

The Mendocino Shrike: Red-backed Shrike (*Lanius collurio*) x Turkestan Shrike (*L. phoenicuroides*) hybrid

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Imagine a group of birds, similar in size and structure, posing subtle identification challenges. Each species has eight or more identifiable plumages, but appearances overlap between subgroups. Molts are confounding and protracted, varying as much within as between taxa, and give rise to shifting transitional plumages and complex interactions between molt timing and plumage expression. Solar exposure affects feathers to varying degrees, further altering appearance, especially in the most migratory taxa. Hybridism occurs between these taxa, in certain cases extensively, and taxonomic disputes add further turmoil.

You are on the northern California coast, in March. Only one group of birds provides such a set of compelling conundra: large *Larus* gulls, correct?

Alder Creek meets the Pacific Ocean where the great San Andreas Fault forsakes the California coast for the Mendocino Triple Junction, one of the least stable places on Earth. Redwood tree trunks, the size of buses, have infiltrated the creek mouth, deposited by titanic winter surges of ages past. Unforgiving spring northwesterlies have sculpted surrounding vegetation, resulting in windswept coastal prairies dotted with occasional prostrate shrubs. Impenetrable coastal scrub, lining the precipitous Alder Creek gulch, conceals the wary and anagogic Point Arena Mountain Beaver (*Aplodontia rufa nigra*), almost never detected by humans. Most of all, this lonely coastal stretch is frequently enshrouded in a fog so thick as to obscure one's vision and, when combined with relentless winds, one's mental composure.

It was here that a lonely itinerant tarried, after its 9000-kilometer journey from one desolate place to another, over tundra and endless, foreboding, coniferous forests, reaching a dramatic backdrop decidedly befitting its tortuous identification.

The Mendocino County, California shrike is one for the ages. It was studied carefully by numerous observers, and over the course of its eight-week stay, it was undergoing and nearly completed its preformative molt. As it molted, the colors of its plumage changed, confounding its observers, who turned to Old World shrike experts for clarity. With the exception of collecting the bird itself, every tool in the arsenal of the amateur and professional ornithologist has been brought to bear in the quest for an identification: photography, audio recording, specimen study, molt study, extensive correspondence, and an exhaustive review of the literature from across Eurasia. The product of this effort is a most unexpected but well-grounded conclusion: that the shrike was a hybrid of two Eurasian species, both unrecorded in North America, moreover two species whose zone of hybridization lies in central Asia, a part of the world that has sent few vagrants to North America: Greater Sand-Plover (*Charadrius leschenaultii*), Blyth's Reed Warbler (*Acrocephalus dumetorum*), Sedge Warbler (*A. schoenobaenus*), Lesser Whitethroat (*Sylvia curruca*), Spotted Flycatcher (*Muscicapa striata*,

and Common Redstart (*Phoenicurus phoenicurus*). Although the identification was difficult, and is by no means certain, its complexity provides the thoughtful birder with a sense of great humility but also great hope in our quests to identify birds utterly unfamiliar to us.

Abstract

The Red-backed (*Lanius collurio*), Turkestan (or Red-tailed, *L. phoenicuroides*), Isabelline (*L. isabellinus*), and Brown (*L. cristatus*) Shrikes comprise an assemblage of related species that breed, migrate, and winter throughout the Old World. The group includes five or more subspecies, and hybridization between Red-backed Shrike and each of the other species is known to occur. An individual of this assemblage was observed at the mouth of Alder Creek, Mendocino County, California, from 5 March through 22 April 2015. In an effort to identify this shrike, we analyzed more than 500 digital images and examined more than 900 specimens to assess variation in molts, plumages, and age/sex-determination criteria within the species assemblage. We also compared recordings of the Mendocino shrike's

Figure 1. The Mendocino shrike when first observed on 5 March 2015 (a) and last observed on 22 April 2015 (b). Despite low resolution, these images demonstrate substantial change in plumage due to body-feather molt over the period of observation, especially in the color of the crown, head, and sides to the underparts. Photographs by Alison Cebula (a) and Murray Brown (b).





Figure 2. The upperparts of the Mendocino shrike during different dates and showing different effects of lighting and variable levels of red saturation: 19 March (a), 27 March (b), 30 March (c), 1 April (d), 6 April (e), and 16 April (f). Careful comparison of field descriptions with these images indicate that images b and c come closest to representing the shrike's actual back coloration, which we describe as rufous-brown. Photographs by Joe Morlan (a), John Sterling (b), Monte Taylor (c), Larry Sansone (d), Barrett Pierce (e), and Mark Rauzon (f).

song with those of the taxa in this assemblage. Although uncertainty is unavoidable when attempting to identify hybrids, we believe that plumage features, along with perhaps more telling wing and tail structural morphologies, point to Red-backed x Turkestan Shrike hybrid as the identification of the Mendocino bird. We also consider how such a hybrid, from a limited breeding area that extends from the Caspian Sea to the Altai region of south-central Russia, might reach California via reverse migration (180° misorientation).

Field encounter and description

On 5 March 2015, Alison Cebula and Robert Kunicki, interns with California State Parks, were conducting a shorebird survey near the mouth of Alder Creek, Manchester Beach State Park, Mendocino County, California, when they spotted what they tentatively identified as a Northern Shrike (*Lanius excubitor*). Cebula obtained a digiscoped image (Figure 1a) and sent it to Richard Hubacek, who believed it more likely a Brown Shrike (*L. cristatus*), a rare vagrant to California. Keiffer received the image on 9 March, agreed that the bird resembled a Brown Shrike, and forwarded it to Dunn and Pyle. Both Dunn and Pyle concurred that it was not a Northern Shrike and was probably a Brown Shrike, although both were puzzled by the grayish

wash to the crown, Dunn supposing that it might be of the southeastern subspecies of Brown Shrike (*L. c. lucionensis*) and Pyle wondering if a duller Red-backed Shrike (*L. collurio*) could be eliminated.

The shrike proved somewhat elusive, disappearing for hours and up to five days at a time, but numerous observers got to see and photograph it over the ensuing six weeks, usually at some distance. It spent most of its time along a brushy ridge bordering open grasslands, on private property across the creek. It was last observed and photographed on 22 April by Murray Brown of British Columbia (Figure 1b), after an absence of observations since 17 April and a general presumption that it had already migrated north. Keiffer observed it on 14 March, Dunn on 24 March, and Pyle on 1 April. During the period of observation, the shrike was undergoing molt of flight feathers and body feathers, resulting in a shifting appearance that elicited shifting opinion as to its age and identity. It was also heard singing, and two recordings by Steve Hampton were posted to xeno-canto (www.xeno-canto.org) under “identity unknown.”

The bird was widely thought to be a Brown Shrike during the first two weeks of observation. Not convinced of this, Pyle sent images to Moores, who has extensive experience with Asian shrikes and

their identification in Korea, where Brown Shrike is a locally common migrant and uncommon breeder (Moores 2004, 2015). Moores's first reaction was that many features were at odds with a pure Brown Shrike, that it did not show indisputable features of any species or subspecies, and that it seemed most likely a dull eastern Red-backed Shrike or perhaps a hybrid between a Red-backed Shrike and either a Turkestan (*L. phoenicuroides*) or Isabelline (*L. isabellinus*) Shrike—three species previously unrecorded in North America.

Interest in the shrike increased substantially after internet discussion turned toward Red-backed Shrike and hybrids. Keiffer contacted observers of the bird to obtain documentary photographs, especially those showing spread wing and tail for analysis of molt, age, and identification. With each new series of posted images, as the bird continued to molt (Figures 1-3), came new rounds of discussion as to its identification, including comments from those familiar with this shrike assemblage in Europe and Asia. Complicating these discussions, digital images (captured with many types of cameras) displayed variable levels of red saturation in the back color (Figure 2). Observers anticipated a secure identification once the shrike had completed its molt, but, unfortunately, this did not occur before the bird was last photographed. By mid-April,



2c

2d



2e

2f





3a



3b



3c

Figure 3. The underparts of the Mendocino shrike during different dates and showing the effects of body molt on the coloration to the sides and flanks: 13 March (a), 21 March (b), 27 March (c), 30 March (d), 4 April (e), and 17 April (f). Careful readings of field descriptions, and direct personal observations, indicate that these images more or less capture the true coloration of the underparts as it changed over the period of observation. Photographs by Steve Stump (a), Thomas Benson (b), John Sterling (c), Monte Taylor (d), Gary Woods (e), and Patricia Bachetti (f).

a general consensus had formed that the bird was either a hybrid involving Red-backed Shrike, or a Brown Shrike of subspecies *L. c. lucionensis*, or (perhaps) *L. c. confusus*, thought by some to represent an intergrade between *lucionensis* and nominate *cristatus*.

As a small *Lanius* shrike showing various grayish, rufous, and brownish tones dorsally, having a distinct dark mask, and being white below with a wash of coloration to the sides, the Mendocino shrike fit well in the assemblage that includes Red-backed, Turkestan, Isabelline, and Brown Shrikes. When the bird was first observed, its crown was dull gray and brown, the back dull rufous-brown, the rump and uppertail coverts a brighter cinnamon to pinkish rufous, and the underparts white with a dull pinkish-buff wash on the sides. As the bird molted, the crown became a brighter silvery gray mixed with some rufous-brown in the nape, the upper back became brighter rufous-brown, the lower back and rump became grayish, and the sides were washed with a brighter apricot-orange tone. The older wing and tail feathers were brownish to cinnamon in coloration, while the replaced remiges were

dusky brown and the replaced rectrices were variously mixed dark rufous-brown and blackish from above and pale grayish basally with indistinct dusky tips from below. The inner web of at least one new rectrix appeared to have a whitish patch at its base, and the newer replaced outer primaries had white bases that extended beyond the primary coverts. A more exhaustive description of individual feathers and feather tracts, within the context of molt progression, is given below.

Overview

Red-backed, Turkestan, Isabelline, and Brown Shrikes form a species assemblage, with as few as one and as many as seven taxa considered distinct species during the course of a checkered taxonomic history (Dement'ev and Gladkov 1954, Vaurie 1959, Pearson 1979, Cramp and Perrins 1993, Kryukov 1995, Worfolk 2000, Panov 2009, Panov et al. 2011, Pearson et al. 2012). Variation in plumage and structure, even among adult males, hybridism and/or character introgression, poorly documented breeding and non-breeding distributions in some cases, and a difficulty in identifying female and first-cycle birds have all contributed to this taxonomic uncertainty. In discussing the identification of the Mendocino shrike, we follow Panov et al. (2011), Dickinson and Christidis (2014), and Gill and Donsker

(2015) in recognizing the above four distinct species within this assemblage, including the Turkestan (or Red-tailed) Shrike as a full species, separate from Isabelline Shrike, where it has often been placed as a subspecies.

Red-backed Shrike breeds in Europe and Turkey east to northern Kazakhstan and the Altai region of south-central Russia and winters primarily in southern Africa (Figure 4). Eastern and southern populations, regarded by many as subspecies *pallidifrons* and *kobylini*, respectively, average smaller, duller, and paler than western populations (Cramp and Perrins 1993). Adult male Red-backed Shrikes have gray crowns, reddish-brown upperparts, and

dusty pinkish or rosy coloration to the sides and flanks. They are unique among this species assemblage in having a distinctly patterned, black-and-white tail.

Turkestan Shrike breeds in Iran north to southern Kazakhstan and east to the southern Altai region (Figure 4). The winter ranges of Turkestan and Isabelline Shrikes are poorly defined and overlap (Worfolk 2000), due in part to an extra degree of difficulty in identifying females and first-cycle birds away from the breeding grounds; however, it appears as though the Turkestan Shrike winters largely in eastern Africa (Figure 4). Adult male Turkestan Shrikes tend to have a reddish-brown crown, a distinct white supercilium, medium brown to grayish back, and white underparts with relatively restricted pale apricot-orange coloration to the sides and flanks. In all age/sex groups, the rump and uppertail coverts are cinnamon-red to pinkish red, and the tail is a fairly bright cinnamon-red.

Isabelline Shrike breeds primarily in Mongolia and north-central China and winters from the southern Arabian Peninsula east through Pakistan and western India (Figure 4). Isabelline Shrike is polytypic, with three subspecies recognized. The more migratory northern subspecies, breeding from the Altai region through Mongolia, is here considered the nominate subspecies, *L. i. isabellinus*, following Pearson et al. (2012; see also Pearson 2000, Panov 2009, Panov et al. 2011). Adult males of this subspecies tend to have uniformly medium to pale brown crowns and backs, lack a distinct supercilium, and show extensive apricot coloration to the sides and flanks that often extends to the throat and auriculars. The rump, uppertail coverts, and tail in all age/sex groups are cinnamon, averaging paler than

in Turkestan Shrike. The subspecies *tsaidamensis* and *arenarius*, which breed to the south of nominate *isabellinus*, are less migratory and show muted pallid plumage features that are too dull for the Mendocino shrike. Therefore, further consideration of Isabelline Shrike in this paper will refer to nominate *isabellinus*.

Brown Shrike is also polytypic, with up to four subspecies recognized. The nominate subspecies, *cristatus*, is the longest-distance migrant of the four, breeding from the western Anadyr River basin to northern Mongolia and wintering primarily in southern India and Southeast Asia (Figure 4). To the southeast, *lucionensis* breeds in eastern China and parts of



3d



3e



3f

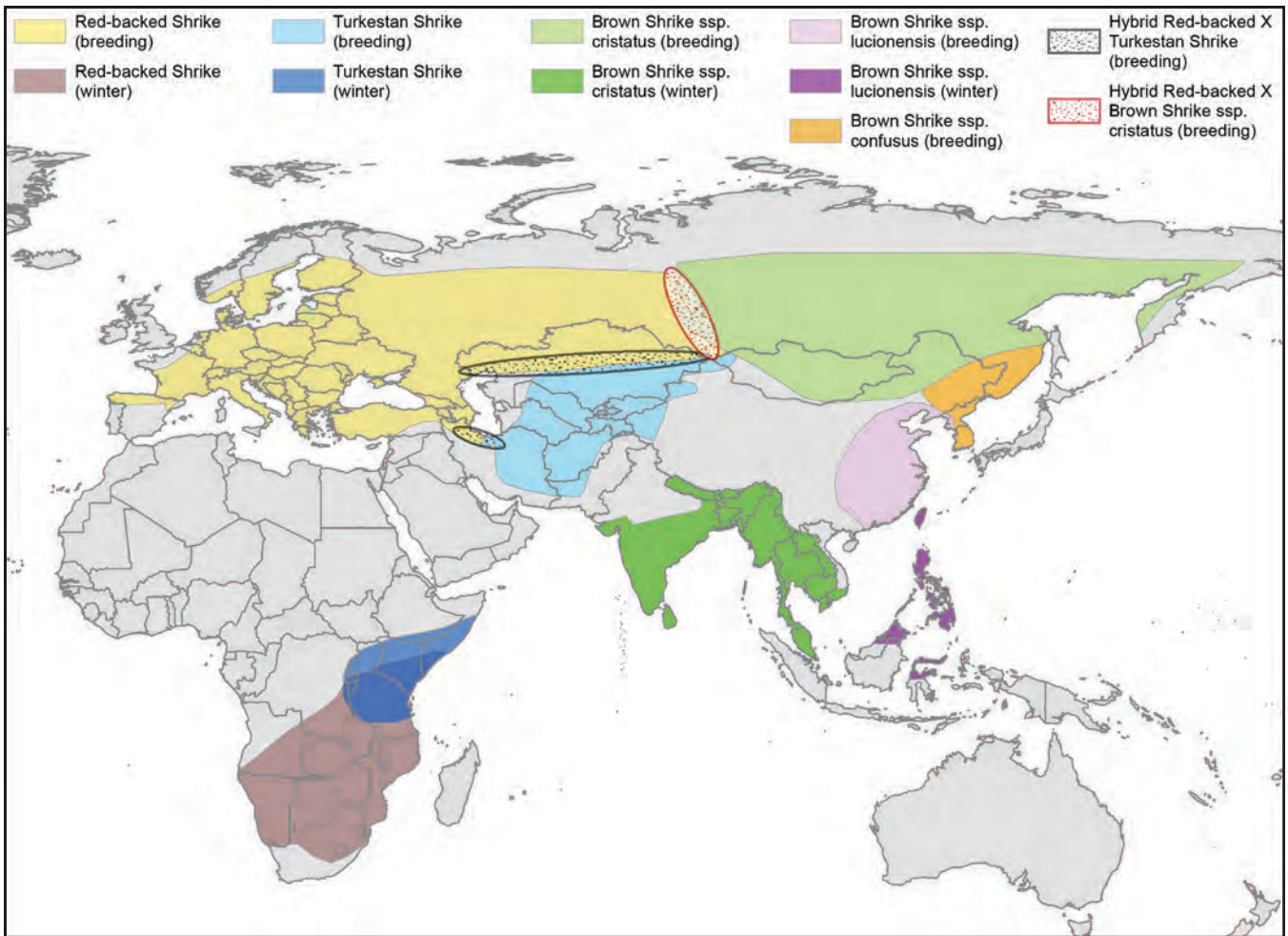


Figure 4. Breeding and winter ranges of shrike taxa considered for the identification of the Mendocino shrike, along with zones of overlap and hybridization between Red-backed Shrike and other taxa. The hybridization zone between Red-backed and Turkestan Shrikes is rather extensive, whereas only occasional hybrids between Red-backed and Isabelline Shrikes and between Red-backed and Brown Shrike have been observed (see text). The two hybrid zones overlap in the Altai range of south-central Russia, an area where all four species of this assemblage occur and may introgress. *Graphic by Shane Feirer, based on Figure 1 in Worfolk (2000), with added detail on the hybridization zones from Kryukov and Gureev (1997), Panov et al. (2011), and V. Dinets and A. Kryukov (pers. comm.).*

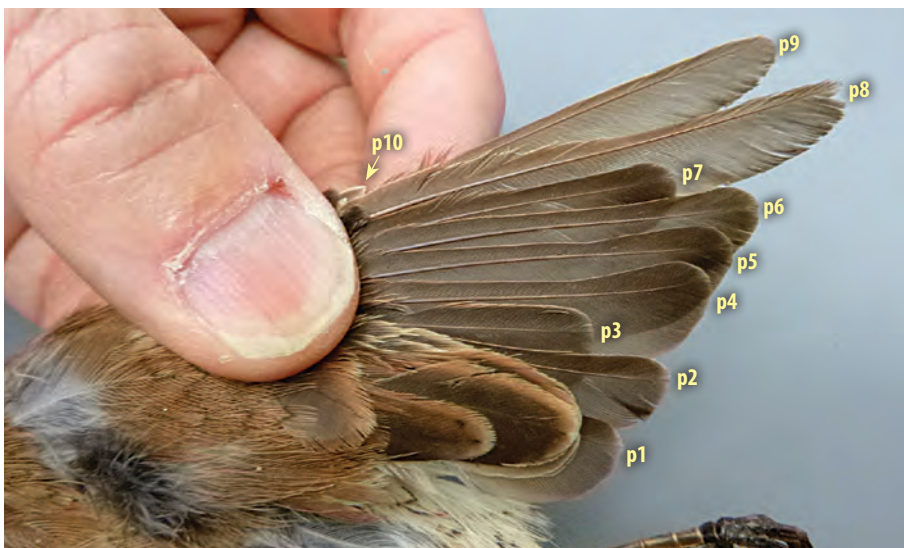


Figure 5. Red-backed Shrike specimen AMNH 661048, collected 7 February 1905 in Angola, Africa, showing bidirectional primary replacement during the preformative molt, likely from a node at p5 (p1-p2 and p8-p10 remain as juvenile feathers). Brown Shrike has been reported to undergo such bidirectional replacement of primaries during both preformative and prebasic molts, whereas Red-backed, Turkestan, and Isabelline Shrikes have been reported to only undergo distal replacement from p1 during these molts (Stresemann and Stresemann 1971, 1972; Cramp and Perrins 1993). Specimen examination for this paper, however, indicates that all four species can demonstrate either strategy, with the majority of individuals undergoing bidirectional replacement (see text). *Photograph by Peter Pyle.*

Korea and winters in eastern Southeast Asia and the Philippine Islands through northern Borneo and the Celebes Islands (Figure 4). A third taxon, *confusus*, is believed to breed in northeastern China, southwestern Siberia, and northeastern Korea; it probably winters primarily in Southeast Asia (Figure 4). Again, our understanding of winter ranges of the Brown Shrike subspecies has been obscured by difficulty in identifying females and first-cycle birds away from the breeding grounds. Subspecies *confusus* could intergrade with *lucionensis* in Korea (Fiebig 1995, in Tomek 2002) and in China and Russia with *cristatus*. A fourth subspecies of Brown Shrike, *superciliosus*, which breeds in southern Sakhalin Island and Japan and winters in Southeast Asia and Indonesia, shows plumage and structural features not shown by the Mendocino shrike (including an extremely long tail and a bright white forehead and distinct supercilium in males) and is not considered further in this paper.

Adult male nominate *cristatus* Brown Shrikes have uniform crowns, upperparts, and tails that vary from reddish brown to brown, whereas *lucionensis* shows a grayish crown transitioning to a duller mud-brown back and tail. Underparts of both subspecies are variable but are often extensively dark buff and occasionally mixed with dull

ochraceous. Subspecies *confusus* shows the widest range of characters; this and its poorly defined distribution suggest that many presumed *confusus* could be intergrades between other taxa (Worfolk 2000, Moores 2015) or in some cases possibly hybrids between Brown Shrike and Isabelline Shrike, though such hybrids may be rare (Kryukov 1995). True to its trinomial, *confusus* is therefore considered here as a catch-all name given to those Brown Shrikes that show a combination of features suggesting *cristatus* or *lucionensis* but that seem to fit neither of these taxa well. Although these four Brown Shrike subspecies vary tremendously in plumage, they share consistent wing and tail morphologies that differ significantly from the other shrike species in this assemblage.

There are 17 records of Brown Shrike from North America, 12 from Alaska in 1978-2015 (nine from fall and three from spring), four from California in 1984-2011 (two from fall and two of wintering birds), and one in November 1997 from Nova Scotia (C.B.R.C. 2007, Howell et al. 2014, Gibson and Withrow 2015; D. Gibson, P. Lehman, pers. comm.). Most records have been assigned to the nominate subspecies, *cristatus*, with the remainder being first-cycle birds that were likely *cristatus* but not confidently determined to subspecies. The first Alaska

record was tentatively identified as *lucionensis* (Gibson 1981) but has subsequently been identified as nominate *cristatus* (Gibson and Withrow 2015).

Hybridization between Red-backed and these other three migratory shrike species has been documented on the breeding grounds (Dement'ev and Glakov 1954, Kryukov and Panov 1980, Andrusenko and Panov 1993, Kryukov 1995, Kryukov and Gureev 1997, Worfolk 2000, Panov 2009, Panov et al. 2011), from Iran to Kazakhstan with Turkestan Shrike and in the Altai region of south-central Russia with all three other species (Figure 4). Individuals thought to be hybrids with Red-backed Shrike have also been recorded on migration or winter grounds, in eastern Africa (Pearson 1979), most countries of the Middle East, including Saudi Arabia (Babbington 2013, 2014), Malaysia (Mun 2015), and Japan (Horimoto and Watabe 2014, Young Guns 2014). Hybridization between Red-backed and Turkestan Shrikes is extensive if not indiscriminate, within a fairly expansive but poorly delineated zone extending from the Caspian Sea to the Altai region (Figure 4). Panov et al. (2011: 475-480, 568-591) speculate that Red-backed and Turkestan Shrikes may be one biological species, and that the two duller eastern

Figure 6. Progression of primary and rectrix molt in the Mendocino shrike on 21 March (a), 27 March (b), and 4 April (c). See text for details. Note also the contrast between cinnamon outer juvenile rectrices and blackish inner formative rectrices on 27 March (b). Photographs by Thomas Benson (a), John Sterling (b), and Larry Sansone (c).

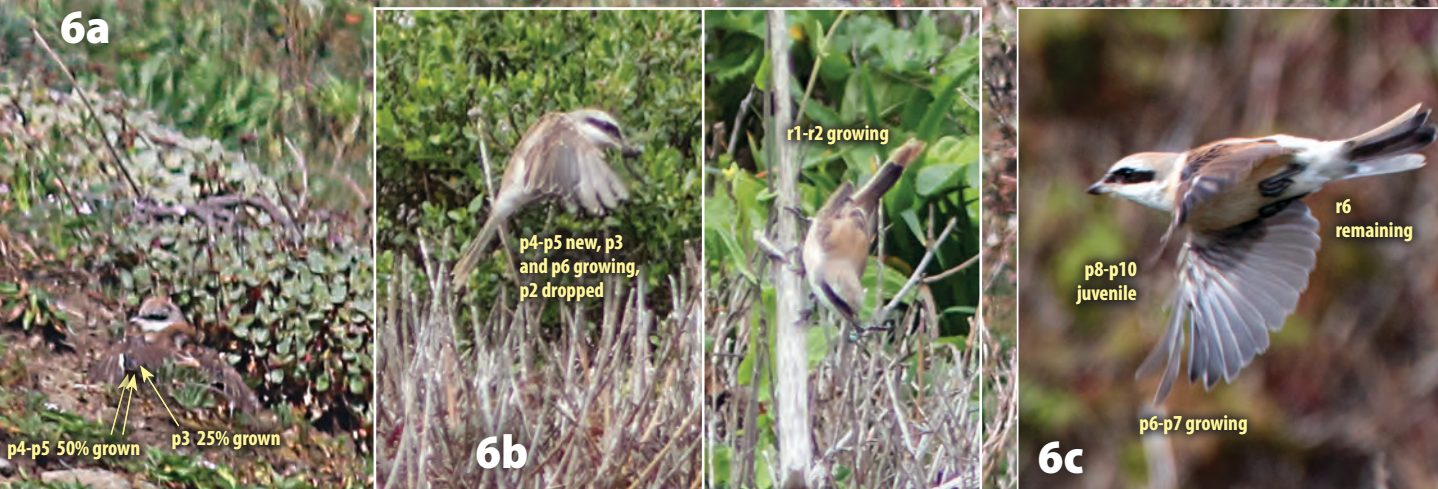




Figure 7. Progression of primary and rectrix molt in the Mendocino shrike on 16 April. Note the mixed blackish and brownish patterns to the formative rectrices (as viewed from below) and the white patches at the bases of the primaries that extend beyond the primary coverts (see also Figure 13). Photograph by Mark Rauzon.

subspecies of Red-backed Shrike (*pallidifrons* and/or *kobylini*) may represent clinally introgressed populations between these two taxa, as perhaps do grayer-backed individuals of Turkestan Shrike (sometimes referred to as subspecies *karelini*). By contrast, evidence from studies on the breeding grounds indicates that hybrids between Red-backed and Isabelline Shrikes are less common and more localized, and those between Red-backed and Brown Shrikes are rare, with mixed pairs usually disassociating before breeding (Kryukov and Panov 1980, Kryukov 1995, Kryukov and Gureev 1997, Panov 2009, Panov et al. 2011; A. Kryukov, pers. comm.).

The contending taxa for the Mendocino shrike, based on range, migratory status, and appearance, therefore, include Red-backed Shrike, Turkestan Shrike, nominate populations of Isabelline Shrike, and Brown Shrikes of subspecies *cristatus*, *lucionensis*, and *confusus*. Hybrids to be considered include those between Red-backed Shrike and all three of the above species. Among the Brown Shrikes, hybridism is limited to subspecies *cristatus*, as the breeding range of Red-backed Shrike is distantly allopatric with those of both *confusus* and *lucionensis* (Figure 4). We restrict further consideration of the Mendocino shrike's identification to these six highly migratory taxa and the above three hybrid combinations.

Molts, Plumages, Age, and Sex

Shrikes of the Red-backed/Turkestan/Isabelline/Brown species assemblage show three

plumages within the first molt cycle and two plumages in definitive cycles, with sex-specific differences beginning with the formative (post-juvenile) plumage. Thus, nine plumages can be recognized within each taxon, resulting in 54 plumages to consider among the six contending taxa noted above, not to mention those of hybrids. Fortunately, the Mendocino shrike showed a distinct black mask and little or no barring to body feathers from the outset (Figures 1-3), indicating a male within either the first or definitive cycle, and thus eliminating the most difficult 42 of these possible plumages from consideration.

Molts of these shrikes are complex, age and sex determination bear critically on identification (Dean 1982, Worfolk 2000), and the fact that the Mendocino shrike was undergoing molt of flight feathers and body feathers necessitates an attempt to untangle molt, age, and plumage variables before proceeding with taxonomic evaluation. A precise determination of feather generations for molted vs. unmolted flight feathers during the course of the shrike's documentary period is also needed to perform detailed assessments of wing and tail morphology (see below). The following interpretation of molts in these shrikes is based upon a synthesis of the literature (Medway 1970; Stressemann and Stressemann 1971, 1972; Svenson 1992; Cramp and Perrins 1993; Jenni and Winkler 1994; Worfolk 2000; Panov et al. 2011) as affirmed and updated by ex-

amination of 911 specimens of the contending taxa by Pyle at the American Museum of Natural History (AMNH), New York, the Museum of Vertebrate Zoology (MVZ), Berkeley, and the California Academy of Sciences (CAS), San Francisco. We apply the molt and plumage terminology of Pyle (2008) for long-distance migrant birds that undergo preformative and prebasic flight-feather molt on winter grounds, allowing that other interpretations are possible in these cases and should be further contemplated (see Pyle and Reid, in press).

Although many inter-taxon differences regarding timing, extent, location, and sequence have been reported, specimen examination for this paper indicates that the molt strategies of these shrike taxa are probably more similar to each other than has been understood thus far. Substantial individual variation in the extents of each molt, both prior to and following southward migrations (of varying distances within each taxon), coupled with an inability to trace the molts of individuals outside of captivity, appears to have resulted in various interpretations for a similar complex molting situation.

We propose that molts and plumages within this shrike species assemblage are similar to those within certain shorebird genera (*Calidris*, for example) in which molt strategy varies as much or more by wintering latitude and breeding status of individuals than it does by taxonomic relationships (Pyle 2008: 500-505). Trans-equatorial mi-



Figure 8. Specimens at AMNH illustrating first-cycle upperpart plumages in male Red-backed Shrikes. From left to right, juvenile (661117 collected 15 October 1902), individuals undergoing the preformative molt (661058 collected 12 October 1886, 661043 collected 8 February 1905, and 661046 collected 7 February 1905), and an individual in first alternate plumage (463918 collected 22 April 1941). Note the dark subterminal chevrons throughout the juvenile feathering, and the variation in the three birds undergoing the preformative molt, including the expression of alternate-male-like plumage as early as October and the lack of chevrons in these birds by commencement of primary molt in February. Note also the variation in the head, back, and rump plumage in the two birds collected a day apart in February. The bird in alternate plumage (463918) was collected in Iran from duller eastern populations of Red-backed Shrike (see also Figure 9). Photograph by Peter Pyle.

grants within each taxon tend to molt more extensively on winter grounds than shorter-distance migrants. This is likely due to adaptations related to elevated solar exposure, which degrades feathers, necessitating more molt, and to increased nutrient availability, which may allow for more feather production, both in the context of two summer seasons per year. Overlaid upon this variation, birds that did not breed or that failed breeding early (including many one-year-olds) tend to commence flight-feather molt earlier and on the breeding grounds, whereas successful breeders tend to migrate southward before commencing this molt at a later date (Pyle 2008: 500-505; Pyle and Reid, in press).

Juveniles of these shrikes proceed to undergo a preformative (post-juvenile) molt that can vary between partial and incomplete or (probably) complete. All body feathers are replaced primarily in August–December, usually commencing on breeding grounds and completing on winter grounds in longer-distant migrants. A few to most or all flight feathers are then replaced primarily in December through April or May. As in shorebirds such as *Calidris* sandpipers, the farther south an individual winters, the more flight feathers are often replaced, from a few tertials and/or central rectrices in northern-wintering individuals, to most or all flight feathers in trans-equatorial and longer-distance migrants. This variation appears to occur at the individual level, as confounded by each taxon's average wintering latitude. A partial first prealternate (first pre-breeding) molt of some to most body feathers occurs in March–May, which can overlap the completion of

preformative flight-feather molt in southern-wintering individuals.

Adults undergo a definitive prebasic (adult post-breeding) molt that parallels the preformative molt but is complete, with body feathers replaced primarily in August–December and flight-feather molt variably commencing sometime in August–January and completing sometime in October–March. In northern-wintering individuals and failed breeders, the molt is often initiated or completed in fall, whereas in trans-equatorial migrants and successful breeders, the flight-feather molt can be suspended for southbound migration and be protracted through spring due to lack of winter-related constraints (Pyle 2008: 500-505); or it can occur entirely on the winter grounds as late as January–March. A definitive prealternate (adult pre-breeding) molt of body feathers then occurs in February–April, overlapping some or most of the flight-feather molt in southern-wintering individuals.

During both preformative and definitive prebasic molts, sequence of primary replace-

ment proceeds bidirectionally (both proximally and distally) from a molt node (or center) at p3, p4, or p5 in most individuals (Figure 5), although in some individuals it may proceed distally from p1, while other individuals may show both of these sequences, e.g., p1 molting before the proximal wave from a central node reaches p2 (Stresemann and Stresemann 1971, Svensson 1992, Cramp and Perrins 1993). Such variation between primary replacement sequences has been recorded for other passerine species (Jenni and Winkler 1994, Neto and Gossler 2006, Junda et al. 2012) and allows birds showing bidirectional replacement to complete molt of primaries more quickly than during unidirectional molt (Pyle 2013a). It is possible that those individuals with nodes at both p4–p5 and p1 are undergoing the second prebasic molt after retaining the juvenile p1 from the year before (see below), as this sort of sequential “memory” between molts (beginning where the previous molt had arrested, as in Staffeldmauser, or step-wise molt, in larger birds) has been recently



9a



9b

documented in other passerines (Pyle et al., in press). Among those specimens examined for this paper that were undergoing remigial molt when collected, 32 were replacing primaries bidirectionally from a medial primary, while only three specimens (Red-backed Shrikes AMNH 661056 and 661086 and Brown Shrike AMNH 661262) were replacing primaries distally from p1. Bidirectional replacement included nodes at p3 (three specimens of Turkestan Shrike), p4 (15 specimens, of all four species), and p5 (14 specimens, of all four species; see Figure 5).

Secondaries are replaced bidirectionally from a node at s8 (the second tertial) and distally from a node at s1, while rectrices are replaced distally from r1 to r6 on each side of the tail, sequences that in each case are typical of passerines (Jenni and Winkler 1994; Pyle 1997, 2013a). During incomplete preformative molts, most or all juvenile inner primary coverts can be retained, even in those individuals that replace most or all primaries. Retained juvenile primary coverts appear most often to correspond to those primaries initially replaced from a central node, among p2-p7, but retention of either all or all but the outer 1-4 juvenile primary coverts was also noted on spring and summer specimens of all four species. Other retained juvenile feathers observed on these specimens included p1-p3, r5-r6, and up to all six secondaries among s1-s6, with proximal feathers (s5-s6) typically replaced before distal feathers (s1-s2). Retention of most or all distal primary coverts, inner primaries, and outer secondaries results in an eccentric-like pattern (sensu Pyle 1997, 2008)

Figure 9. Variation in upperpart coloration of alternate-plumaged males among specimens at AMNH identified as five taxa considered for the Mendocino shrike: Red-backed Shrike (a), Turkestan Shrike (b), Isabelline Shrike (c), *cristatus* Brown Shrike (d), and *lucionensis* Brown Shrike (e); see Figure 10 for underpart coloration of these same specimens. Specimen identification as indicated on the labels may not always be accurate, especially that between Turkestan and Isabelline Shrikes (b and c), formerly considered conspecific. Brown Shrike subspecies *confusus* (not shown) also displays a broad range of characters, some of which are intermediate between those of *cristatus* and *lucionensis*, whereas others are not shown by either of these subspecies (see text); the warm tones to the right-hand *lucionensis* in these series (e) suggest that it may represent *confusus*. Among the specimens of Red-backed Shrike and the other taxa, a comparison with dates of collection indicates that variation in reddish plumage is not attributable to specimen foxing. Photograph by Peter Pyle.

for retained flight feathers during the preformative molt, similar to retention patterns of some migratory North American passerines (e.g., *Empidonax* and *Myiarchus* flycatchers) in which eccentric molts can occur in longer-distant migrants (Pyle 1997, 1998). These shrikes differ from species showing eccentric molts in that fewer juvenile primaries and primary coverts are retained due to bidirectional rather than the unidirectional (distal) replacement within this tract found in most birds.

Adult *cristatus* Brown Shrikes have been reported to undergo two complete molts per year (Medway 1970, Stresemann and Stresemann 1971, Svensson 1992, Cramp and Perrins 1993, Jenni and Winkler 1994), but confirmation of this is lacking due to an inability to trace feather replacement in wild individuals throughout a molt cycle in a natural setting. It is possible that this interpretation was based on separate individuals undergoing the complete molt at variable times of year; for example, some individuals may molt flight feathers in August–November, others in January–March, and some may molt throughout this period with one or more molt suspensions, while few or no individuals molt flight feathers twice within a cycle. Specimens examined for this paper, collected in both late sum-





mer and late winter, show worn flight feathers typical of those not replaced for nearly a year, or else show apparent suspensions indicating a single long protracted molt. A careful reading of both Medway (1970) and Stresemann and Stresemann (1971), furthermore, indicates little evidence for two molts per year and some evidence (e.g., very worn feathers being replaced in spring, fresh non-molting birds in April, and spring molts proceeding distally from medial primaries after suspensions), suggesting single variable flight-feather molts, as has been documented in Red-backed Shrike (Snow 1965) and Turkestan and Isabelline Shrikes (Stresemann and Stresemann 1972). We would consider it unusual for two complete molts per year to be confined to one taxon within the Red-backed/Turkestan/Isabelline/Brown shrike species assemblage. The above conclusions on molt in the Brown Shrike were arrived at independent of those of Neufeldt (1978, summarized by Panov et al. 2011: 71-73), who came to several similar suppositions. Specimen examination otherwise revealed few differences in molt strategies among the taxa considered for the Mendocino shrike, differences in timing and extents depending more on migratory status and wintering latitude of the individual.

Most first-year individuals of this shrike species assemblage can be aged by the retention of brown and worn juvenile primary coverts, with one to five distal feathers replaced. Juvenile outer primaries and rectrices are also narrower and more worn as compared to formative and definitive basic feathers, and these differences can be used to age molting individuals and those that do not undergo complete flight-feather molt (Svensson 1992, Jenni and Winkler 1994). Further investigation may be needed to determine what proportion of these shrikes, especially Red-backed Shrikes, may undergo a complete preformative molt (including all primary coverts), as these appear not to be reliably separated from older adults in spring and summer.

Careful analysis by Pyle of dozens of im-

Figure 10. Variation in underpart coloration of alternate-plumaged males among specimens at AMNH identified as five taxa considered for the Mendocino shrike: Red-backed Shrike (a), Turkestan Shrike (b), Isabelline Shrike (c), *cristatus* Brown Shrike (d), and *lucionensis* Brown Shrike (e); see Figure 9 for comments on the identification of these specimens and on Brown Shrike subspecies *confusus*. All variation among certain taxa is not captured in these images; in particular, many male Turkestan and Red-backed Shrikes show brighter apricot-orange sides than are captured here. Photograph by Peter Pyle.

ages and video clips of the Mendocino shrike allowed assessment and progress of its flight-feather molt (Figures 6-7). By 13 March, p3-p5 were noted to be missing by one observer (Jeff Petit) and by 21 March, p4 and p5 were growing equally at about 50% of full length and p3 about 25% of full length (Figure 6a). A replacement node occurring synchronously at two adjacent feathers (p4 and p5) is of interest and indicates that the node's position may be fluid within a defined area along the alar tract, as found in other birds (Pyle 2013a). By 27 March, replacement of primaries had proceeded bidirectionally to p3 and p6, which were growing at about 80% and 70%, respectively, p2 had dropped, and p1 and p7-p10 remained as old feathers (Figure 6b). By 16 April, p1 was still old, p2-p6 were fully grown, p7 was 80% grown, p8 was 30% grown, and p9-p10 had dropped (Figure 6b). The old inner primary coverts had been retained, and the outer three or four were being replaced concurrent with the outer primaries (cf. Figure 13). A rough calculation of feather growth rates based on molt scores, along with total length of all primaries (529 mm, the mean of one each of Red-backed, Turkestan, and Brown Shrike specimens measured by Pyle),

Continued on page 20





Figure 11. The Mendocino Shrike on 4 April (a) and 16 April (b), showing characters indicative or diagnostic of Red-backed Shrike among the six taxa under consideration (Table 1; see text). The apparent white patch to the inner web of r3 (a) was noted on images taken by different observers, and close examination of the images further suggests that it is not a photographic artifact. No other images taken subsequent to this shows the inner webs of these rectrices from above, while images from below (e.g., Figure 7) might not be expected to show the same pattern. Several features of the Mendocino shrike, however, do not indicate a pure Red-backed Shrike including, notably, reddish-brown alternate feathers in the hindcrown (a) and the lack of more-extensive white bases to r3-r5, as typically found in this species (c; MVZ 21374); see also Figure 7. *Photographs by Gary Woods (a), Richard Hubacek (b), Peter Pyle (c).*



Table 1. Plumage (a) and structural morphological (b) characters of the Mendocino shrike along with those for five taxa under consideration for its identification. Plumage characters and biometrics were derived from descriptions and images for the Mendocino shrike as compared to the literature and specimen examination for alternate-plumaged males of the five contending taxa. Analyses of morphological ratios in specimens of males with juvenile, formative, and basic outer primaries and rectrices yielded no significant effects of age or feather generations, so ages were lumped in calculating the ratios from specimens. See text for details. For Isabelline Shrike, it is possible that some of the specimens were of subspecies *arenarius* or *tsaidemensis*, misidentified as *isabellinus*, which may have resulted in shorter wing and tail morphologies than is true of *isabellinus*; *isabellinus* likely should match *phoenicuroides* more closely in wing and tail structure (Svensson 1992; L. Svensson, pers. comm.). Not enough Brown Shrike specimens confirmed to subspecies *confusus* were available to include in this table; see text for discussion of plumage features, largely intermediate between *cristatus* and *lucionensis*.

	Red-backed Shrike	Turkestan Shrike	Isabelline Shrike	Brown Shrike	Brown Shrike	Mendocino Shrike
Character	<i>L. collurio</i>	<i>L. phoenicuroides</i>	<i>L. isabellinus isabellinus</i>	<i>L. cristatus cristatus</i>	<i>L. cristatus lucionensis</i>	

TABLE 1a: PLUMAGE

Crown	Pale to medium pale gray; supercilium lacking or indistinct	Rufous-cinnamon to tawny; distinct white supercilium	Pale grayish brown to ginger; indistinct buff supercilium	Cinnamon-brown; distinct white supercilium	Grayish lavender; moderately distinct, whitish to grayish-white supercilium	Bright silvery gray; indistinct whitish supercilium
Back	Bright chestnut to reddish brown; contrasts distinctly with crown	Dull brown to brownish gray; contrasts with crown	Pale grayish brown to sandy brown; little or no contrast with crown	Brown to cinnamon-brown; little or no contrast with crown	Dull dark brown to gray-brown; contrasts distinctly with crown	Medium dull rufous-brown; contrasts distinctly with grayer crown
Rump	Gray	Pale to medium brown	Pale brown	Brown to cinnamon-brown	Dull dark brown	Pale brownish gray
Juvenile rectrices	Brown	Cinnamon to pale rufous	Cinnamon	Brown to reddish brown	Brown	Cinnamon
Formative and basic rectrices	Black with white bases; r6 edged and tipped white	Rufous	Pale rufous to cinnamon	Brown to rufous	Brown to warm brown	Mixed blackish brown and rufous-brown above; darker tips from below
Sides and flanks	Pale to dark vinaceous pink, not extending to throat or auriculars	Mixed ochraceous and brown, not extending to throat or auriculars	Pale cinnamon to cream, extending to throat and auriculars	Warm yellow-buff to tawny, not extending to throat or auriculars	Deep yellow-buff to tawny; less white in center	Mixed pink, ochraceous, orange, and brown, not extending to throat or auriculars
Tertial edging	Rufous and white	Off-white to pinkish buff	Buff to pale cinnamon	Whitish to pale cinnamon	Whitish to pale cinnamon	Rufous and white
White bases in primaries	Occasionally extend beyond primary coverts	Usually extend beyond primary coverts; white	Usually extend beyond primary coverts; washed buff	Very rarely extend beyond primary coverts	Very rarely extend beyond primary coverts	Extend beyond primary coverts

TABLE 1b: STRUCTURE AND MORPHOLOGY

Bill size and shape	Medium-long and shallow	Short and shallow	Short and shallow	Long and deep	Long and deep	Medium-short and shallow
Wing morphology						
n	56	36	25	49	23	8
p9-p8 (a)	3-8 (5.7)	5-11 (8.3)	7-12 (9.5)	8-15 (11.6)	8-14 (11.8)	
p9-p coverts (b)	45-51 (47.6)	42-49 (45.5)	40-47 (43.8)	35-46 (40.5)	37-43 (39.6)	
Ratio a/b	0.90-0.155 (0.126)	0.136-0.230 (0.187)	0.170-0.255 (0.211)	0.233-0.313 (0.274)	0.225-0.309 (0.268)	0.102-0.138 (0.120)
Tail morphology						
n	52	35	25	48	23	11
r5-r6 (c)	6-11 (8.3)	7-12 (9.6)	7-13 (10.3)	14-24 (18.8)	13-20 (16.7)	
r6 to tail base (d)	59-68 (63.9)	62-70 (65.7)	63-74 (68.7)	54-62 (57.9)	56-61 (58.2)	
Ratio c/d	0.091-0.157 (0.126)	0.113-0.181 (0.149)	0.113-0.180 (0.148)	0.248-0.364 (0.304)	0.223-0.335 (0.277)	0.098-0.129 (0.114)

suggests that primary molt had commenced around 12 March and would have completed around 8 May, barring suspended or arrested molt following the last observation.

Replacement of secondaries and rectrices proceeded largely as described above. By 21 March, the central tertial (s8) was growing, and the remaining eight secondaries had not yet dropped, and by 16 April the inner two tertials (s8-s9) were new, s7 was 90% grown, s5-s6 had dropped, and the remaining secondaries (s1-s4) were old (Figure 7). Given that this was the preformative molt (see below), we suspect that, at most, the s4 might have been replaced by the time the molt completed, leaving p1 and s1-s3, along with most of the inner primary coverts, as retained juvenile feathers, a pattern noted in specimens of first-spring/summer shrikes of all four species. By 13 March, the four central rectrices (r1-r2 on each side) had apparently dropped, and by 21 March these were growing at about 50% of full length (Figure 6b). Sometime during this period, the right central rectrix was lost and, by 3 April, was re-growing at about 40% of full length, at which point the other three central rectrices had fully grown, the r3s were growing at about 20% of full length, r4-r5 had dropped, and r6 on each side of the tail remained. By 16 April, r1-r3 were full-length, and r4, r5, and r6 were growing, at 70%, 30%, and 20% of full length, respectively (Figure 7).

Based on molt timing and replacement patterns, then, the Mendocino shrike was a first-cycle bird, as confirmed by the retention of brown inner juvenile primary coverts, contrasting with the replaced corresponding pri-

maries and the outer primary coverts (Figure 13). According to the molt terminology used here, it was thus completing the preformative molt of flight feathers and had initiated the first prealternate body-feather molt during the period of observation. Unmolted outer primaries and rectrices were narrow, tapered, and worn, and the new and growing feathers of these tracts were substantially dusker or blacker in appearance (Figure 6), indicating replacement of juvenile with formative feathers. Despite some plumage features suggesting definitive basic plumage in early March, the body feathering changed coloration rather substantially (Figure 1), indicating transition from formative to first alternate plumage as opposed to the more static appearance change between definitive basic and definitive alternate plumage in males. The bill was also dusky with a substantial pinkish base to the lower mandible throughout the period of observation (Figures 2-3), further suggesting a first-cycle bird for a male (Svensson 1992, Cramp and Perrins 1993).

The first prealternate body-feather molt had commenced by early April, as indicated by mixed worn and fresh feather generations visible in photographs, along with a shifting plumage appearance (Figures 1-3). Body-feather molts in birds generally proceed from head to rump and breast to vent (Jenni and Winkler 1994, Pyle 1997), and this is also reflected in photographs of the Mendocino shrike. Molt of the head and upper back had largely completed but that of the lower back,

rump, and uppertail coverts had not completed by the time these areas were last photographed, in mid-April.

Plumage tones

The variable molts and plumages of the shrike species assemblage considered here, coupled with molt-plumage interactions (see Pyle 2013b) and age/sex-specific differences within each species, results in complex and variable plumages within each taxon (Dean 1982, Svensson 1992, Cramp and Perrins 1993, LeFranc and Worfolk 1997, Harris and Franklin 2000, Worfolk 2000, Panov et al. 2011). The following analysis is based on information from these references, with an emphasis on males in formative and fresh alternate plumages, as verified by specimen examination by Pyle and extensive field experience by Moores and Dunn (primarily with Brown Shrike).

The timing and sequence of the preformative and first prealternate molts in the Mendocino shrike, described above, offer little direct elucidation as to its identification due to the similar overall but individually variable nature of these molts among the shrike



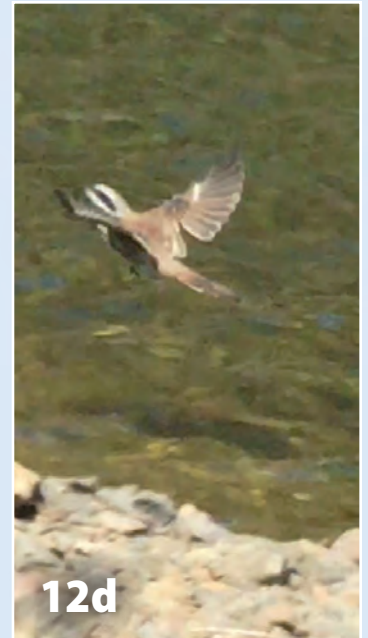


Figure 12. The Mendocino shrike on 30 March (a), 6 April (b), 13 April (c), and 17 April (d), showing coloration to lower back, rump, uppertail coverts, and base of the rectrices as it transitioned from formative to first alternate body feathering and replaced juvenile with formative rectrices. The first prealternate molt of body feathers progressed slowly through this period and had not completed by the time the bird was last observed, resulting in the lower back and rump becoming increasingly but not entirely grayish. In formative plumage, the contrast between cinnamon to pinkish-rufous rump and uppertail coverts with browner back (a, b) is not typically found in *cristatus* Brown Shrikes and favors the influence of Turkestan or Isabelline Shrikes (Table 1). Note also the reddish juvenile rectrices (a) and the rufous bases to the formative rectrices (d, the latest image taken of the Mendocino shrike in flight). Photographs by Monte Taylor (a), Bruce Pierce (b), Shirley Wilkerson (c), and Patricia Bachetti (d).



taxa under consideration. However, the preformative molt occurring largely on the winter grounds and the relatively late timing to the flight-feather molt of the Mendocino bird supports the shrike's origin as one of the longer-distance migratory populations. The slightly later-than-normal and complete primary molt, despite a more northerly wintering location, might be attributed to the vagrant status of the Mendocino shrike (see Howell et al. 2014, regarding similar molt in a vagrant sand-plover).

In all four species, juveniles are heavily marked with black crescents, the result of V-shaped subterminal bars on both upperpart and underpart feathers (Figure 8). In males, formative feathers can either show or not show these crescents, perhaps based on early and later timing to the preformative molt, respectively, and some formative males with later molts can assume a duller expression of definitive alternate body plumage as well (Figure 8). Following the first prealternate molt, first-cycle males become much brighter and are very similar to definitive alternate males in body plumage, although they may average slightly duller (Cramp and Perrins 1993; specimen examination; Figure 8). Definitive basic males largely maintain alternate-like coloration, with the addition of brown fringing to basic feathers that subdues plumage tones when fresh. Definitive basic males can also have a few dark crescents, especially in the sides and flanks (Cramp and Perrins 1993, specimen examination).

Although many males in first or defini-

tive alternate plumage are readily diagnosed to species and subspecies, these plumages within each taxon can show substantial variation in the saturation, tone, and brightness of both upperpart and underpart coloration (Figures 9-10). For example, back coloration in Red-backed Shrike can vary from a bright brick-red to a dull reddish brown, and back coloration among Turkestan and Isabelline shrikes can vary in the shade of brown, to the extent of approaching or overlapping with each other in tone (Figure 9). The sides and flanks can vary substantially in coloration in all taxa under discussion (Figure 10). These differences appear to reflect both geographic and individual variation within each taxon, complicated further in some instances by hybridism or introgression.

Intra-taxon variation in plumage color, coupled with different color saturations captured by different cameras, rendered it challenging to analyze the plumage of the Mendocino shrike for taxonomic placement. Assessment of its plumage was also hindered by shifting proportions of formative and first alternate body feathering, requiring consideration of prealternate molt extent throughout the period of observation. When first observed, the shrike showed subdued alternate-like patterns to the formative body plumage and few or no dark crescents (Figures 1-3). This perhaps suggests that it had undergone a late preformative molt on the winter grounds that produced relatively definitive-like formative plumage (see Pyle 2013b). In formative plumage, its crown and nape were

mixed with grayish and brown feathering, its mask was dusky, its back, rump, and uppertail coverts were dark pinkish rufous to cinnamon rufous with the rump contrastingly brighter and paler, and its sides and flanks were whitish washed pinkish buff (Figures 1-3). Juvenile rectrices were reddish to cinnamon (Figures 2-3, 6, 12a).

As the Mendocino shrike molted during the period of observation, its crown became a brighter more-silvery gray mixed with some rufous on the nape, its mask became blacker and bordered above by an indistinct whitish supercilium, its underparts became whiter, and its sides and flanks were washed with brighter pale apricot-orange tones (Figures 1-3). By the last week of observation, newly molted lower back and rump feathers appeared grayish (Figures 11-12). The uppertail coverts largely remained pinkish rufous (formative feathers), although during the final week of observation one or two mixed rufous-and-gray feathers appeared to be molting in.

Incoming formative primaries were dusky blackish (Figures 6-7). When last photographed, p2-p6 showed white bases that exceeded the tip of the primary coverts by an estimated 1-2 mm on the closed wing and by an estimated 2-4 mm on the open wing (Figures 7, 12-13). New formative tertials were blackish edged rufous and white (Figures 2, 11a). From above, the formative central rectrices were blackish brown, paling slightly subterminally, and darkening to blackish terminally (Figures 2, 6, 11-12).

Figure 13. The Mendocino shrike on 16 April (a,b), showing white to the bases of the formative primaries extending an estimated 2-4 mm beyond the primary coverts in the open wing. The primary showing the maximum extent of white beyond the primary coverts, p7, had not fully grown by this date (see Figure 7); once fully grown, more white would be expected beyond the coverts (see text for details). Note also the retained, brown, juvenile inner primary coverts contrasting with the outer three coverts, being replaced at the time these images were taken. Photographs by Mark Rauzon.

13a



13b





Figure 14. Wing and tail morphology of male Red-backed Shrike (a, b; AMNH 661158), Turkestan and Isabelline Shrikes (c, d; AMNH 661351 of Turkestan Shrike), and Brown Shrike (e, f; AMNH 106777 of nominate *cristatus*), in each case with juvenile primaries and rectrices. The p9 and r6 are proportionally longer in Red-backed Shrike, followed by Turkestan and Isabelline Shrikes, and then all subspecies of Brown Shrike (Table 1b). The r6 is proportionally narrower as compared to r5 in the Brown Shrike group than in the Red-backed, Turkestan, and Isabelline Shrikes. These differences appear to be useful for identifying the Mendocino shrike (see text and Figures 15, 18-21). Photographs by Peter Pyle.

Photographs taken on 4 April, with the tail partially spread, appear to show a white patch on the basal inner web of r3 (Figure 11a); otherwise, however, the bases of the formative rectrices were not extensively white as is shown in non-juvenile male Red-backed Shrikes (compare Figures 7 and 11c). By the last week of observation, incoming formative outer rectrices were chestnut to reddish, darker toward the tips; the outer two rectrices (r5 and r6) showing distinct white borders (Figure 11b, 12c-d). From below, the rectrices were pale grayish basally (translucent at certain light angles) with indistinct dusky tips (Figure 7).

In Table 1a, we present differences in definitive alternate body plumage and formative or basic flight feathers among males of the four species under consideration, including two subspecies of Brown Shrike, *cristatus* and *lucionensis* (subspecies *confusus* largely combines features of these other two subspecies). We also present a plumage summary of the Mendocino shrike based on descriptions and photographs taken after 5 April, when its first alternate body plumage appearance was becoming established and its incoming formative flight-feather patterns could be assessed.

The plumage of the Mendocino shrike does not fit a pure individual of any of the four species. The bright grayish head contrasting distinctly with the bright reddish-brown back eliminates pure Turkestan and Isabelline shrikes, as well as the *cristatus* subspecies of Brown Shrike. Features that are inconsistent with *lucionensis* and *confusus* Brown Shrikes include the crown and back plumage mentioned above and the mixed blackish and rufous formative rectrices with white tips to the outer rectrices and apparent white patches to the inner webs of others (Figure 11). No Brown Shrike shows a combination of grayish head and reddish-brown back; those with grayer heads (e.g., *lucionensis*) typically show this gray more restricted to the crown and blending indistinctly with a dull brown or mud-brown nape and back. The

largely white underparts with apricot-orange flanks and sides, and the white bases of the primaries, would also be exceptional for *lucionensis* (compare Figures 2, 3, and 11 with Figures 9-10), although both of these characters may sometimes be shown by some *confusus* (see below). Gray molting into the rump and the blackish-brown formative rectrices with rufous-washed bases are also inconsistent with Brown Shrike of any subspecies. Although the Mendocino shrike initially showed some features resembling *lucionensis* while in formative plumage, the incoming first alternate plumage, as described above, showed substantial differences with this taxon.

Most of the first alternate plumage features of the Mendocino shrike at least partially matched those of Red-backed Shrike, some of them diagnostically so (Table 1a, Figures 11-12). In particular, the bright grayish head contrasting with rufous-brown back, rufous-and-white tertial edging, blackish coloration to the tail with bright white tips to the outer rectrices, and apparent white bases to some rectrices are not found in any of the other shrike taxa. However, compared with a pure Red-backed Shrike, the juvenile rectrices appeared more reddish than in most birds, the incoming formative rectrices appeared too brownish (as opposed to black), and the outer rectrices (r3-r5, at least) should have shown more-extensive white bases by the time it was last photographed (Figures 7, 11b-c). Other features that appeared to be inconsistent with a pure Red-backed Shrike included the whitish supercilium, apricot-orange tones in the sides and flanks, rather extensive white to the bases of the primaries (see below), and perhaps too little blackish on the forehead. However, all plumage features at least partially indicated Red-backed over the other shrike taxa under consideration, giving us confidence that the Mendocino shrike was a hybrid between Red-backed and one of the other three shrike species (Figures 11-12). An identification of a hybrid involving Red-backed Shrike was supported by almost all outside reviewers of

this paper from Europe and Asia (Alan Dean, Alexey Kryukov, Paul Leader, Evgeny Panov, Brian Small, Lars Svensson, Yoshiki Watabe, Tim Worfolk, in litt.)

Assuming such hybrid parentage, careful analyses of plumage characters suggest the additional genetic influence of Turkestan rather than Isabelline or nominate *cristatus* Brown Shrikes (Table 1a, Figure 12). Features less consistent with *cristatus* Brown Shrike than Turkestan Shrike include reddish juvenile rectrices and bases to the incoming outer formative rectrices (Figures 1-2, 12) and predominantly white underparts with a rather restricted apricot-orange wash to the sides (Figures 3, 12b). Although both Red-backed and Brown Shrikes can occasionally show reddish juvenile rectrices, it seems unlikely that they would appear this richly cinnamon in a hybrid between the two. The rich, apricot-orange coloration to the sides, furthermore, is found in some proportion of both Turkestan and Isabelline Shrikes (Dean 1982, specimen examination) and is more orange-toned than the coloration seen in Red-backed and Brown Shrikes. The formative rump and uppertail coverts also appeared to be a brighter pinkish to cinnamon rufous than the back (Figure 12a-b). Brown Shrikes, by contrast, more often show the back and rump colorous brown to reddish brown and the uppertail coverts brown to rufous-brown, although uncommon variants may show a brighter rump than back.

Another plumage character indicating Turkestan or Isabelline Shrike as opposed to Brown Shrike introgression was the extent of white in the bases of the formative primaries (Figure 13). This white patch often reaches its maximum extent on p7 or p8 (Cramp and Perrins 1993, specimen examination); thus, as these feathers had not fully grown by 16 April, when the opening of the Mendocino shrike was last photographed, it is likely that the white patch would have extended even farther beyond the primary coverts once growth of the primaries had completed (Figures 7, 12, 13).

It has been widely documented that white extending beyond the primary coverts occurs only occasionally in Red-backed Shrike, in 8-9% of individuals according to Glutz von Blotzheim and Bauer (1993, in Panov et al. 2011); Chylarecki (1991) and Panov et al. (2011) further suggest that an apparent increase in extent of the white primary patch toward eastern portions of the breeding range may relate to introgression with Turkestan Shrike. White extending beyond

the primary coverts is also very rare in nominate *cristatus* Brown Shrikes (Svensson 1992, Cramp and Perrins 1993, Worfolk 2000, Panov et al. 2011). Although extensive white bases in the primaries appear to be shown by a larger proportion of *confusus* Brown Shrikes (Moore 2004, 2015), this subspecies is unlikely part of a hybrid combination with Red-backed Shrike due to the distantly discrete breeding ranges of these two taxa (Figure 4).

Specimen examination by Pyle of males with basic or formative primaries indicated that in Red-backed Shrikes white bases were absent in 50% and extended beyond the primary coverts in 8.3% of specimens ($n=36$), while in *cristatus* Brown Shrikes white was absent in 72% and extended beyond the primary coverts in no specimens ($n=18$); similar results were found among 21 male *lucionensis* specimens and among 41 *cristatus* Brown Shrikes of other ages

Figure 15. Distances between the tips of primaries and primary coverts (a; 3 April), and between rectrices (b, c; 27 and 30 March, respectively) in order to calculate wing and tail morphology ratios of the Mendocino shrike for identification. The distances are between the tips of p8 and p9 (a), between the tips of p9 and the primary coverts (b), between the tips of r5 and r6 (c), and the estimated total length of r6 from point of insertion to tip (d). Ratios a/b and c/d from juvenile feathers were calculated from photographs and compared to the same measures taken on specimens (Table 1b). For example, ratios from these images are a/b = 0.115 (a), c/d = 0.132 (b), and c/d = 0.102 (c); see Table 1b. Photographs by Don Roberson (a), John Sterling (b), and Monte Taylor (c).

15c





16a

Figure 16. Images of the Mendocino shrike taken 30 March (a), 3 April (b, c), and 4 April (d), indicating that the juvenile outer rectrix (r6) appears similar in width to other juvenile and replaced formative rectrices. Juvenile rectrices are narrower than formative rectrices in shrikes and other passerines (Svensson 1992, Pyle 1997), further indicating relatively wide outer rectrices for the Mendocino shrike after accounting for age. *Photographs by Monte Taylor (a), Don Roberson (b, c), and Gary Woods (d).*

and sexes. Only one specimen of Red-backed Shrike was examined that had white extending >3 mm beyond the primary coverts (MVZ 108600, collected in Czechoslovakia). By contrast, in the Turkestan and Isabelline Shrikes combined, a white patch was present on all birds, it extended beyond the primary coverts in 91% of specimens, and it extended >3 mm past the primary coverts in 79% of specimens (n=33). Although the white patch extends slightly farther beyond the primary coverts when the wing is partially open than when it is closed (Cramp and Perrins 1993, specimen and photograph examination), on balance we believe that the extent of white in the primaries on the Mendocino shrike, estimated to be >3 mm past the primary coverts on a partially spread wing once molt would have completed (Figures 12c-d, 13), is more likely to be expressed in a hybrid between Red-backed and either Turkestan or Isabelline Shrikes than in a hybrid between Red-backed and nominate *cristatus* Brown Shrike (but see Figure 19).

Plumage features that favor Turkestan over Isabelline introgression for the Mendocino shrike include the darker brownish tone to the upperparts, the apricot underpart coloration not extending to the auriculars and resulting in a distinctly defined white throat, the indistinct whitish supercilium (lacking or less distinct in both Red-backed and Isabelline Shrikes), the richer rufous tones in the bases of the formative rectrices, and the white (rather than buff) coloration in the bases of the primaries (Table 1a). The black mask tends to be more abbre-

viated in Isabelline Shrike than in Turkestan Shrike, less often meeting across the forehead (Panov 2009, Panov et al. 2011). However, study of specimens and images indicates overlap between the two species in this feature and that photographic effect can make this difficult to assess in images (e.g., Figures 2-3). This mark in the Mendocino shrike therefore seems equivocal in respects to the identification of either Isabelline or Turkestan Shrike influence. Overall, we believe that the plumage of the Mendocino shrike would fall within the range of variation shown for Red-backed x Turkestan Shrike hybrids in Figures 17.1 and 17.7 of Panov et al. (2011), and its relatively dark formative and first alternate feathering would be unlikely to be seen in a Red-backed x Isabelline Shrike hybrid.

However, given a number of complicating factors, the plumage-based evidence alone is not strong enough for identification in the case of the Mendocino shrike, other than to conclude that Red-backed Shrike genes are clearly involved. Extensive variation within *cristatus* Brown Shrikes could result in a recombination (albeit unlikely) of plumage features that fit characters of the Mendocino shrike not contributed by Red-backed Shrike genes. This may especially be the case since phenotypic plumage expression by hybrids can show any combination of parental phenotypes and occasionally contradictory plumage patterns atypical of either parental species (Graves 1990, 1996; Rohwer 1994, Rohwer et al. 2000), perhaps representing ancestral

character states no longer found in either parent. While all plumage features could be considered intermediate between Red-backed and Turkestan Shrikes, we cannot claim that any plumage feature is necessarily contradictory to a Red-backed x Brown Shrike cross, including the extent of white at the bases of the primaries. Furthermore, had the Mendocino Shrike originated from the Altai Region of south-central Russia, where hybridization between Red-backed and all three other shrike species is known to occur (Figure 4), there is a possibility that it was comprised of genetic recombination from three or even all four species. Therefore, other variables beside plumage need to be considered in the identification of the Mendocino shrike.

Size, structure, and flight feather morphology

All of the taxa under consideration for the Mendocino shrike show roughly the same body size (Worfolk 2000). Thus, field descriptions of the Mendocino bird, as variously being about the size of a Loggerhead Shrike (*L. ludovicianus*) to the size of a Black Phoebe (*Sayornis nigricans*), are not helpful for identification. Bill size is larger and deeper in the Brown Shrikes than in the other three species (Svensson 1992, Cramp and Perrins 1993, Worfolk 2000), and most observers and those commenting on posted photographs thought that the bill of the Mendocino shrike appeared too small, stubby, and with a lower mandible too straight (rather than convex) for

THE MENDOCINO SHRIKE

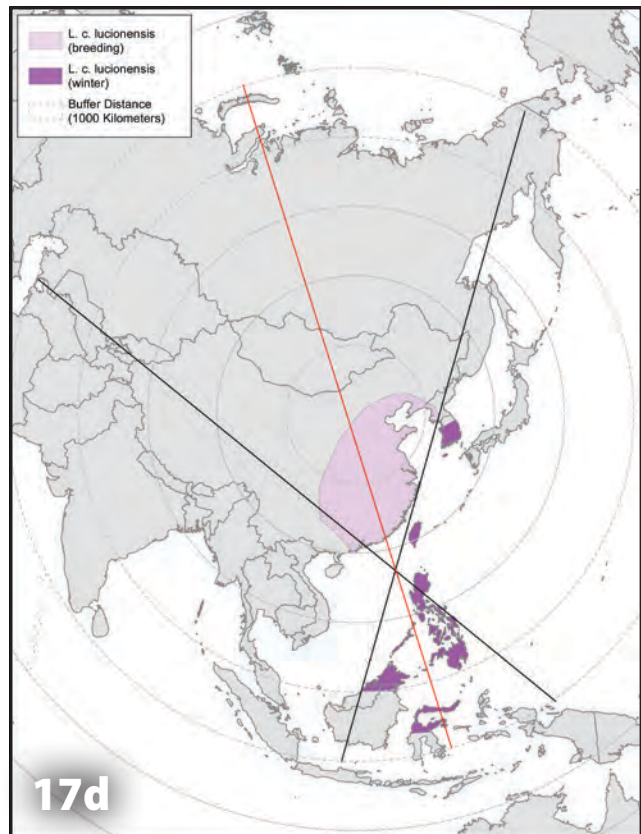
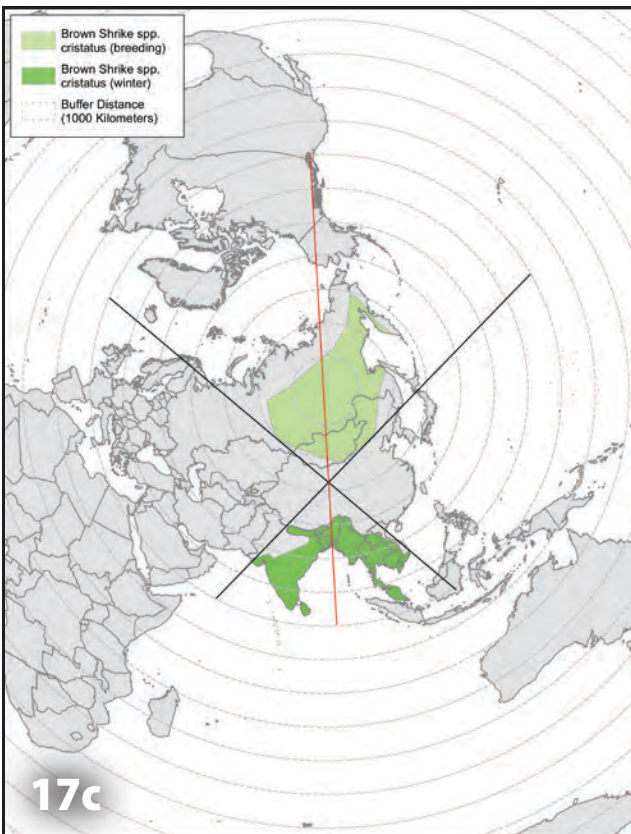
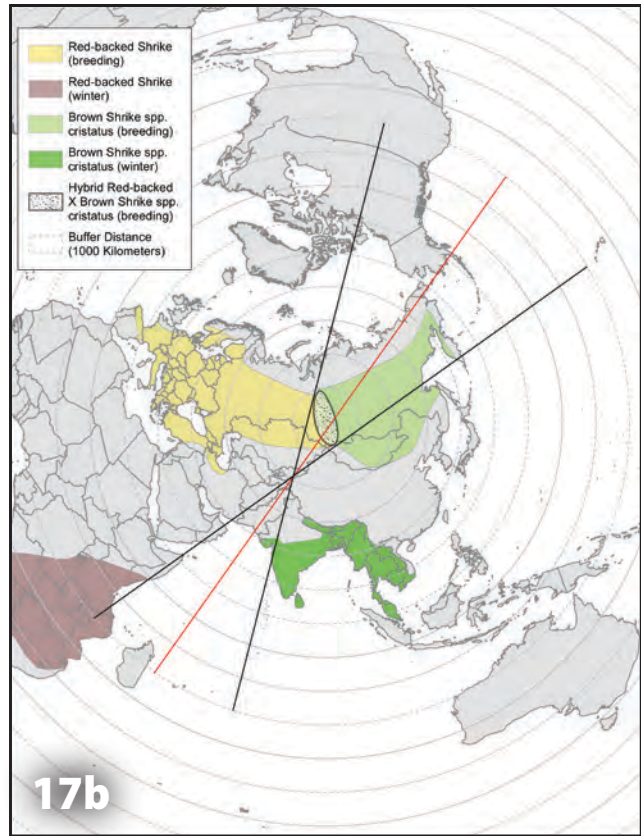
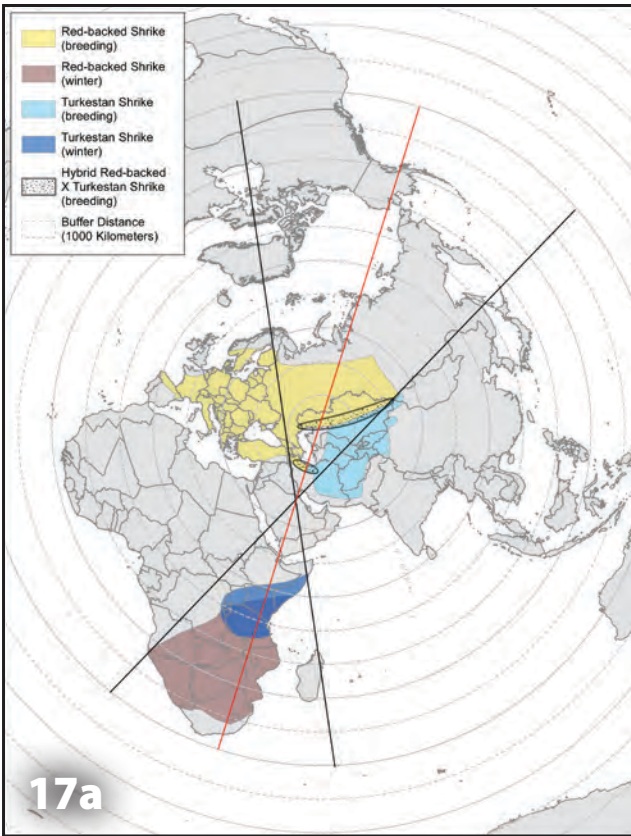


Figure 17. Projected range of migratory pathways for shrikes assuming reverse migration (see Howell et al. 2014) and based on projected breeding and winter ranges. Black lines indicate the range of potential vectors given breeding and winter ranges, red lines indicate the mid-point, and concentric gray rings indicate 1000 km distances from the centers of hybridization zones and subspecies ranges. Shown are 180° misorientation projections based on the Red-backed/Turkestan Shrike hybridization zone (a), the Red-backed/Brown Shrike hybridization zone (b), the range of *cristatus* Brown Shrike (c), and the range of *lucionensis* Brown Shrike (d). See text for discussion. Graphics by Shane Feirer.

Brown Shrike, especially for a male. Moreover, first-year male Brown Shrikes typically show a gray-based lower mandible that becomes black by April, rather than a pinkish base as shown through mid-April by the Mendocino shrike.

Red-backed Shrikes average longer wing lengths than Turkestan and Isabelline Shrikes, which in turn average longer wings and greater primary projections than any of the Brown Shrike taxa (Svensson 1992, Cramp and Perrins 1993). On the other hand, Brown Shrikes average slightly longer tails than Turkestan and Isabelline Shrikes, which in turn average longer tails than Red-backed Shrike. Wing-to-tail ratios can be useful in the hand but, unfortunately, are nearly impossible to determine with confidence in photographs due to uncertain angles of orientation to feather tracts relative to the plane of an image. Comments from those familiar with the identification of these shrikes indicated that the primary projection of the Mendocino shrike appeared to be too short for Red-backed Shrike but too long for most Brown Shrikes and that the tail appeared too long for Red-backed Shrike but too short for Brown Shrike. Relative wing and tail proportions are also affected by camera angle, bird posture, and the fact that the Mendocino shrike was molting both primaries and rectrices during the period of observation.

Primary and rectrix morphologies, the relative distances between the tips of certain feathers within each of these tracts, differ fairly substantially among shrikes in this assemblage (Dement'ev and Gladkov 1954, Dean 1982, Svensson 1992, Cramp and Perrins 1993, Worfolk 2000; Figure 14). The penultimate primary (p9) is longest in Red-backed Shrike, falling 3-9 mm short of the wing tip and equidistant to the tips of p6-p7 inclusive (Svensson 1992, Cramp and Perrins 1993); it is a bit shorter in Turkestan Shrike and migratory nominate Isabelline Shrike (5-9 mm short of the wing tip and equal to p5-p6); and it is shortest in the Brown Shrikes, including nominate *cristatus* (6-12 mm short of the wing tip and equal to p4-p5). Likewise, the outer rectrix (r6) is relatively long and wide in Red-backed, Turkestan, and nominate Isabelline

Shrikes, falling 7-14 mm short of the tail tip and roughly equal in width with the other rectrices, whereas in all subspecies of Brown Shrike, r6 is substantially shorter, falling 14-27 mm short of the tail tip, and also averaging over 1 mm narrower than the other rectrices (Svensson 1992, Cramp and Perrins 1993; Figure 14).

On non-molting birds in the hand, feathers can be compared directly and distances between tips measured to separate these taxa, but obtaining such specific biometrics is not possible with images of the Mendocino shrike due to feather positions, camera angles, and the fact that it was molting critical primaries (p3-p6) and rectrices (r1-r2) by the time adequate images could be obtained to evaluate structural morphology. Most reviewers of the images thought that both the juvenile p9 and the juvenile outer rectrix (r6), prior to these feathers molting, looked too long for a Brown Shrike, and that r6 looked roughly equal in width to other un-molted rectrices. In order to confirm these impressions and to assess wing and tail structure as related to the identification of the Mendocino shrike, Pyle obtained biometrics from specimens to calculate ratios between feather tips that could be applied to the same ratios in the images. This process carries the assumption that ratios will be less affected by angle of the feather tract relative to the plane of the image than are estimated biometrics.

Primary and rectrix morphology ratios could not be applied to the newer formative feathers of the Mendocino shrike, as the outer primaries and rectrices were not fully grown when it was last observed (Figures 7, 13), so ratios were based on its juvenile feathers. The outer three juvenile primaries (p8-p10) were present (had not yet molted) in photographs up through at least 4 April, and the outer two juvenile rectrices (r5-r6) were present until 31 March, so ratios between these feather tips were used in images taken through these dates (Figure 15, Table 1b). The distances between p8 and p9 (a) and p9 and the primary coverts (b) were measured in specimens in order to calculate the ratio a/b and apply it to images showing these feathers. The upperwing and underwing primary coverts

Figure 18. Presumed Turkestan x Red-backed Shrike hybrids photographed in Saudi Arabia (Babbington 2013, 2014) on 27 April 2013 (a, b) and 13 April 2014 (d, c). Note the similarities between the plumage of these birds and the Mendocino shrike, including indistinct whitish supercilia, rufous or mixed rufous-and-gray uppertail coverts contrasting with browner backs, rufous bases to the outer rectrices, whitish underparts with pinkish to apricot sides and flanks, and white extending beyond the primary coverts. Note also that tail morphology of these hybrids (b, c) is similar to that of the Mendocino Shrike (Figure 15b, c) and would be expected of Red-backed x Turkestan hybrids (Table 1b); the ratio c/d was calculated as 0.118 (image b) and 0.132 (image c). Photographs by Jahed Alammadi (a, b) and Jem Babbington (d, c).

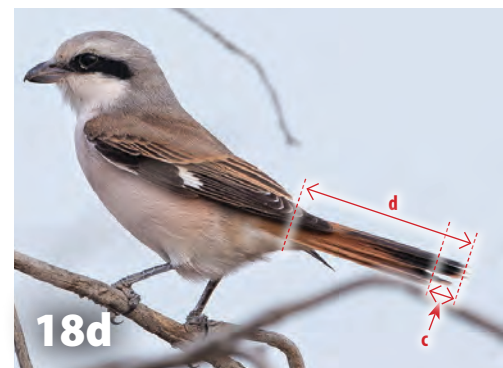
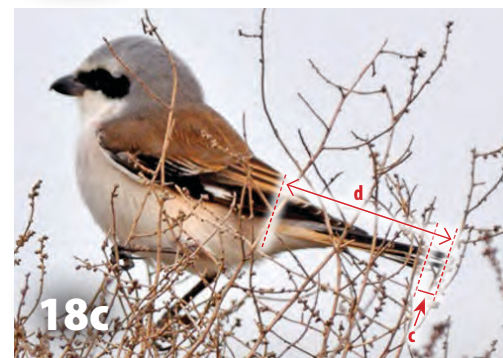




Figure 19. Specimen of a presumed Red-backed x Turkestan Shrike hybrid undergoing the preformative or definitive prebasic molt, collected 5 January 1927 in Ethiopia (FMNH 83458). Features resembling the Mendocino shrike include the coloration of the head, back, tertial edging, and (especially) the underparts, and a pinkish-based bill. The rectrices were grayish with white patches at the bases that were not extensive enough for a pure Red-backed Shrike. The bird was completing molt when collected, with r6 still growing (precluding full analysis of tail morphology) but p8 and p9 fully grown, resulting in morphology suggesting this hybrid combination (see text). Three other specimens identified as Red-backed x Turkestan Shrike hybrids are located at FMNH (200775-200777), which allowed further assessment of wing and tail morphologies of this hybrid combination (see text). *Photographs by Josh Engle.*

are about the same length (specimen examination) and were used for this ratio rather than the tip of p10, as the length of p10 showed substantial individual variation relative to the primary coverts (see Cramp and Perrins 1993), leading to less consistent ratios within each taxon than those using the primary coverts. Similarly, the distances from the tip of r6 to the tip of r5 (c) and from the tip of r6 to its insertion point (d) were taken on specimens to compare with ratios of c/d in images (Figure 15). The distance from r5 to r6 rather than r1 to r6 (as in other studies) was used due to molt of one or the other of these rectrices during a large part of the observation period.

The ratios a/b and c/d, calculated from 11 images of the wing and eight images of the tail

of the Mendocino shrike (Figure 15), were all fairly consistent (Table 1b), indicating a degree of reliability to this method. They indicated that both p9 and r6 were long relative to the overall wing and tail dimensions, falling within the range of Red-backed Shrike measurements from specimens. Among the images of the Mendocino shrike, even those ratios at the maximum end of the range, indicating p9 and r6 to be relatively short, still fell within the range of Red-backed Shrike and the lower extreme of the range for Turkestan Shrike but outside of the ranges for the other taxa (Table 1b). Despite some probable inherent inaccuracy in the calculation of ratios from images, we are confident that the results of this exercise suggest the identification of the Mendocino

shrike as a Red-backed x Turkestan Shrike over a Red-backed x Brown Shrike hybrid, which we would expect to show ratios well above those of Red-backed Shrike. The width of the juvenile r6 in images appeared about equal to those of other rectrices, both juvenile and formative (Figure 16), further suggesting Turkestan rather than Brown Shrike in the genetic make-up of the Mendocino shrike.

Habitat and vocalizations

On winter grounds, Brown Shrike tends to favor forest edges and large trees, whereas Turkestan and Isabelline Shrikes favor arid open country and edges of cultivated fields (Cramp and Perrins 1993). Habitats surrounding the mouth of Alder Creek in 2015 largely

consisted of open, grazed, and drought-stricken marine-terrace habitats with scattered low scrub, which might be favored more by Turkestan than by Brown Shrike. However, given the influence of Red-backed Shrike, which appears to occupy habitats somewhat intermediate to those of Brown and Turkestan Shrikes (Cramp and Perrins 1993), and unknown habitat usage when the Mendocino shrike was not at the mouth of Alder Creek (a majority of the time searchers were present), we believe that habitat selection is of little value in the shrike's identification.

The Mendocino shrike was heard singing on several dates, and the song was recorded on 4 April 2015 by Steve Hampton and archived at xeno-canto (www.xeno-canto.org; accessions XC234213, XC234214, under "identity unknown"). We have labelled these vocalizations as an "advertising song" (Cramp and Perrins 1993) given by male *Lanius* shrikes, which typically involves extensive mimicry learned from other species on either the breeding or winter grounds. The song of the Mendocino shrike consisted of a long string of quiet warbling musical notes, recalling to Moores those of *Acrocephalus* or *Sylvia* warblers, interspersed with occasional soft chatter as is typical of the genus.

The advertising songs of Red-backed, Turkestan, and Isabelline Shrikes as well as their hybrids are reported to be quite similar, all averaging softer and more musical than the advertising songs of Brown Shrike taxa (Cramp and Perrins 1993, Harris and Franklin 2000, Panov et al. 2011, Wassink 2015). At least in Korea, Brown Shrike taxa often include quite harsh phrases that recall vocalizations given by Thick-billed Warbler (*Arundinax aedon*) and Siberian Rubythroat (*Calliope calliope*), species that share a similar habitat and range with breeding Brown Shrikes (Moores, pers. obs. and audio recordings). However, comparisons between each of these taxa are hindered by individual variation in these songs, in large part owing to extensive mimicry. Although we believe that this vocal evidence is at least consistent with the Mendocino shrike involving Turkestan as opposed to nominate *cristatus* or other Brown Shrikes, more detailed spectrographic analyses of the recordings as compared to those of other vocal studies (see Panov et al. 2011) may refine this assessment. The call notes of these shrikes are reported to differ more diagnostically than the songs (Cramp and Perrins 1993, Harris and Franklin 2000, Panov et al. 2011), but we have no descriptions or recordings of call notes given by the Mendocino shrike.

Migration trajectories and vagrancy

Early concerns about the identification of the Mendocino shrike as a Red-backed x Turkestan Shrike hybrid included the unlikelihood that a bird from a population breeding in interior southwestern Asia would occur in California. But we propose that such a vagrant occurrence is possible given the migratory pathways that such a hybrid would take between this breeding area and wintering areas in Africa (Figure 4), and given 180° misorientation (reverse migration) theory that has been proposed for several other highly migratory, central Eurasian shorebirds and passerines reaching California and North America (Abbott et al. 2001, Howell et al. 2014). Vagrants misorienting in an approximately 180° opposite direction from normal migratory paths may proceed over far-northern regions on a great-circle route to reach North America and may have an intrinsic clock resulting in approximately the same distance of flight as would be found in normal migrants of the species.

Applying 180° misorientation theory based on the southwestern and northeastern ends of the hybridization zone between Red-backed and Turkestan Shrikes (Figure 4) results in a pathway that includes the Pacific North American coast, including Mendocino County and adjacent offshore waters (Figure 17a). The distance traveled to reach Mendocino County (9000 km) would be at the higher end of the usual migratory distance for such a hybrid (6000-9000 km). However, we believe that in this case the shrike may have found



Figure 20. Presumed Red-backed x Brown Shrike hybrids photographed at Perlis, Malaysia 28 February 2015 (a; Mun 2015) and 21 February 2015 (c) and in Kanagawa Prefecture, Japan 27 February 2013 (b) and 21 April 2013 (d). Although resembling the Mendocino shrike in many respects, note a lack of whitish in the supercilial region, brownish uppertail coverts, similar in color to the back, brown or brownish-tinged rather than rufous bases in the formative rectrices, and more extensive and deeper buff tones in the sides and flanks. Note, however, white extending beyond the primary coverts in the hybrid from Japan (b, d), a plumage feature only occasionally shown by Red-backed and rarely by *cristatus* Brown Shrikes (see text). The tail morphology of these hybrids (c, d) differs rather substantially from that of the Mendocino Shrike (Figure 15b, c) and would be expected of a Red-backed x Brown Shrike hybrid (Table 1b); the ratio c/d was calculated as 0.230 (image c) and 0.258 (image d). The Malaysian bird (a, c) was as an adult that had yet to replace its formative or basic outer rectrix when photographed on 21 February (c); this rectrix had dropped by 28 February (a). Photographs by Choy Wai Mun (a), Shinichiro Ueno (b), Piyapong Chotipuntu (c), and Yoshiki Watabe (d).



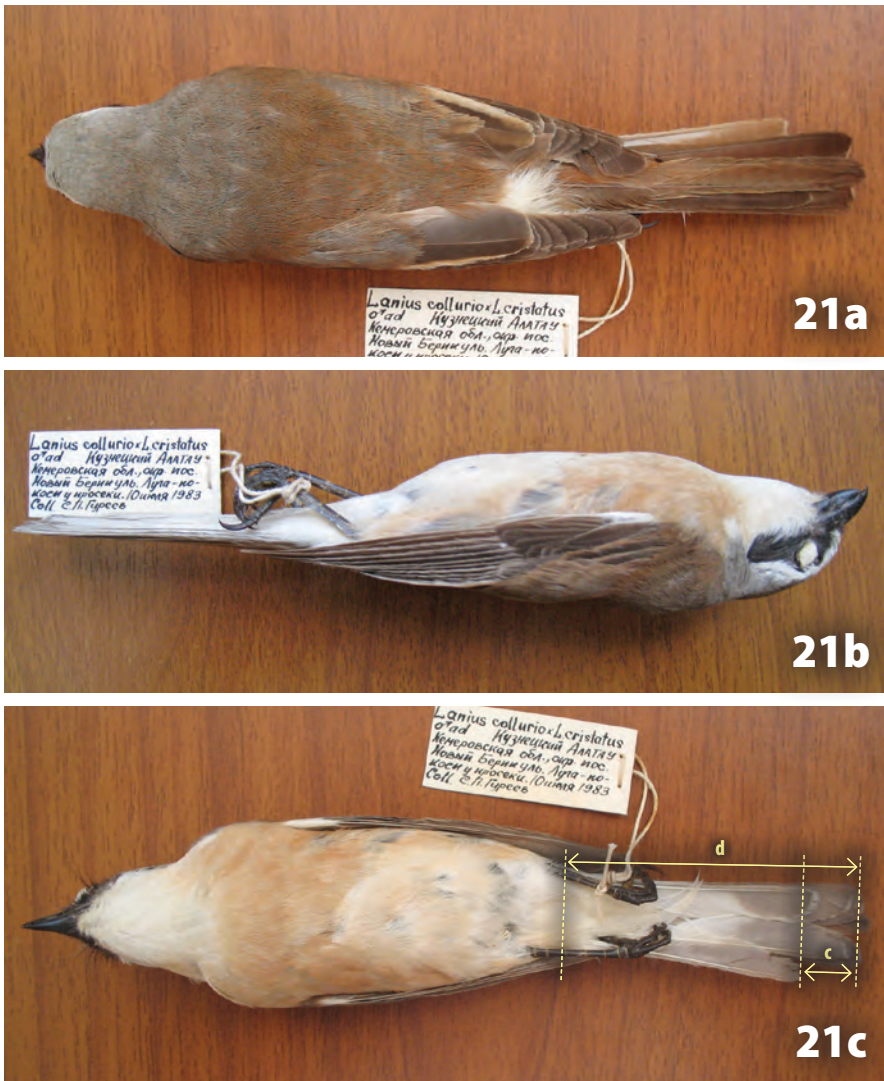


Figure 21. Specimen of a presumed male Red-backed x Brown Shrike hybrid collected in the zone of sympatry between the two species, in the Kuznetsk Alatau range of Russia, on 10 July 1983, after having raised young with a female Red-backed Shrike (see Kryukov and Gureev 1997; specimen at the Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia). Although superficially resembling the Mendocino shrike, note differences summarized in Figure 20. The ratio of c/d for this specimen’s tail morphology (see Figures 15, 18-20) is 0.161, well above the ratios calculated for the Mendocino shrike (Table 1b). Photographs by Alexey P. Kryukov.

Comparison with other hybrid shrikes

We have established that the Mendocino shrike was a hybrid involving Red-backed Shrike and one or more of Turkestan, Isabeline, and/or nominate *cristatus* Brown Shrikes. In this section, we compare the plumage and morphology of the Mendocino shrike with those of other reported hybrids. We examined photographs in the literature and online of 34 male shrikes reported to be hybrids, not including those shown in Figures 17.1 and 17.7 of Panov et al. (2011).

Twenty-eight of these reported hybrids were photographed in Kazakhstan and countries of the Arabian Peninsula (e.g., Babbington 2013, 2014; Figures 18a-b) and were identified as or showed characters of Red-backed x Turkestan Shrike hybrids. These 28 hybrids display substantial variation in plumage, from those resembling Red-backed Shrike with a slight red tinge to the bases of the outer rectrices to those resembling Turkestan Shrikes with a slight grayish tinge to the crown and a dusky wash to the central rectrices. Most showed tail patterns resembling that of the Mendocino Shrike, with brownish-black central rectrices, a dusky subterminal band, variably rufous to cinnamon-whitish bases to the outer four pairs of rectrices, and whitish to white tips to the outermost rectrices. The range of plumage variation shown by these 28 hybrid shrikes is consistent with a broad zone of genetic introgression as has been documented to occur between Red-backed and Turkestan Shrikes (Panov et al. 2011).

Many of these 28 presumed Red-backed x Turkestan Shrike hybrids, including those photographed in Saudi Arabia and shown in Figure 18, resemble the Mendocino shrike in most or all plumage features. In addition to the pattern of the rectrices, notable similarities to the Mendocino shrike shown by these hybrids include an indistinct whitish supercilium, rufous or mixed rufous-and-gray rump and uppertail coverts contrasting with brown-er back, largely white underparts with pinkish to apricot-orange wash in the sides and flanks, and white extending beyond the primary co-

itself over the Pacific Ocean, as predicted by the midpoint of such trajectories, and continued on or drifted to reach the closest point of coastal land, as has been proposed for both North American and Asian vagrants that reach the Pacific North American coast (Howell et al. 2014).

The same calculations applied to a prospective Red-backed x Brown Shrike hybrid results in a 180° misorientation trajectory more westward in the Pacific (Figure 17b) than the projected path of a Red-backed x Turkestan Shrike hybrid, although the same possibility mentioned above may apply to a Red-backed x Brown Shrike hybrid that finds itself over the Pacific Ocean flying or drifting until it makes landfall. Distance traveled would also be slightly longer to reach Mendocino County (8000-9000 km) than it would be to reach prospective wintering grounds for such a hy-

brid (6000-8000 km; Figure 17b). These 180° misorientation calculations applied to *cristatus* Brown Shrike show how this subspecies might be expected throughout most of North America, including Nova Scotia, with the midline of these pathways directing birds close to the California coast (Figure 17c), and distance traveled being about the same (5000-7000 km) in each direction. On the other hand, a *lucionensis* Brown Shrike, based on a maximum normal migratory distance of about 4500 km, would result in destination end-points throughout northern Russia east to the tip of Siberia, and some 3500-4500 km from the California coast (Figure 17d). Many caveats need to be applied to vagrancy theories, however, with some vagrants defying these sort of calculations and others affected by weather systems, disorientation, and other vagrancy mechanisms (Howell et al. 2014).

verts (Figure 18a-b), the latter of which was present in 25 of the 28 (perched) individuals.

Notably, these 28 hybrid shrikes show tail structural morphologies that match that of the Mendocino shrike. Among 14 individuals for which the outer rectrix tips were visible, using the methods applied above (Figure 15), the ratio of the tips of r5 to r6 to the estimated length of r6 in the images (c/d in Figure 15) ranged from 0.093 to 0.135 (e.g., Figure 18c-d). This ratio in two specimens identified as Red-backed x Turkestan Shrike hybrids at the Field Museum of Natural History (FMNH 200775 and 200777; see Figure 19a) was also similar, being 0.103 and 0.102, respectively (J. Engle, pers. comm.). These ratios are similar to those calculated from images of the Mendocino shrike and specimens of Red-backed Shrike and overlap with the lower end of the ranges from Turkestan Shrike specimens (Figure 15b-c, Table 1b). Similar variation in these ratios appears evident from a visual examination of the series of Red-backed x Turkestan Shrike hybrids shown in Figure 17.1 of Panov et al. (2011). The tip of p9 was insufficiently visible in images of these 28 hybrid shrikes, precluding a comparison of wing morphologies (see Figure 15a) with that of the Mendocino shrike. However, in three specimens at FMNH identified as Red-backed x Turkestan Shrike hybrids (83458, 200776, and 200777; see Figure 19), the ratio of p9-p8 to p9-primary coverts (a/b in Figure 15, above) was 0.078, 0.099, and 0.191 (J. Engle, pers. comm.), similar to or shorter than estimated ratios calculated from images of the Mendocino shrike. Ratios for both wing (a/b) and tail (c/d) morphologies from these presumed Red-backed x Turkestan Shrike hybrids all fall well below the ranges of these ratios calculated from Brown Shrike specimens (Table 1b).

The remaining six hybrids were photographed in Malaysia (Mun 2015; Figure 20a) and Japan (e.g., Horimoto and Watabe 2014, Young Guns 2014; Figure 20b), with most of those in Japan being identified as Red-backed x Brown Shrike hybrids (Y. Watabe, in litt.; we have excluded the shrike documented by Furuichi et al. 2010, which may well represent a pure Red-backed Shrike). We also analyzed images of the specimen of Red-backed x Brown Shrike hybrid collected in 1983 in the Kuznetsk Alatau range of Russia, where both species were breeding and mixed pairs were observed (Kryukov and Gureev 1997; Figure 21). The plumage of these seven shrikes appeared more comparable to each other than those of the 28 presumed Red-backed x Turkestan Shrike hybrids discussed above, showing characters more consistent with F₁ hybrids

than with products of genetically introgressed populations. The plumage of these seven hybrids generally resembled that of the Mendocino shrike (Figures 20a-b, 21), but most of them showed a lack of whitish to the supercilial region, browner or mixed brown and gray uppertail coverts that did not contrast in color with the back, brown (or brownish-tinged) rather than rufous bases to the outer rectrices, more extensive and deeper buff (rather than apricot) tones to the sides and flanks, and white not extending beyond the primary coverts. However, at least one of the seven hybrids showed each of these features analogous to those of the Mendocino shrike, with the exception of rufous at the base of the tail. For example, the specimen from the Kuznetsk Alatau range showed a whitish supercilium (Figure 21), and an individual photographed in Japan (Figure 20b; Figures 8, 9 in Young Guns 2014) showed white at the bases of the primaries extending beyond the primary coverts. This appears to confirm the risk of plumage assessment in hybrids, due to variable combinations of phenotypic expression contributed by each parent, along with occasional contradictory character states, as noted above.

The tip of the outer two rectrices (r5 and r6) were visible on six of these seven hybrid shrikes from eastern Asia (e.g., Figures 20c-d, 21), allowing assessment of tail morphology. The proportion of the distance between r5 and r6 to that of the length of r6 in the images (c/d in Figure 15) ranged from 0.137 to 0.230, not overlapping the range in these proportions calculated from images of the Mendocino shrike or of the 16 presumed Red-backed x Turkestan Shrike hybrids noted above, instead being consistent with what might be expected of Red-backed x Brown Shrike hybrids (see Table 1b). The length of the outer rectrix (r6) was shorter relative to the overall tail length in all seven presumed Red-backed x Brown Shrike hybrids than it was in the Mendocino shrike or any of the 14 presumed Red-backed x Turkestan Shrike hybrids in which this could be assessed.

Primary morphology could also be assessed in photographs of two of the Japanese hybrids, shown in Figure 2 of Horimoto and Watabe (2014) and Figure 9 of Young Guns (2014). Using the methods described above, the distances between p8 and p9 and between p9 and the primary coverts in the images (a/b in Figure 15) resulted in ratios of 0.233 and 0.188, respectively, consistent with what would be expected of a Red-backed x Brown Shrike hybrid but greater than that expected of a Red-backed x Turkestan Shrike hybrid, according to specimen-based data, and greater

than the ratios calculated from images of the Mendocino shrike (Figure 15a, Table 1b). The bills of these seven hybrid shrikes also appear larger and stouter than those of the 28 hybrid shrikes from Kazakhstan and the Arabian Peninsula, as well that of the Mendocino shrike (compare Figures 2-3 with Figures 18-21).

Both plumage and structural features thus suggest that hybrids from Kazakhstan and the Arabian Peninsula are primarily Red-backed x Turkestan Shrikes, whereas those from Malaysia and Japan are primarily Red-backed x Brown Shrikes, as generally identified by the observers of these shrikes, and as would be expected based on the breeding and winter ranges of parental populations. Both plumage and morphological features also suggest that the Mendocino shrike is better placed with the former group, as an individual from the zone of hybridization between Red-backed and Turkestan Shrikes. Studies of hybrids have shown that, whereas plumage characters can be determined by multiple alleles resulting in various combinations of parental traits and occasionally traits shown by neither parental species, structural traits of recombinants more consistently show states intermediate between those of parentals (Rohwer et al. 1994, Graves 1996). A possible dominance of Red-backed Shrike genes, as displayed by both plumage and morphological characters, might further suggest that the Mendocino shrike was a product of a broadly introgressed zone of overlap and hybridization as found between Red-backed and Turkestan Shrikes but not extensively between Red-backed and Isabelline Shrikes or Red-backed and Brown Shrikes (Panov et al. 2011), although at least one presumed male of the latter hybrid combination has been documented successfully raising young with a female Red-backed Shrike (Kryukov and Gureev 1997; Figure 21).

Conclusions

We recommend that the Mendocino shrike be considered a product of the Red-backed/Turkestan Shrike zone of hybridization. As in all identifications involving hybrids (and many involving pure species), a degree of uncertainty is unavoidable. We believe, however, that the combination of suggestive plumage and perhaps vocal features with more reliable and indicative wing and tail morphologies, as compared with these criteria in both specimens and other hybrids, indicates this as the most parsimonious conclusion and a reasonable one within the realm of identification certainties. The Red-backed/Turkestan Shrike hybridization zones from the Caspian Sea to the Altai region of south-central Russia repre-

sent a much larger population source for the Mendocino shrike than the occasional hybrids produced by Red-backed and either Isabelline or Brown Shrikes from nearby areas, and such hybrids could reach North America via a 180° misoriented migration.

TO SUMMARIZE:

1 • Features indicating Red-backed Shrike influence rather than pure *lucionensis* Brown Shrike include:

- a) gray first alternate head and crown contrasting distinctly with reddish-brown back;
- b) blackish formative rectrices;
- c) white tips to outer formative rectrices and apparent white in bases of some rectrices;
- d) gray first alternate lower back and rump feathers; and
- e) wing and tail morphologies matching those of Red-backed Shrike and far below those of Brown Shrike.

2 • Features unresponsive of pure Red-backed Shrike include:

- a) chestnut and blackish formative rectrices lacking sufficient white in bases;
- b) apricot-orange tones in the underparts;
- c) rufous-brown tinges among first alternate nape feathers; and
- d) white at base of formative primaries extending past primary coverts.

3 • Features suggesting Turkestan over Brown Shrike influence include:

- a) white underparts with apricot-orange tones restricted to sides;
- b) bright cinnamon juvenile rectrices and chestnut bases to formative rectrices;
- c) cinnamon to pinkish-rufous formative rump and uppertail coverts contrasting with browner back;
- d) white at base of formative primaries extending past primary coverts;
- e) rufous-brown first alternate feathers in nape; and
- f) wing and tail morphologies far outside of ranges for Brown Shrike or presumed hybrid Red-backed x Brown Shrike hybrids.

We cannot rule out an introgressed individual of three or more species from the Altai region of southern Russia, and for this and other reasons an alternate conclusion would leave the parental make-up of the Mendocino shrike, other than involving Red-backed Shrike, as indeterminable given current knowledge. However, given especially the wing and tail morphologies and the sizes of potential source populations, a hybrid between Red-backed

and Turkestan Shrike seems most likely. We welcome further discussions on the Mendocino shrike, and naturally we hope that the bird returns to winter in California in the future. The bird may hold the distinction of being the only individual bird to represent two species new to North America. In any case, the intense scrutiny, interest, and accumulated series of images of the Mendocino shrike provided an opportunity to refine our understanding of these captivating and complicated Eurasian shrike taxa.

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