognized as the default form in most or all of the state.

Macaulay Library file	ML465491991	ML184156581	ML184161861	ML184168921	ML465482071
County in Montana	Lincoln	Lincoln	Lincoln	Lincoln	Flathead
Male position note					
Macaulay Library file	ML465492841	ML465496011	ML356522921	ML395441521	ML171292351
County in Montana	Flathead	Flathead	Flathead	Flathead	Flathead
Male position note					
Macaulay Library file	ML202296	ML465489251	ML108560051	ML106043391	ML357975851
County in Montana	Lake	Mineral	Missoula	Missoula	Missoula
Male position note					
Macaulay Library file	ML363478981	ML349682111	ML167048221	ML458600501	ML458502401
County in Montana	Missoula	Cascade	Lewis and Clark	Lewis and Clark	Lewis and Clark
Male position note					
Macaulay Library file	ML453531551	ML465487911	ML465487871	ML465482681	ML169557931
County in Montana	Lewis and Clark	Hill	Hill	Blaine	Fergus
Male position note					

Presumed Cordilleran Flycatcher fledglings. Gila Co, Arizona. 9 Aug 2020. *Photo © Gordon Karre.*

Currently, however, sound recordings and photographs of Western Flycatchers breeding in Mexico are few and far between. This presents an exciting opportunity for both birders and researchers, who can help clarify the nature of this tricky complex and perhaps uncover a new North American bird species in the process.

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References

Alberta Bird Records Committee (2022). *Official List of the Birds of Alberta.* Accessed 25 Jun 2022. royalalbertamuseum.ca/collections/life-sciences/ornithology/birds-list/taxonomy

British Columbia Bird Records Committee (2018). *Checklist of British Columbia Birds.* Accessed 25 Jun 2022. bcfo.files.wordpress.com/2018/09/j102594m-1_bc-bird-checklist-bcfo_scp-rev5_prf.pdf

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, M. C. E. McNall, and G. E. J. Smith (1997). *The Birds of British Columbia. Volume 3. Passerines: Flycatchers Through Vireos.* University of British Columbia Press.

Cracraft, J. 1981. Toward a phylogenetic classification of the recent birds of the world (class Aves). *Auk.* 98: 681–714

Dice, L. R. (1918). The birds of Walla Walla and Columbia counties, southeastern Washington. *Auk* 35:40-51.

eBird: An online database of bird distribution and abundance. Accessed 14 Jul 2022. ebird.org

Howell, S. N. G. & Cannings, R. J. (1992). Songs of two populations of the Western Flycatcher *Empidonax difficilis* complex. *Condor.* 94: 785–787.

Howell, S. N. G. (2021). What Isn't a Species? *North American Birds.* 72, 1: 16–25.

Idaho Bird Records Committee (2020). *Checklist of Idaho Birds.* Accessed 25 Jun 2022. ibrc.idahobirds.net/checklist

Isacoff, Jonathan B. (2021). The "Western Flycatcher" Problem in Eastern Washington: Latest Findings and Spectrogram Analysis. *Journal of the Washington Ornithological Society*. 13 (April): 97–102.

Irwin, D. E. (2020). Assortative mating in hybrid zones is remarkably ineffective in promoting speciation. *American Naturalist*. 195 (6): E150–E167.

Jewett, S.G., Taylor, W.P., Shaw, W.T., and Aldrich, J.W. (1953). *Birds of Washington State.* Univ. Wash. Press.

Johnson N.K. (1980). Character Variation and Evolution of Sibling Species in the Empidonax difficilis-flavescens Complex (Aves: Tyrannidae). Univ. of California Press 112: 1–151.

Johnson, N. K., & Marten, J. A. (1988). Evolutionary Genetics of Flycatchers. II. Differentiation in the Empidonax difficilis Complex. *The Auk.* 105 (1): 177–191.

Johnson, N. K. (1994). Old-School Taxonomy versus Modern Biosystematics: Species-Level Decisions in Stelgidopteryx and Empidonax. *Auk.* 111 (3), 773–780.

Linck, E., Epperly, K., Van Els, P., Spellman, G. M., Bryson, R. W., McCormack, J. E., … Klicka, J. (2019). Dense Geographic and Genomic Sampling Reveals Paraphyly and a Cryptic Lineage in a Classic Sibling Species Complex. *Systematic Biology*. 1–23.

Lowther, P. E., P. Pyle, and M. A. Patten (2020). Pacific-slope Flycatcher (*Empidonax difficilis*), version 1.0. *In Birds of the World* (P. G. Rodewald, Editor). Cornell Lab of Ornithology.

Lowther, P. E., P. Pyle, and M. A. Patten (2020). Cordilleran Flycatcher (Empidonax occidentalis), version 1.0. *In Birds of the World (P. G. Rodewald, Editor)*. Cornell Lab of Ornithology.

Manthey, J. D., Klicka, J., & Spellman, G. M. (2012). Is Gene Flow Promoting the Reversal of Pleistocene Divergence in the Mountain Chickadee (*Poecile gambeli*)? *PLoS ONE*. 7 (11).

Martins, A. B., De Aguiar, M. A. M., & Bar-Yam, Y. (2013). Evolution and stability of ring species. *Proceedings of the National Academy of Sciences of the United States of America*. 110 (13): 5080–5084.

Marks, J. S., Hendricks, P., and Casey, D. (2016). *Birds of Montana.* Buteo Books.

Mayr, E. (1942). Systematics and the origin of species. Columbia University Press.

Monroe, B. L., Banks, R. C., Fitzpatrick, J. W., Howell, T. R., Johnson, N. K., Ouellet, H., … Storer, R. W. (1989). Thirty-Seventh Supplement to the American Ornithologists' Union Check-List of North American Birds. *The Auk.* 106 (3): 532–538.

Montana Bird Records Committee (2022). *Official State List of Montana Birds.* Accessed 25 Jun 2022. montanabirdadvocacy.org/state-list

Pieplow, N. 2011. The 'Western Flycatcher' Problem. Accessed 10 Jul 2022. earbirding.com/blog/archives/2996.

Rocha-Méndez, A., Sánchez-González, L. A., González, C., & Navarro-Sigüenza, A. G. (2019). The geography of evolutionary divergence in the highly endemic avifauna from the Sierra Madre del Sur, Mexico. *BMC Evolutionary Biology*. 19 (1): 1–21.

Rush, A. C., Cannings, R. J., & Irwin, D. E. (2009). Analysis of multilocus DNA reveals hybridization in a contact zone between *Empidonax* flycatchers. *Journal of Avian Biology*. 40 (6): 614–624.

Van Els, P., Spellman, G. M., Smith, B. T., & Klicka, J. (2014). Extensive gene flow characterizes the phylogeography of a North American migrant bird: Black-headed Grosbeak (*Pheucticus melanocephalus*). *Molecular Phylogenetics and Evolution*. 78 (1): 148–159.

Washington Bird Records Committee (2021). *Official Washington State Checklist of Birds.* Accessed 25 Jun 2022. wos.org/documents/WBRC/2021/WA-checklist-Nov2021.pdf