Solving the Dowitcher Problem: Frank Pitelka, Rollo Beck, and the Merced Wetlands

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ABSTRACT

The taxonomic status of the Long-billed (*Limnodromus scolopaceus*) and Short-billed (*L. griseus*) dowitchers remained unsettled and controversial for over 150 years until the publication of a now-legendary monograph *(Geographic Variation and the Species Problem in the Shore-bird Genus Limnodromus)* by University of California, Berkeley, ornithologist Frank Pitelka in 1950. The solution to the dowitcher "problem" began in 1945 when bird collector Rollo Beck arrived in Berkeley and presented to Pitelka, in dramatic fashion, boxes of dowitcher specimens he had collected from the wetlands of Merced County. This consequential encounter with tireless collector Beck inspired Pitelka to commence a years-long, museum-based study that clarified the taxonomic relations and geographical distribution of these similar and confusing shorebirds. This comprehensive study examined dowitcher morphology, molt, age and sex variation, areas of breeding, migration timing and routes, and ecology. Multiple lines of evidence were presented to support the determination that the two dowitcher forms were indeed distinct species. A new subspecies of the Short-billed Dowitcher (*L. griseus caurinus*) also was described, which breeds from southwestern Alaska along the Pacific coast to northwest British Columbia. I present brief biographical sketches of Pitelka and Beck that touch on their careers and personalities. The major research results and conclusions in the monograph are summarized as well as the personal connections between the two men.

The dowitchers (*Limnodromus* sp.) perplexed generations of avian taxonomists. The first dowitcher was described in 1789 by Johann Gmelin, a German naturalist and protege of Carl Linnaeus, based on a specimen that had been collected on Long Island, New York. Gmelin named it *Scolopax grisea*, known today as the Short-billed Dowitcher (*L. griseus*). In the decades that followed, a different dowitcher with a slightly longer bill was discovered in Council Bluffs, Iowa. This prompted American naturalist Thomas Say to designate it a new species in 1823, the Long-billed Dowitcher (*L. scolopaceus*).

A century later, the general view was that the two forms were subspecies of a single dowitcher species rather than different species (AOU 1931, Grinnell and Miller 1944). A brief look at some of the events that occurred 75 years ago — events centered in central California — illustrate how specimen collecting and museum research combined to resolve the confusing systematics of the dowitchers.

Early California ornithologists (e.g., Dawson 1924, Bent 1927, Hoffman 1927) followed the American Ornithologists' Union Check-list (AOU 1931), which included an eastern subspecies ("Short-billed Dowitcher") and a western subspecies ("Long-billed Dowitcher"), although the Short-billed Dowitcher was considered uncommon or perhaps absent entirely in the state. British Columbia ornithologist Allan Brooks (1934) recognized this error and remarked, "The practice of calling all western birds *scolopaceus* has perpetuated a mass of error." By 1944, enough new information had accumulated for Grinnell and Miller (1944) to accept the occurrence of the short-billed form in California, but they still cautioned readers that their comments on the status of the dowitchers should be "taken with a margin of flexibility". Consensus on the dowitcher "problem" remained elusive. Were these shorebirds — both similar in size and appearance but differing most obviously in average bill length — members of a single species, or were they separate "good" species? Although their general appearance clearly indicated that the two dowitchers were very closely related, slight differences and variation in plumage had prevented a full understanding of their relationship. A shroud of uncertainty and confusion would persist until the middle of the 20th century, when the work of two ornithologists, Frank Pitelka and Rollo Beck, converged. Reflecting on the state of knowledge of prior decades, Pitelka (1950) would write in his characteristic direct style, "The literature on dowitchers, especially that dealing with the western half of the North American continent, is an almost inextricable confusion of records", and "…a good part of what has been written about the distribution of dowitchers since the 1850s is virtually worthless."

FRANK A. PITELKA: MUSEUM SCIENTIST AND ECOLOGIST

Frank Pitelka (1916–2003) grew up near Chicago, and as a teenager he helped in the Birds Division of the Chicago Field Museum. After completing a Bachelor of Sciences degree, he moved west in 1940 to begin a doctoral program at the University of California, Berkeley (Koenig and Sherman 2004, Root and Batzli 2004). He had planned to study under Joseph Grinnell, the director of UC's Museum of Vertebrate Zoology (MVZ). Grinnell, however, had passed away a year before Pitelka arrived, so he became a graduate student of Alden Miller, Grinnell's replacement as director. MVZ is one of the nation's premier research museums in the fields of vertebrate systematics, ecology, and natural history.

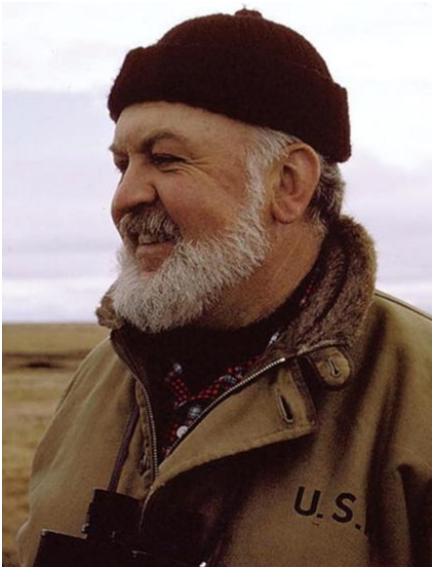

Figure 1. Frank Pitelka. 1975. at Utqiagvik (Barrow), Alaska.

Photo by Peter Connors.

From MVZ's founding in 1908, scientists under Grinnell's leadership had identified and described hundreds of new forms of birds and mammals; thus, in 1940 Pitelka had joined a lineage of prominent vertebrate zoologists. Although Pitelka's early work centered on avian speciation and taxonomy, his later career was devoted to vertebrate behavioral ecology, predator-prey relations, and factors that regulated populations. Pitelka became a dominant figure in the field of modern ecology and received the Eminent Ecologist Award from the Ecological Society of America and the Brewster Medal of the American Ornithologists' Union (Koenig and Sherman 2004, Root and Batzli 2004). He was a larger-than-life presence on the UC Berkeley campus and among the Bay Area field ornithologists and birders he encountered. Those of us on the periphery of his influence could appreciate his insights and strong opinions first-hand at seminars in the Life Sciences Building, where he held forth during question time following talks, not infrequently to the distress of the speaker.

ROLLO H. BECK: BIRD COLLECTOR AND EXPLORER

In the early 1900s, the Merced County wetlands and agricultural fields were rich collecting grounds for Rollo Beck. Beck (1870–1950) was born in Los Gatos, California, grew up near San Jose, and lived intermittently in Planada (eastern Merced County). Beck's serious interest in birds began in 1894 when he joined a collecting trip to the Sierra Nevada, Yosemite, and Lake Tahoe. Those mountain trips launched him on a celebrated 30 year career. Beck had no formal scientific training — and apparently no schooling beyond the 8th grade — yet he was a chief zoologist on six major expeditions, gaining a reputation as an outstanding leader and field collector. Beck explored Alaska

with prominent ornithologists Alexander Wetmore and Arthur Cleveland Bent. He participated in the Rothschild Expedition to the Galapagos Islands and the Brewster-Stanford Expedition to South America. From 1920 to 1928, he led the American Museum of Natural History's Whitney South Sea Expedition, at that time the largest ornithological expedition ever conceived. On that voyage to the Southern Ocean with Museum curator Robert Cushman Murphy, Beck returned with over 7,800 bird specimens.

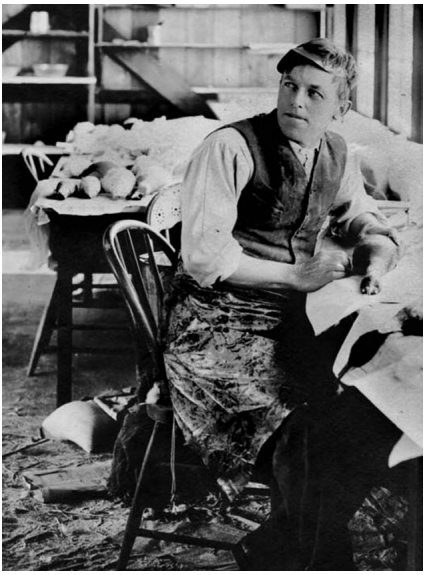

Figure 2. Rollo Beck in Planada in 1906, shortly after returning from the California Academy of Sciences' Galapagos expedition.

Photo from the Rollo Beck Collection, California Academy of Sciences Archives.

Beck's skill as a field worker with a shotgun put him in "a class by himself" (Murphy 1936). "A tray of Beck's specimens was as uniform in appearance as so many cigarettes in a box," Murphy stated. "He stands today as the most successful worker in this branch of ornithology that the world has known." He could collect and flawlessly prepare 40 specimens of petrels in a single day, or a single specimen every 10–15 minutes (Dumbacher and West 2010). While he was living part-time in Pacific Grove, Beck collected seabirds for the California Academy of Sciences (CAS) from a small boat he rowed single-handedly out onto Monterey Bay. Peter Pyle remarked that Beck had collected roughly half of the thousands of museum specimens he examined and measured while preparing the *Identification Guide to North American Birds: Part 2* (Pyle 2008). MVZ alone holds over 4,000 Beck specimens.

After travelling the world for three decades, in 1930 he settled into homelife in Planada where he and his wife Ida Menzies managed their apricot orchard and where he could continue collecting dowitchers and other birds. For more on Beck's remarkable life and his many contributions to ornithology, see James (2017) and the Beck (2008) Collection at California Academy of Sciences.

MERCED COUNTY HOLDS THE ANSWER

In 1900, the town of Merced, a few miles from Planada, had fewer than 10,000 inhabitants. The region consisted of small agricultural fields, many natural wetlands, and meandering waterways that flooded in winter and spring. Even in Beck's day, the San Joaquin Valley landscape had changed markedly from the natural conditions that existed before the Gold Rush. Conversion of lands to agricultural uses caused rivers to be reclaimed and channelized for irrigation, wetlands and vernal pools drained or graded, and groundwater pumped causing widespread land subsidence (Galloway and Riley 1999, Garone 2011, Arax 2019). It's hard to imagine how vast this natural landscape was a century ago, but a visit today to the federal wildlife refuges in Merced County gives a glimmer of what much of the San Joaquin Valley once looked like. Despite these tremendous environmental alterations, habitats for shorebirds and other wintering and migratory waterbirds were still available.

From his ranch in Planada, Beck ranged throughout central San Joaquin Valley in search of birds. From July through April, flocks of dowitchers could be found probing for invertebrates in the soft mud. Between 1911 and 1940 Beck collected 52 dowitcher specimens near Los Banos. Over the next seven years, he collected another 234 dowitchers in the wetlands near the town of Merced. Gustine and Dos Palos were other places he frequented. More than two-thirds of these birds were collected during late winter and early spring when numbers of migrants generally peak in the Central Valley (Shuford et al. 1998). Beck's interest in dowitchers had been further stimulated after reading a paper by Robert Orr (1940) on dowitcher distribution in California. Although Orr confirmed that both the long-billed and short-billed forms occurred in California, he incorrectly concluded that short-billed birds were "five times" more common than long-billeds. Orr's error reflected the fact that almost all of the 178 specimens he examined were collected from saltwater habitats in the San Francisco Bay region and thus did not include the birds' distribution away from the coast and throughout the state. With his own large collection of dowitcher specimens, Beck was in a unique position to examine their characteristics and form an opinion on their identity. Orr's paper was at odds with what Beck was finding in Merced County where all of his specimens had 'long' bills. To satisfy his growing curiosity, Beck boxed up his specimens in the fall of 1945 and drove to Berkeley to meet with a scientist who might shed light on the situation.

2,900 SPECIMENS!

Pitleka had initially been skeptical that dowitchers were the same species, so the timing of Rollo Beck's appearance at the museum seemed ideal to initiate a new investigation. Pitelka knew of Beck, but the two men had never

met. Forty years later, Pitelka (1986), described their pivotal meeting: "When I approached him (Beck), as we greeted each other he was spilling, helter-skelter, onto the table the contents of one, then the other box, heap after heap of well-made dowitcher specimens - 311 in all, and all of them of the long-billed form." Prior to this, Pitelka had worked on scrub-jay systematics for his doctoral dissertation (Pitelka 1951), which gave him the experience and research approach needed to take aim at dowitcher taxonomy. A collaboration was begun that would last for five years, settling once and for all the "problem" of the dowitchers.

Even though Beck's Merced County collection of dowitcher specimens was large, they were almost all from one small area of California. For a thorough assessment, more specimens were needed from throughout their migratory and wintering range across North America. Pitelka acquired specimens from 16 other museums and private collections, eventually obtaining 2,908 specimens. Almost all (85%) had been collected on the migratory or wintering grounds, and over 1,000 specimens (from Beck and other collectors) alone were from California.

Essential for Pitelka's analysis was this large number of specimens now at his disposal and his decision to disregard all published records that were not supported by specimens that he personally examined. Considering the number of past misidentifications, it was essential to carefully inspect and measure every dowitcher specimen. Each museum specimen bore a tag with the date and place of collection, age and sex determination, and the name of the collector – data crucial for his analyses.

Standard measurements were made of bill (culmen) length, wing chord, and tarsus length, nearly 9,000 individual measurements in all – a tremendous amount of precise work with dial calipers. Armed with this mass of data, Pitelka initially separated specimens into categories based on size and color, then further divided them based on plumage, age, molt stage, and degree of ventral coloration and spotting. Table 1 summarizes Pitelka's data on bill, wing, and leg lengths of his California dowitcher specimens. It is apparent that long-billeds have longer bills and legs than short-billeds, but short-billeds have longer wings. These three mensural characteristics were essential for separating the two forms in the hand. The short-billeds in his California sample represented a new subspecies that Pitelka described in the monograph.

Importantly, for many years it was not fully appreciated that females of both types (as in many shorebirds) on average have longer bills than males. The average bill lengths of the two forms differ by only 5 to 10 mm; however, owing to sexual dimorphism the full range is more extreme, from the shortest bill at 52 mm for a male short-billed to the longest at almost 81 mm for a

female long-billed (Figure 3; from Pitelka, 1950). A female short-billed might therefore be misidentified as a male long-billed. Errors like this occurred in both published observational records and on museum specimen tags.

Well into the 20th century, little was known about the species' breeding and wintering ranges, migration patterns, molt, or habitat use. The nesting grounds were in the far north where few ornithologists ventured, so nothing was known about whether interbreeding occurred between the two forms. Rowan (1932) described the nest of the Short-billed Dowitcher as, "about the hardest of all shorebirds to find." On their migratory and wintering grounds, as many birders know, it is a challenge to distinguish the two in their non-breeding plumage. Using the data on the museum specimens combined with the existing literature, Pitelka was able to determine the timing and routes of migration, broad-scale distribution across the continent, and breeding and wintering grounds.

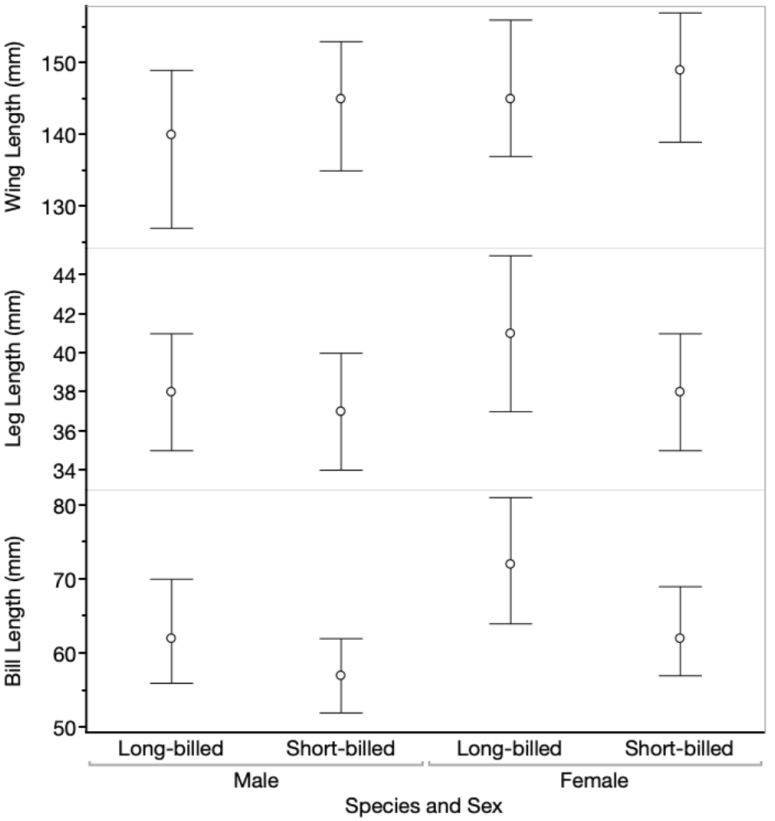

Figure 3. Mean (circles) and range of bill, leg, and wing lengths of Long-billed and Short-billed dowitchers, from measurements made by Pitelka (1950).

Pitelka's sample of Short-billed Dowitchers specimens from Alaska and along the U.S. west coast were distinct enough morphologically from the two known subspecies that breed in central and eastern Canada for him to designate them a new subspecies, *L.g. caurinus*. *Caurinus* is larger than the other two subspecies and, in breeding plumage, is somewhat intermediate, yet variable, in the amounts of white on the belly and spotting on the underparts. He created a map of their breeding distribution in coastal Alaska.

Table 1. Highlights of Pitelka's dowitcher study.

- Long-billed and Short-billed dowitchers are full species and do not interbreed within the apparent narrow zone of overlap in the breeding ranges just north of the Alaska Peninsula. No hybrids between the two dowitchers are known.
- Long-billeds have longer bills, longer legs, and shorter wings than short-billeds.
- Bill length and plumage characteristics must be used together for correct classification.
- In both dowitchers, females are larger than males in bill, leg, and wing length, and in weight.
- Plumages of the downy young differ markedly.
- The species use different foraging habitats during migration and in winter: long-billeds prefer freshwater habitats, whereas short-billeds prefer tidal estuarine or saltwater habitats with open mudflats.
- In California, Long-billed Dowitchers are common inland in the Central Valley during the non-breeding season, whereas short-billeds are abundant coastally but very rare inland; long-billeds (mostly juveniles) occur on coastal estuaries where they prefer interior ponds and salt marsh vegetation rather than open mudflats.
- Three subspecies of the Short-billed are delineated and the breeding grounds of the "eastern" Short-billed Dowitcher (*L.g. griseus*) extends east into the Ungava Peninsula. A new, larger western subspecies (*L.g. caurinus*) is described with breeding grounds along the coast of southern Alaska.
- Differences in foraging ecology likely accounts for the differences in bill, leg, and wing length between Long-billed and Short-billed dowitchers.
- A "phylogenetic history" suggests that speciation occurred when the two forms became separated geographically during the early Pleistocene epoch

Pitelka's monograph, which included 30 tables, 9 figures, and 10 photographs, evaluated and discussed the merits of important earlier studies by Rowan (1932), Brodkorb (1933), Orr (1940), and Conover (1941). He built his case with thorough analysis, a compelling rationale, and a detailed discussion. Pitelka argued against the idea that dowitchers were a single species and presented multiple lines of evidence to support his conclusions.

His study firmly established the morphological and ecological distinctness of the two forms, ending this long-standing controversy. The importance of his paper was quickly recognized by Dean Amadon (1951), another eminent avian evolutionary biologist. Pitelka's recommendation to split the dowitchers into two species was supported and published in the AOU Check-list (AOU 1957). Highlights of the results in the monograph are shown in Table 1.

Figure 4. Short-billed Dowitchers (top two) and Long-billed Dowitchers (bottom four) used in the study. All in non-breeding plumage, collected in California.

From Pitelka (1950).

BILLS, LEGS, AND WATER DEPTH

Addressing dowitcher foraging ecology, Pitelka (1950) wrote, "a remarkable degree of ecological separation is shown to occur" between the two species. He found that long-billeds generally avoided estuarine habitats except during migration, and strongly preferred freshwater ponds and wetlands in most parts of their range at all seasons. In contrast, short-billeds in winter are found almost entirely on coastal, estuarine mudflats with tidal flow. These differences led him to speculate about the adaptive value of the differences in bill and leg length between the two species and how each species appeared to be well-adapted to the particular wetland habitat each preferred.

In estuaries, water depth varies with the tidal stage, thus offering short-billeds more area available with optimal feeding conditions; they can forage in deeper water during high tide, and on exposed mud when the tide is low.

Their shorter bill and legs serve them well under all tidal conditions. In freshwater wetlands where tides are absent and the availability of suitable foraging area is correspondingly less, long-billeds find adequate foraging conditions by virtue of their longer bill and legs that are suited for temporary, uniformly deep water. Wing length could have evolved as an adaptation related to foraging habitats. Pitelka speculated that the shorter wing of the long-billed dowitcher would allow them a faster more effective takeoff while feeding in water than the Short-billed Dowitcher with its longer wings. Fast takeoff is crucial for evading shorebird predators such as Peregrines and Merlins–something to ponder while watching dowitchers probe in deep water.

DOWITCHER ORIGINS

Pitelka speculated that the Long-billed Dowitcher was derived from a form similar to the Short-billed Dowitcher. He also suggested that speciation occurred during or shortly before the Pleistocene glaciation (up to 2.5 million years ago), when the long-billed became isolated from the short-billeds in ice-free areas (glacial refugia) of northern Alaska.

How did environmental conditions across Canada and Alaska over two million years ago lead to speciation and the formation of the two dowitchers? Generally, the first step in the process of species formation begins when a geographical feature such as an uplifting mountain range, zone of unsuitable habitat, or oceanic island isolates and divides a formerly contiguous population (Mayr 1963). Glaciers and ice sheets also separate and isolate populations, as existed across all of Canada during the Pleistocene Epoch. When the glaciers began expanding southward 2.5 million years ago, populations of many animals were forced south. After the glaciers retreated at the close of the ice ages, birds returned to northerly breeding grounds.

During the Pleistocene epoch, the unglaciated Bering Sea-Yukon refugium remained along northern Alaska bordering the Bering Sea and another existed along the coast of southeast Alaska and adjacent northwestern British Columbia (Holderegger and Thiel-Egenter 2009). The extent of the northern Alaska refugia conforms with the current breeding range of the Long-billed Dowitcher. The population persisted there throughout the ice ages, a long time period when this population was not in contact with Short-billeds. The current ranges of the three subspecies of the Short-billed Dowitcher also suggests that glaciation played a role in initially isolating populations, which allowed them to evolve and develop into the three forms. Today, the Rocky Mountains and Hudson Bay serve as barriers that maintain this separation.

Figure 5. Long-billed Dowitcher in non-breeding plumage. 30 March 2014. Bolsa Chica Ecological Reserve, Orange Co. California.

Photo by Mark Chappell.

Figure 5. Short-billed Dowitcher in non-breeding plumage. 23 August 2009. Bolsa Chica Ecological Reserve, Orange Co. California.

Photo by Mark Chappell.

WHAT'S BEEN LEARNED SINCE 1950

Although Pitelka greatly clarified our understanding of dowitcher taxonomy and distribution, much has been learned since about their migration, distribution, ecology, and habitat preferences in California and elsewhere in the west (e.g., Shuford et al. 1998, Page et al. 1999, Pandolfino and Handle 2018). How has his study held up over time? Information on shorebird population size in the first half of the 20th century was largely non-existent when Pitelka prepared his monograph, so he did not include estimates of dowitcher populations. However, the general migration chronology through coastal areas in the West that Pitelka described holds true today and seems similar for both species (Takekawa and Warnock 2020). Shuford et al. (1998) noted that long-billeds substantially outnumber short-billeds in at least northern and central California in winter, but short-billeds outnumber long-billeds in migration, particularly in spring. In most of the interior of the state, short-billeds are generally rare in migration but more frequent at saline lakes than at freshwater wetlands (D. Shuford, pers comm.). Although there have now been many studies of distribution and migration across North America (Takekawa and Warnock 2020), the current size of dowitcher populations in the Central Valley and where Beck collected, is not known (D. Shuford, pers. comm.). The only comprehensive surveys of Central Valley shorebirds, conducted in 1992–1994 well after much of the historical wetland habitat had been converted to agriculture, showed that in April the San Joaquin Valley supported about 37,000 dowitchers (all likely long-billeds) or 40% of all of those found in the entire Central Valley (Shuford et al. 1998).

Long-billed Dowitchers are the only species found inland away from the coast as Pitelka explained, however, the San Francisco Bay estuary is actually the most important wintering area for Long-billed Dowitchers on the Pacific Flyway where they prefer muted tidal impoundments and salt pond habitats in the north bay (Takekawa et al. 2002). Long-billeds use mudflats just like short-billeds, but these are often near freshwater inflows with muddy substates, with saltmarsh pools likely used mostly after tides inundate the mudflats (Shuford et al. 1998, D. Shuford, pers. comm.).

Pitelka drew intriguing inferences regarding "ecological separation" from his measurements of bill, leg, and wing length that led him to speculate about adaptations of each species to their preferred freshwater or saltwater foraging habitats. Long-billeds with their longer bills and legs were better adapted to freshwater habitats, whereas short-billeds with shorter bills and legs were better suited to estuarine mudflats. Was he correct? D. Shuford (pers. comm.) replies, "knowing that long-billeds also use estuaries, I'm not sure how tidal conditions alone differentiate habitat use of the two species. By this reasoning, with longer bills and legs, long-billeds could forage over an

even greater range of depths and tidal conditions. For short-billeds, I wonder if this has something to do with adaptation to saline conditions and the sandier substrates more often found in estuaries. For example, short-billeds are more likely to occur than long-billeds at Mono Lake, perhaps for these reasons." Pitelka had also speculated that the long-billed's shorter wings (than short-billed's) could allow faster takeoff from the substrate, an advantage for birds foraging in water. Recent research on shorebird wing shape (pointedness, length, and overall shape) has shown that multiple factors such as migration distance, habitat changes, and even predator pressure can lead to differences in wing shape (Minias et al. 2015, Lank et al. 2017).

Avise and Zink (1988) used molecular techniques and mitochondrial DNA to confirm Pitelka's determination that the two forms are good species. However, they placed the dowitcher speciation event at 4-million years ago, well before Pitelka's conjecture. If their conclusion is correct and speciation occurred prior to the ice sheets pushing south across Canada and into the northern United States, then the exact forces that separated the forms remain unclear. Before he passed away, Pitelka suggested that studies of the area of breeding sympatry between Long-billed and Short-billed dowitchers from Kuskokwim to Goodnews Bay, Alaska, could shed light on how these two species evolved (Takekawa and Warnock 2020).

In 1950, Pitelka had only a few Alaska breeding records available to delineate and map the range of the Short-billed Dowitcher (*L.g. caurinus*). Subsequent field studies throughout southern Alaska and into Canada have expanded this range into southwestern Yukon Territory and northwestern British Columbia (Godfrey 1986, Jehl et al. 2020, Breeding Bird Atlas of BC, https://www.birdatlas.bc.ca/).

The two dowitcher forms still present a significant challenge to differentiate, and much has been written in recent decades about subtle marks that can help to distinguish the two in the field (Prater et al. 1977, Wilds and Newlon 1983, Hayman et al. 1986, Jaramillo and Henshaw 1995, Chandler 1998). Today, field guides emphasize these marks, most of which were probably not fully appreciated by Pitelka and others. For example, he described somewhat in passing, "conspicuous edgings and subterminal bars" of the tertials on juvenile specimens. These characters – the presence or absence of conspicuous buffy edges and inner markings of the longer tertial and greater covert feathers – have been found to be especially useful for distinguishing juveniles of the two species in the fall when birds are in fresh fall plumage (Dunn and Alderfer 2017). By the 1940s, separation of the species in the field became less problematical when it was discovered that each gives distinctly different call notes (first noted by Peterson in 1947), making it possible to firmly identify many individuals. Adding to knowledge of

calls, Lenna (1969) and D. Shuford (pers. obs.) have noted that Long-billed Dowitchers are more vocal (soft calls) while in feeding flocks (see also, Hayman et al. 1986) than are short-billeds, which they speculated is because long-billeds need to call frequently to maintain contact when foraging in freshwater habitats (which often have more vegetation) compared to short-billeds which forage primarily on the open estuarine mudflats.

CONCLUSIONS

Frank Pitelka's 1950 dowitcher monograph is a model of careful analysis and forceful interpretation of results that remains legendary in the annals of systematic zoology of North American shorebirds. His conclusions, most of which hold up today, were based on detailed museum work using a large number of specimens, combined with his own knowledge of distribution and the foraging habitats where birds were collected. Former students Richard Root and George Batzli (2004), wrote in an obituary, "In two monographs, one on shorebirds (dowitchers in the genus *Limnodromus*) and the other on the American jays (*Aphelocoma*), Frank developed hypotheses about how speciation may have proceeded within each of these two groups of closely related species. These monographs set new standards, broadened the conceptual scope of museum-based studies, and continue to figure importantly in the analyses of biogeographic patterns, largely because of the extensive and carefully gathered data that they contain."

Just as important as Pitelka's analysis was Beck's persistent collecting of specimens over decades in Merced County, and Beck's own curiosity about dowitchers, which gave Pitelka the impetus for his investigation into this pair of shorebirds. The Merced County wetlands in the San Joaquin Valley and the Long-billed Dowitchers collected there over 75 to 100 years ago were key to bringing this long-standing controversy to a resolution. Thirty-six years after Beck's death, Pitelka (1986) wrote that it was his friendship and collaboration with Beck that led to "my immersion in the distribution, taxonomy and nomenclatural chaos of American dowitchers…"

ACKNOWLEDGMENTS

Thanks to Patricia Bacchetti for useful comments and to Judith Hurley for excellent editorial assistance. Nils Warnock, Dan Airola, and especially David Shuford, provided many helpful suggestions which improved an early draft. Thanks to Gregory Bulte for help with the graph in Figure 3.

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Author's note: My uncle Henry E. Childs, Jr., and my graduate school advisor Howard L. Cogswell, both received their doctorates in zoology in the 1950s under Frank Pitelka. While a graduate student at California State University, East Bay (1978–1983) and shortly thereafter, I assisted three of Pitelka's very last PhD students with their bird studies in far-flung places. As a result, I've had a long interest in his research and contributions.