AN APPARENT HYBRID BLACK × EASTERN PHOEBE FROM COLORADO

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ABSTRACT: From 21 April to 11 May 2007 an apparent hybrid male Black × Eastern Phoebe (*Sayornis nigricans* × *S. phoebe*) was observed in Loveland, Larimer County, Colorado. The bird's plumage was intermediate between the species, with paler upperparts, darker flanks, and a less distinct border between dark and white on the breast than expected on the Black Phoebe and darker upperparts, less head/back contrast, and a darker and more sharply demarcated upper breast than expected on the Eastern. Sonograms of the bird's territorial song show numerous characteristics intermediate between the typical songs of the two species. Although the Colorado bird provides the first strong evidence of hybridization in *Sayornis*, other sightings suggest the Black and Eastern Phoebes may have hybridized on other recent occasions. Range expansions of both species may increase the frequency of hybridization in the future.

The Black (*Sayornis nigricans*) and Eastern (*S. phoebe*) Phoebes are similar medium-sized flycatchers that historically occupied allopatric breeding ranges. The Eastern Phoebe is a common breeding species of mixed woodlands, riparian gallery forest, and human-altered habitats, nesting on cliffs, banks, and man-made structures in the eastern two-thirds of the lower 48 states and in Canada from Nova Scotia west and north to southwestern Nunavut and northeastern British Columbia (Weeks 1994). The Great Plains were probably a barrier to the species' range expansion until channelization and stabilization of river banks encouraged the growth of extensive gallery forests along east-flowing rivers, particularly the South Platte and Arkansas (Knopf 1991). The Black Phoebe is mostly resident in a wide latitudinal range from the western United States south through Central and South America (A.O.U. 1998). In the United States it was formerly restricted to areas west of the continental divide, except in southern New Mexico and western Texas.

Recent eastward and northward expansion of range by the Black Phoebe into Colorado and northern New Mexico (Faulkner et al. 2005) and concomitant expansion west by the Eastern Phoebe into the southeastern foothills of Colorado (Andrews and Righter 1992) and northern New Mexico (S. O. Williams pers. comm.) have brought the two species into contact at a few locations in those two states (Leukering pers. obs.). With such contact comes the possibility of hybridization, a phenomenon previously unknown in the genus *Sayornis* (Weeks 1994, Wolf 1997, Schukman and Wolf 1998). Below, we provide details on an individual that we believe was a hybrid Black × Eastern Phoebe and provide additional information on previous occurrences of suspected hybridization by the two species.

Figure 1. The Loveland phoebe, 26 April 2007.

Photo by Rachel Hopper

Figure 2. The Loveland phoebe, 26 April 2007. Note that in lighting such as this, the bird looked very dark and was easily mistaken for a Black Phoebe.

Photo by Rachel Hopper

Figure 3. The Loveland phoebe, 29 April 2007. Note that in lighting such as this, the bird looked paler and more similar in coloration and pattern to an Eastern Phoebe.

Photo by Tony Leukering

OBSERVATION

The suspected hybrid phoebe was first found 21 April 2007 by Coley near a dam and water-diversion structure on the Big Thompson River just east of Wilson Avenue in Loveland, Larimer County, Colorado (40.398° N, 105.107° W). On 25 April, Coley found a Black Phoebe in association with the apparent hybrid, and both were present daily until 6 May, the last date that the Black Phoebe was seen. The apparent hybrid continued, though became difficult to find, until at least 11 May.

From 21 to 25 April the putative hybrid sang frequently during the day and was best located by song. As singing by female phoebes is fairly rare and brief (Smith 1969), we believe that the singer was a male. After 25 April, the male was heard to sing almost exclusively between 0515 and 0545 hrs, usually from low perches overhanging the water just upstream from the dam; the only other vocalizations heard with any frequency were contact notes. Both birds were reliably found within about a 100-meter radius of the dam, usually right along the main watercourse.

On 26 April, Rachel Hopper (pers. comm.) reported apparent nesting behavior, with visits to a potential nest site in the water-control structure. Subsequently, we found some minimal additions of fine nest materials to an old Barn Swallow (*Hirundo rustica*) nest. Larger, thicker, flatter mud nests that resembled old phoebe nests were visible on other parts of the dam, but apparently none were being occupied or modified. The activity at the suspected nest site, particularly the interest in the Barn Swallow nest, seemed to taper off prior to the Black Phoebe's disappearance on 6 May.

At approximately 0900 hr on 24 April, Pieplow was able to record approximately 1 minute of the male phoebe's advertising song. Weather conditions were poor and did not allow much recording, but analysis of the recordings made a strong case for the bird's hybrid parentage. Pieplow made more recordings of the song and some calls on 2 May and 6 May, when

the male vocalized nearly continuously from approximately 0515 to 0545 hrs but only briefly or not at all thereafter. The recordings made on these dates total 68 minutes. That the male sang at 0900 hr on dates before the second phoebe was observed, and for only a half-hour at dawn thereafter, is consistent with the hypothesis that the birds were paired (Smith 1969).

Plumage

With only brief views, the putative hybrid could easily be (and was) misidentified as an Eastern Phoebe. Closer inspection, however, disclosed characteristics intermediate between those of the two likely parental species. On all parts of the bird where the Black Phoebe is black or blackish, the Loveland bird was paler and browner, though this coloration was darker (for most parts) than is typical for the Eastern Phoebe (Figures 1, 2, 3). Table 1 provides a suite of characters in which the Loveland phoebe differed in appearance from both the Black and Eastern Phoebes.

We believe that the Say's Phoebe (*S. saya*) is readily eliminated from consideration as a parental species, as it probably would have provided some warm tones to the bird's plumage, particularly on the belly, that were not present. Say's lacks white in the outer web of rectrix 6, and we believe that had it been one of the parental species, the outer web of the Loveland phoebe would have been less extensively white. Finally, the vocalizations of the Say's Phoebe differ significantly from those of its congeners, and the vocalizations of the Loveland bird, discussed below, do not reflect these differences.

Vocal Evidence

As is considered typical for suboscine passerines (e.g., Kroodsma 2005), Eastern Phoebes do not learn their songs. Song in this species is apparently controlled completely by genetic factors (Kroodsma 1985, Kroodsma

Table 1 Plumage Characters Distinguishing Black and Eastern Phoebes and Phenotype of the Loveland Phoebe

Plumage character	Black Phoebe	Loveland phoebe	Eastern Phoebe
Head color	black	dark brown	dark brown
Throat color	black	intermixed dark brown and whitish	whitish
Chest color	black	dark brown with darker streaking	pale with smudgy dark streaking
Back color	black	medium to dark brown	dark olive
Belly color	white	whitish with a few dark streaks	pale yellow (wears to whitish)
Chest/belly interface	strong demarcation	vague demarcation with streaks	vague demarcation with blurry streaks on sides
Tail color	black	dark brown	dark brown
R6[a] outer web color	white	basal 2/3 white, distal 1/3 brown	basal 1/2 white, distal 1/2 brown

[a]R6, rectrix 6 (outermost tail feather).

and Konishi 1991), and we assume that the Black Phoebe is similar in that regard. Several authors working with a variety of avian taxa have convincingly demonstrated that genetically determined vocalizations take intermediate form in hybrid individuals (e.g., *Coturnix* quail, Collins and Goldsmith 1998; *Alectoris* partridges, Ceugniet et al. 1999; *Streptopelia* doves, de Kort et al. 2002, den Hartog et al. 2007; *Callipepla* quail, Gee 2005). Berner and Kroodsma (2005) used intermediate vocalizations as a primary line of evidence to argue for hybrid origin of an apparent Acadian × Least Flycatcher (*Empidonax virescens* × *E. minimus*).

The advertising song of the Eastern Phoebe was well studied by Smith (1969), who termed it the "regularly repeated vocalization" (RRV). Smith found that the RRV in this species consists of two phrase types, RR_1 (Figure 4a) and RR_2 (Figure 4b), which he correlated with the phonetic transliterations "phee-bee" and "phee-b-be-bee," respectively. Smith (1970a) also provided the most complete description and analysis of the vocal repertoire of the Black Phoebe, but it is much less detailed than was his study of the Eastern Phoebe. He identified an RR_1 (Figure 4c) and RR_2 (Figure 4d) in the

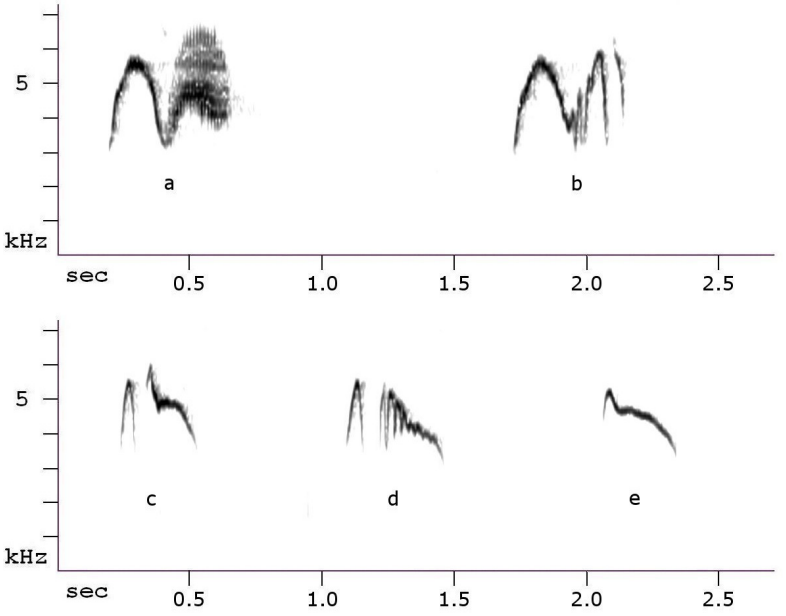

Figure 4. Typical vocalizations of the Eastern Phoebe (a, RR_1; b, RR_2; Baca County, Colorado, 15 April 2006) and Black Phoebe (c, RR_1; d, RR_2; e, htIPV; Clark County, Nevada, 30 September 2007). Note that all RRV phrases in both species consist of an introductory portion, which is identical in both phrases, and a terminal portion, which distinguishes the RR_1 from the RR_2.

Recordings and sonograms by Nathan Pieplow

Black Phoebe's repertoire but also noted that the Black's "song-like displays," unlike those of the Eastern, frequently include a third component which he named the "high-tailed initially peaked vocalization" or htIPV (Figure 4e). In predawn singing, the htIPV is frequently given "alone, or occasionally in strings of two or three units, amid RR_1s and RR_2s"; Smith considered it an "important component of the song" (1970a). As is considered typical in the Tyrannidae, all song (RRV) components of both these species are quite stereotyped, with minimal individual and geographical variation (Kroodsma 1985, Weeks 1994), although the htIPV is somewhat more variable (Smith 1970a).

The advertising song of the Loveland phoebe consisted of three somewhat variable but easily distinguished phrase types; its first phrase (Figure 5, a–c) and second phrase (Figure 5, d–f) appear most similar to RRV phrases of the two putative parent species, while its third phrase (Figure 5, g–i) appears most similar to the htIPV of the Black Phoebe.

In the Black and Eastern Phoebes, each RRV consists of two parts, an introductory note and a terminal portion. In both species, the introductory notes of RR_1 and RR_2 are identical; the two song phrases are distinguished entirely by their terminal portions (see Figure 4, a–d). The Loveland phoebe's introductory notes were highly variable, while its terminal portions were much more stereotyped. The full range of variation of introductory notes was used with both terminal portions; note the similarity in these notes between Figures 5b and 5e and between Figures 5c and 5f. In general, the introductory notes of the Loveland bird were quite similar to those of the Black Phoebe and very different from those of the Eastern Phoebe.

The terminal portion of the Loveland bird's first phrase (Figure 5, a–c) appears intermediate between the terminal portions of the Eastern Phoebe's RR_1 (Figure 4a) and the Black Phoebe's RR_2 (Figure 4d); in particular, it begins like the latter, but it quickly develops much faster and more intense modulations than the Black Phoebe's RR_2 ever does; this is a trait of the terminal portion of the Eastern Phoebe's RR_1. Meanwhile, the terminal portion of the Loveland bird's second phrase (Figure 5, d–f) varies little from a rounded "M" shape very similar to the terminal portion of the Eastern Phoebe's RR_2 (Figure 4b) and very different from any terminal portion of any Black Phoebe phrase.

The Loveland bird's third phrase (Figure 5, g–i) appears very similar to the htIPV of the Black Phoebe (Figure 4e), except that it is always strongly and rapidly modulated or "burry." Smith (1970a) illustrated a number of variants of the IPV; the variant most frequently given during bouts of RRV closely matches the Loveland bird's third phrase in overall shape, and one of the variants does include some slight modulation, but it does not come close to matching the Loveland bird in rate or intensity of modulation. This may indicate influence from the terminal portion of the Eastern's RR_1 or from the Eastern Phoebe call that Smith (1969) termed the "locomotory hesitance vocalization" (LHV), which contains modulations at a rate similar to those of the Eastern's RR_1 and which in certain variations somewhat resembles the Loveland bird's third phrase.

The variability of the Loveland phoebe's third phrase, and of the introductory notes of the RRV phrases, may be an additional indicator of hybridization.

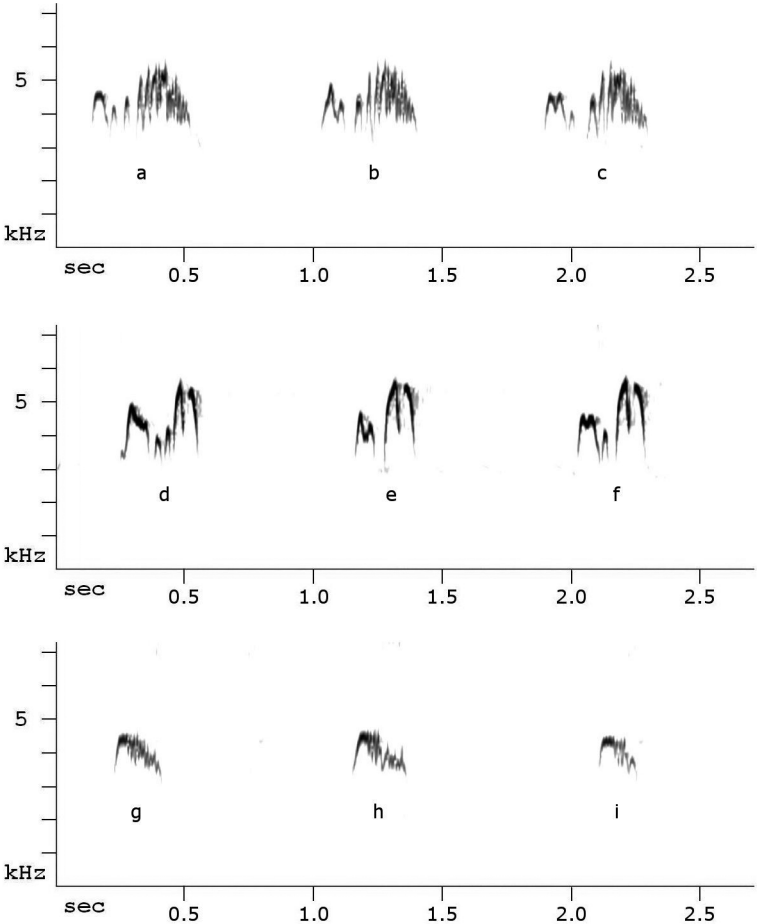

Figure 5. Vocalizations of the Loveland phoebe (a, b, c, phrase type 1; d, e, f, phrase type 2; g, h, i, phrase type 3), 2 May 2007. Three examples of each phrase type are given to represent the bird's full range of variation. Note that phrase types 1 and 2 consist of a variable introductory portion and a more stereotyped terminal portion. The introductory portion varies independently of the terminal portion and somewhat resembles the introductory portion of the Black Phoebe's RRV phrases. However, the modulation of the terminal portion of phrase type 1 is more rapid than that in any Black Phoebe vocalization and more closely resembles the terminal portion of the Eastern Phoebe's RR_1. In addition, the terminal portion of phrase type 2 resembles the terminal portion of the Eastern Phoebe's RR_2.

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In addition to intermediate form, at least one study has found that hybrids may have vocalizations less stereotyped than those of the parental species (Collins and Goldsmith 1998). In late summer and autumn at least some Black and Eastern Phoebes do give distinctly variable renditions of their RRV phrases (Pieplow pers. obs.), a phenomenon that may have to do with seasonal hormonal levels. No authors, however, have noted this variability in spring.

In some respects the sounds of the Loveland bird resemble those of the Black Phoebe more closely than they resemble those of the Eastern Phoebe, and it is possible that the bird is a backcross hybrid with the Black Phoebe. On the basis of an appearance relatively equidistant from both parental species, however, and the distinct similarity of the terminal portions of the Loveland bird's second phrase and the Eastern Phoebe's RR_2, we believe it more likely that the Loveland bird is a first-generation (F1) hybrid.

OTHER POSSIBLE HYBRIDS

We are aware of the following reports of possible hybridization or interspecific pairing in *Sayornis*. Berner and Kroodsma (2005), citing a personal communication from J. P. Hubbard, mentioned a report of a possible Black × Eastern Phoebe hybrid in New Mexico. This report apparently refers to a pair of phoebes seen by Hubbard along the upper Pecos River in San Miguel County, New Mexico, on 4 April 1981. Hubbard reported these birds as a pair of Eastern Phoebes but noted "one darker, may be hybrid with Black Phoebe?" (NMOS 2007, database record 14355). Sartor O. Williams (pers. comm.) notes that although Eastern Phoebes had colonized this area as early as 1969, April 1981 produced the first report of (pure) Black Phoebes at this location, and that both species have apparently continued to breed there since without subsequent reports of hybridization, though the area may not receive much attention from observers.

On 19 May 2000, Leukering encountered an apparent mixed pair of phoebes at the Burnt Mill Bridge on the St. Charles River in Pueblo County, Colorado (Leukering and Wood 2000), and these birds were seen again on 21 May by Leukering and others. On both dates, both birds responded to playback of Eastern Phoebe song and calls and did not interact agonistically. Other observers noted this pair until sometime in July. But when Leukering walked 2 km of the river on 4 June, he did not detect any phoebe at or near the bridge. He did, however, observe three pairs of Eastern Phoebes and one pair of Black Phoebes in typical linear territories (Leukering and Wood 2001). Summer reports of the possible mixed pair included the finding of a nest, but no details of whether the nest was attended or whether the birds produced young were provided (Leukering and Wood 2001).

Brandon K. Percival (pers. comm.) found an intermediate-appearing phoebe at Rock Canyon in Pueblo Reservoir State Park, Pueblo County, Colorado, on 29 August 2007; the site is less than 20 miles from the Burnt Mill Bridge. The bird appeared fairly similar to the Loveland bird, but no photographs or sound recordings were obtained.

On 20 July 2008, Ted Floyd and Chip Clouse (pers. comm.) found up to three possible hybrid phoebes along the Purgatoire River and Trinchera Creek in Las Animas County, Colorado. They reported that one bird "looked

like a dark Eastern, and gave a call like a Black," while the other two appeared darker than normal for an Eastern Phoebe; one of these gave an "atypical" vocalization. In the same area on the same day, they found ten adult and juvenile Eastern Phoebes and one adult Black Phoebe.

DISCUSSION

The plumage and vocalizations of the Loveland phoebe are strong evidence of hybridization between a Black and an Eastern Phoebe. Virtually all of the plumage characters were intermediate between those of the suggested parental species, and the songs incorporated unique aspects of songs of both species. As suboscines have been found to have genetically determined vocalizations, a hybrid would be expected to sing intermediate songs.

In Colorado (and, presumably, in northern New Mexico), both the Black and Eastern Phoebes are near-obligates of riparian habitat (Leukering pers. obs.). The Black Phoebe is usually found in canyons. The Eastern Phoebe is typical of the flatter stretches of rivers on the eastern plains, though it also occupies canyons in southeastern Colorado. The Loveland location is, interestingly, outside the known breeding range of both species in Colorado, being west of the known breeding range of the Eastern Phoebe in northern Colorado (Andrews and Righter 1992) and north of the known breeding range of the Black Phoebe in eastern Colorado (Faulkner et al. 2005). However, like the St. Charles River site farther south in Pueblo County, the Loveland site is very close to the foothill/plains interface. The habitat criteria for both species may be met in such situations, increasing the likelihood of contact between these two otherwise generally segregated species. From Leukering's surveys along the St. Charles River canyon at and below the Burnt Mill Bridge in summers 2000–02, we believe that in situations where the two species are syntopic, they typically occupy mutually exclusive linear territories. As populations are quite small (probably <12 pairs of Black and Eastern phoebes, combined, within 15 km of the Burnt Mill Bridge), it seems likely that a lack of males of the appropriate species might encourage surplus females to accept as a mate a male of the other species.

As both species continue to expand their ranges, such juxtapositions may become more widespread and may enable more instances of *Sayornis* hybridization. Such hybridization should be sought particularly along the foothill/plains interface in eastern Colorado and northern New Mexico. Interestingly, though the Say's Phoebe breeds syntopically with the Black Phoebe in western Colorado and with the Eastern Phoebe in eastern Colorado (and on the uplands adjacent to the St. Charles River canyon), hybridization involving Say's remains unreported. This is perhaps unsurprising given that a molecular phylogeny by Cicero and Johnson (2002) suggests that the Eastern and Black Phoebes are sister taxa and that Say's is the outlier in this genus.

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