

## A REASSESSMENT OF HOMOLOGIES IN THE VOCAL REPERTOIRES OF PHOEBES

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**ABSTRACT:** During the breeding season, phoebes (*Sayornis*) sing vigorously at dawn with two or three highly stereotyped, probably innate, song types. All song types are combinations of a species-specific introductory note and a terminal phrase. Building on a classic assessment of repertoire structure by W. J. Smith, we recognize three phrase types for the genus (I, II, and III), all of which are used by Say's Phoebe (*S. saya*) but only two of which (I and II) are used by the Black (*S. nigricans*) and another two of which (II and III) are used by the Eastern (*S. phoebe*) Phoebe. A recently discovered hybrid male Black  $\times$  Eastern used all three phrase types and sang like Say's Phoebe by embedding single type II and III songs in longer strings of type I songs. Thus, what appears to be the primitive sequencing of song types was potentiated through reconstitution of the complete repertoire via hybridization. For future studies, we recommend replacement of Smith's terminology with a simpler scheme recognizing three homologous song types.

As biological lineages diversify via speciation, specific characters (e.g., skeletal organization of the hand) often evolve slowly enough that the equivalent character is recognizable in closely related species and higher taxa. Called "homologues," these characters share "primitive," i.e., unchanged, states that have been inherited from the same character in a common ancestor. Homologies are often recognizable even when the form and function of the character has changed under natural selection (e.g., the hand of a dog and a bird).

In birds, the vocal repertoire is a complex of components, like a somatic organ, in which homologies can be recognized and evolutionary history can be reconstructed. Vocal repertoires are richly structured compilations of simple vocal elements, which may be combined into songs or other stereotyped signals, which may then be combined into singing performances (Smith 1986, 1991). Combination rules assemble the static sounds into signaling behavior (Smith 1977, 1997), just as human syntax assembles words into speech. Like the signals themselves, the rules that govern them are amenable to evolutionary analysis.

W. John Smith, a leading theorist on animal communication (Smith 1977, 1986, 1991), published a series of ground-breaking and now classic studies (Smith 1966, 1969, 1988, Smith and Smith 1992, 1996), both observational and experimental, on the singing behavior of tyrant flycatchers (Tyrannidae). These were significant not only because of Smith's pioneering analysis of the rules used in combining acoustic units into singing performances, thereby illuminating the messages encoded in these performances, but also because they remain among the few studies of the singing behavior of suboscines (suborder Tyranni of order Passeriformes, but see Murphy et al. 2008), which have been thought, on the basis of studies by Kroodsma (Kroodsma 1984, 1985, Kroodsma and Konishi 1991; reviewed

by Kroodsma 2005) as well as on morphological grounds (Suthers 2004, Amador et al. 2008), to produce species-specific songs innately.

In his comparative studies of the three phoebes, the Eastern (*Sayornis phoebe*), Black (*S. nigricans*), and Say's (*S. saya*), Smith used the term "regularly repeated vocalization" (RRV) for acoustically distinct sounds that are typically called songs or song types. He gave each distinct song type a numerical designator, so each species had types RR1 and RR2. Other sounds received descriptive labels such as "simple vocalization" (SV) and "initially peaked vocalization" (IPV).

Although Smith focused on current utility and did not perform formal analyses of homology, he did compare his results for the three species, writing, "the names assigned to different signals are intended where possible to provide an indication of comparability in form and/or usage between signals of this genus" (Smith 1969:286). Such a naming system implies homology, and Smith himself occasionally used the word "homologue" (e.g., Smith 1970a:77) and the phrase "apparently homologous displays" (e.g., Smith 1970b:105) to describe these vocalizations. Subsequently, the authors of the species accounts in the *Birds of North America* series (Weeks 1994, Wolf 1997, Schukman and Wolf 1998) have referred to RR1, RR2, etc., of the three phoebes as though they were homologues. This assumption, however, remains untested.

One potential problem with Smith's analysis is that he began with a thorough study of the Eastern Phoebe and then generalized his findings to the genus on the basis of rather limited exposure to the two western species. He noted (e.g., Smith 1970b:105) several ways in which the Eastern Phoebe's repertoire is distinctive, but these differences turn out to be autapomorphies (uniquely derived rather than primitive character states) and therefore not suitable as bases for comparison. On the basis of mitochondrial DNA sequences Cicero and Johnson (2002) reported that Say's Phoebe is the basal member of this distinctive three-species clade. On the basis of this finding, as well as our wider experience with the two western species, the abundance of recordings now available for all three species, and the recordings of the first known hybrid in the genus (Pieplow et al. 2008), we assessed homology and repertoire organization in the genus *Sayornis* independently.

Broadly, we wished to determine which, if any, vocal elements (song types) used by *Sayornis* in dawn singing are homologous and whether the syntax revealed by dawn singing is homologous. This broad approach allowed us to evaluate whether Smith's terminology delineates homologues accurately—e.g., whether "RR1" is homologous across species. We limited our investigation to noninteractive broadcast singing, typically delivered around dawn, because patterns of song-type alternation at this time are more likely to reflect species-wide rules rather than the socially mediated modulations seen with daytime singing (e.g., Smith 1969, 1988, Smith and Smith 1992, 1996, Kroodsma 1985).

## METHODS

Assessing homology in any suite of characters can be difficult because one cannot be certain whether character states are similar because they

are homologous or appear homologous because they are similar. Remane (1956) proposed three criteria for recognizing true homology. As repeated by Brooks and McLennan (1991:7), these are similarity of position in an organ system, special quality, and continuity through intermediate forms. These three criteria are as applicable to behavioral data as they are to morphological data (Brooks and McLennan 1991), especially for innate vocalizations, those that develop normally in the absence of environmental input, such as the vocalizations of the Eastern Phoebe (Kroodsma 1985, Kroodsma and Konishi 1991). We discuss each criterion and its applicability to our study briefly.

*Similarity of position in an organ system.* Although this criterion was developed to assess morphology, it can also be adapted to the assessment of behavioral systems. The topology of an organ system carries a phylogenetic signal because an organ system is a co-adapted functional complex that is likely to change only under selection. By analogy, behavioral complexes that are essential to fitness are likely to be canalized and thereby consistent. We propose that the syntax of dawn song in phoebes is one such complex and that homologies of dawn-song elements can be inferred from the positions of these elements relative to one another in a singing performance.

*Special quality* (e.g., commonalities in fine structure or development). In the case of vocalizations, fine structure of sounds is clearly revealed by high-resolution spectrograms and oscillograms, which can indicate the likelihood of similar production mechanisms. The intricacies of avian phonation (reviewed by Suthers 2004) may carry clear phylogenetic signals.

*Continuity through intermediate forms.* Intermediate forms are provided by the behaviors of hybrids. The recordings of a bird morphologically identifiable as a *nigricans* × *phoebe* hybrid (Pieplow et al. 2008) are very useful in this regard.

We assembled a library of dawn-singing performances, daytime-singing performances, and social interactions from numerous individuals of all three species throughout their U. S. breeding ranges (Appendix). Included in this sample were 68 minutes of recordings of a hybrid Black × Eastern Phoebe (Pieplow et al. 2008). Online material from the Borror Laboratory of Bioacoustics (BLB) and Macaulay Library (ML) public catalogues was played as streaming media with a QuickTime player and rerecorded with WaveDisk software (Engineering Design, Berkeley, CA). We confirmed that compression of streaming media had not resulted in measurable distortion by comparing spectrograms of rerecorded and original source material. McCallum's recordings were recorded in analogue format and digitized at 50,000 points per second with NIDisk software (Engineering Design, Berkeley, CA) with a National Instruments DAQCard 6062E analogue-to-digital acquisition card. Pieplow's recordings were recorded digitally in linear PCM format on a Sony Hi-MD MZ-NH900 minidisc recorder.

To characterize singing performances, we "paged" through continuous recordings of dawn singing spectrographically and logged the start and stop times and the minimum and maximum frequency of each phoebe sound with the on-screen cursor in Signal Sound Analysis Software, Version 4.02.04 (Engineering Design, Berkeley, CA). We displayed 6 sec at a time in a 900-pixel × 400-pixel window, yielding a measurement resolution of

## REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

7 msec  $\times$  29 Hz. Concurrently, we assigned each sound to one of the song types or call types defined by Smith (1970a). After we had passed through the recordings once, we revisited each identified song, checked its song-type assignment for error, and measured the duration and bandwidth of the introductory note and song phrase from a subset of these (see Results for these distinctions) to assess variability within and among species. We chose this subsample deliberately to capture variation.

We used SAS Version 6 (SAS Institute, Inc., Cary, NC) to manage the resulting data table. We used the Tables option in SAS Proc Freq to calculate transition probabilities to and from each song type for each species and to test these transitions for independence. We prepared histograms of the time intervals separating each song from those immediately preceding and following it with SAS Proc Chart. Summary statistics were calculated with SAS Proc Univariate and Proc Means. Highly skewed (to the right) distributions of intervals between songs were the rule, but these distributions were unimodal. We therefore used the mode (from 0.2-sec bins) to characterize the “typical” interval. We infer that the longer intervals in the tail of the distribution resulted from interruptions or movements by the singers and therefore do not reflect syntactical rules accurately. The mode nicely captures the shorter, limiting intervals that are probably most reflective of singing rules. Intervals lengthen as the day progresses (Smith 1969, 1970a, Kroodsma 1985, 2005; pers. obs.), so we restricted our analyses of dawn-singing syntax to samples recorded within an hour of sunrise.

We used order of homologous song types (Remane’s principle 1) to address whether the patterns of combination of the song types indicated homology among entire performances, i.e., whether syntax was homologous.

## RESULTS AND DISCUSSION

### Descriptions of Repertoire Elements Used in Dawn Singing

We examined 93 recordings from 15 states and measured the start times and stop times of 2248 songs from 27 individuals (Appendix). The seven song types of the genus (Figure 1a, b, c, d, e, i, j) range in duration from 290 to 550 msec (Table 1) and, within a species, occupy the same frequency band. Say’s Phoebe songs barely overlap in frequency with the much higher songs of the sympatric Black Phoebe (Table 1), while the Eastern, which is largely allopatric with both Say’s and Black, is intermediate.

An arresting characteristic of these seven sounds is that each begins with a species-specific note, which we refer to generically as the “*pip*.” In all three species the frequency trend of the *pip* is similar: it is a simple overslur (a rising and then falling trace on the spectrogram). The species, however, differ strongly in the duration and bandwidth of the *pip* (Table 1). Species identity is thus encoded in the acoustic characteristics of this note, and it may exist primarily for the purpose of broadcasting the specific identity of the singer during the dimly lit dawn. The hybrid also uttered a *pip*, which was intermediate in duration but narrower in bandwidth than those of the parental species (Table 1). It had a unique double-peaked frequency contour (Figure 1g, h). The hybrid’s *pip* is surprising on two counts: it was poorly stereotyped (see

REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

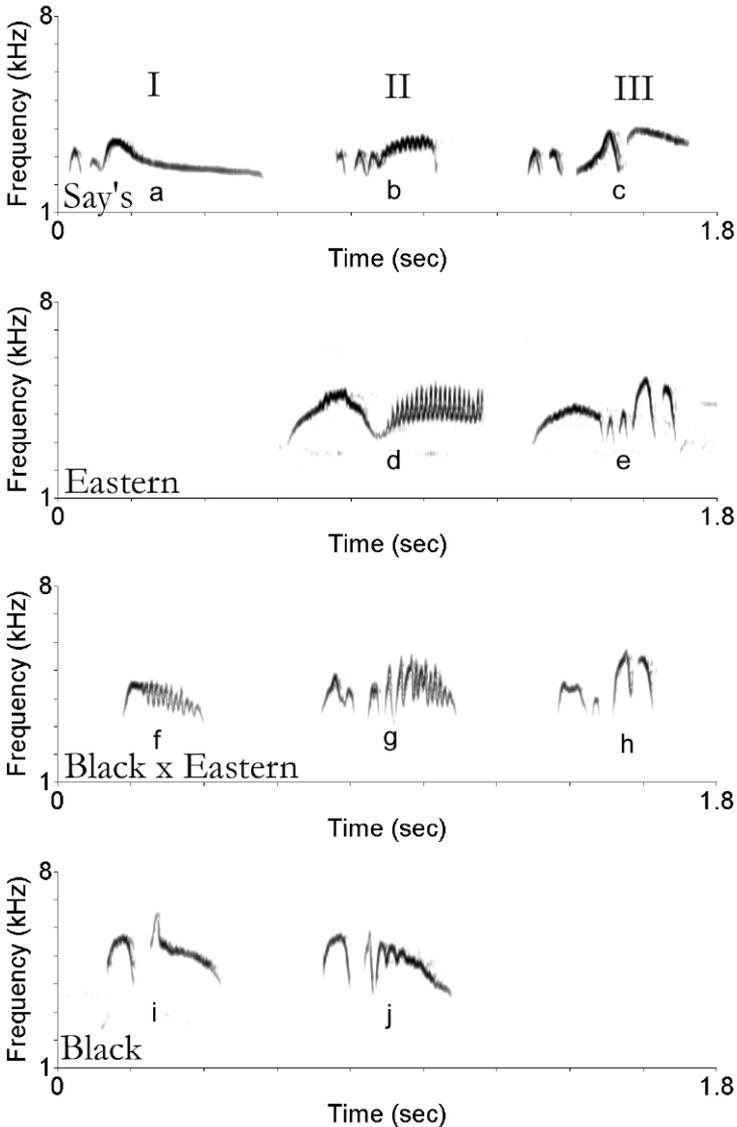


Figure 1. The seven highly stereotyped song types of the phoebes, arranged to show similarity within species horizontally, and similarity within a song type vertically. Say's Phoebe, the basal species in the phylogenetic reconstruction of Cicero and Johnson (2002), is at the top, while a hybrid Black  $\times$  Eastern Phoebe (Pieplow et al. 2008) is displayed between its parental species. Roman numerals across the top of the figure designate the three song types we propose as homologous (see text).

REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

**Table 1** Species-Specific Characters of Introductory *Pip* Notes and Entire Songs<sup>a</sup> of the Three Phoebes and one Hybrid Black × Eastern

Variable <sup>b</sup>	<i>Pip</i> <sup>c</sup>	Song type		
		I	II	III
Duration (msec)				
Say's	37 (9), 9.4	551(9), 6.1	279 (9), 21.3	438 (8), 7.4
Eastern	242 (10), 19.1		506 (10), 13.9	461 (11), 13.8
Black	66 (10), 11.4	290 (11), 10.2	336 (10), 8.5	
Hybrid	101 (12), 15.6	207 (10), 27.1	411 (12), 7.0	282 (17), 7.0
Bandwidth (Hz)				
Say's	872 (9), 19.1	1435 (9), 5.4	1571 (9), 9.5	1728 (8), 20.3
Eastern	2153 (10), 9.8		2529 (10), 10.7	2677 (11), 7.3
Black	2003 (10), 16.5	2759 (11), 13.8	2649 (10), 10.6	
Hybrid	1596 (12), 11.3	1835 (10), 13.4	2599 (12), 7.6	2749 (17), 8.5
Maximum frequency (Hz)				
Say's	3314 (9), 6.9	3748 (9), 3.8	3909 (9), 4.8	4090 (8), 8.0
Eastern	5077 (10), 5.1		5444 (10), 5.4	5644 (11), 3.7
Black	5677 (10), 2.7	6271 (11), 6.7	5921 (10), 5.2	
Hybrid	4652 (12), 3.2	4700 (10), 3.7	5570 (12), 2.5	5812 (17), 2.6
Minimum frequency (Hz)				
Say's	2442 (9), 5.7	2317 (9), 4.9	2342 (9) 3.6	2376 (8), 4.5
Eastern	2924 (10), 5.0		3071 (10), 5.5	3147 (11), 7.1
Black	3674 (10), 7.5	3610 (11), 5.6	3301 (10), 5.2	
Hybrid	3056 (12), 5.2	2865 (10), 5.5	2970 (12), 3.5	3063 (17), 4.7

<sup>a</sup>Songs consists of *pip* + intervening notes + main song phrase.

<sup>b</sup>Summary statistics are the mean of means for individual birds, number of individuals measured, and the coefficient of variation (CV) of the individual means. The CV rather than the standard deviation is presented to facilitate comparison. The sample sizes and CVs reported for the hybrid are for individual songs. Sample sizes for individual means are 1–9 songs.

<sup>c</sup>Data on *pips* are from song type II only, but results for *pip* from different song types within each species are highly consistent.

Pieplow et al. 2008 for discussion), and it was completely absent from one of the hybrid's song types (Figure 1f; see below for discussion).

The extent of the *pip* is unambiguous in the Black Phoebe because it is clearly separate from the terminal portion of the song, which we call the “song phrase.” In the Eastern the *pip* of song type II is continuous with the song phrase, as seen in Figure 1d, and the *pip* of song type III ends with zero to several frequency modulations that could be considered part of the song phrase. (These chevrons are unattached in Figure 1e, but they are often attached to the introductory note.) For consistency with the Black Phoebe, we defined the end of the Eastern's *pip* as the low-frequency point following the frequency maximum. In Say's the *pip* may be absent or reduplicated (e.g., Figure 1a). We measured the largest *pip* available, whether it was isolated or attached to the main song phrase.

For consistency within and across species, we defined song phrase III as the terminal two notes seen in Figure 1c, 1e, and 1h. These were always present, while small chevron-shaped notes, as seen in Figure 1e and 1h, were variable in number, shape, and presence. In Say's, Black, and the hybrid

song phrase II typically began with an accentuated chevron, as in Figure 1, while such a feature was absent from the evenly modulated song phrase II of the Eastern. We included the accentuated chevron in measurements of song phrase II.

### Homologies among Song Types

The introductory *pip* note is clearly homologous across the genus by all three of Remane's criteria: position in the finished song type, similarity of frequency trend, and continuity through the intermediacy revealed in the hybrid. This well-supported hypothesis of homology means that the genes that are ultimately responsible for the neurological circuitry that directs the production of these prefixes during singing performances have in all likelihood been inherited from the common ancestor of all three phoebes. This type of introductory note is seen not only in all species of *Sayornis* but also in several pewees (*Contopus*) and in two species of *Empidonax* (McCallum unpubl. data). Use of principle 1 (position) here, within song type, does not invalidate our using it also for homology of syntax in analysis of complete song types.

The existence and stereotypy of the *pip* reveals that the completed song types are combinations, generated with a rule that prefixes the introductory note to one of several terminal phrase types. Because the finished product is generated by rules, the combining forms may vary independently, and it is possible for the prefix to be inherited from one parent and the terminal phrase type from another. Therefore, in order to determine homology in the phoebes' dawn-song system, we needed to assess it among the seven terminal phrase types rather than among the completed song types. We did that by using Remane's second and third criteria, saving the positional criterion for an assessment of the rules by which song types are combined into singing performances.

*Phrase type II.* The clearest homology within the seven phrase types is between the highly modulated "buzz" phrases of the Say's (Figure 1b) and of the Eastern (Figure 1d). Both feature a carrier frequency that initially rises and then levels off and is frequency-modulated at a constant rate. Although the note is nearly twice as long and the depth of frequency modulation is roughly twice as great in the Eastern, the rate of modulation in the two species is actually very similar. Overall, the two types differ quantitatively but are qualitatively very similar. These similarities in fine structure abundantly satisfy the "special quality" criterion. We designate song types with this "buzz" phrase song type II. (The choice of designators for the three song types is based on syntactical relations; see below.)

One of the hybrid's phrase types (Figure 1g) provides a link between these periodically modulated "buzzes" and one of the phrase types (Figure 1j) of the Black Phoebe, which is shallowly and irregularly modulated at the outset but "smooth" terminally (Pieplow et al. 2008). The hybrid's version is irregularly modulated at the outset, like the Black parent's, and more regularly modulated terminally, like the Eastern parent's. The hybrid's carrier frequency rises and then falls evenly, which can be interpreted as a pasting together of the initial half of the Eastern parent's and the terminal half of the Black parent's carrier frequencies. Note that the modulation rate

and frequency trend are not correlated with regard to parental species and hence are probably inherited independently of each other. These assignments mean that all three species and the hybrid have song type II in their repertoires. Assignment of Figure 1j to song type II rather than to song type I (see below) is supported by the similarity of the semi-attached chevron that always begins this phrase type in the Black and the unattached chevron that begins the hybrid's song type II.

*Phrase type III.* Although they appear dissimilar at first glance, the “stutter” phrases of Say's (Figure 1c) and the Eastern (Figure 1e) are probably homologous, on the basis of the fine-structure criterion. The last two notes of each have similar frequency trends. The Say's form is an elongated version of the Eastern's form, just as the Eastern's buzz (song phrase II) is an elongated version of the Say's buzz. In other words, as we have seen in both the phrase types and in the introductory *pip* notes, the duration of song elements appears to be rather more labile in this genus than frequency trend. The “stutter” song-phrase of the Eastern Phoebe, which we designate III, is clearly the unadulterated source of one of the hybrid's song phrases (Figure 1h), while the Black apparently lacks song phrase III.

*Phrase types I and IPV.* Also likely homologues are the two phrase types with an overslurred frequency trend (Fig 1a and 1i). Although the Black's version is typically shorter (Table 1), an abruptly rising, then more gradually falling frequency trend unites them. Bolstering the argument for homology is in all three species' giving a *pipless* note with this frequency trend (Figure 2), designated IPV (“initially peaked vocalization”) by Smith (1969, 1970a, b). As noted by Smith (1970a:80), it is highly plausible that Say's and Black simply generate this song type by affixing their species-specific version of *pip* to their species-distinctive IPV. We therefore consider the IPV in these two species the same as the terminal phrase of song type I (Figure 1), i.e., song type I is a “pipped” IPV. The Eastern has lost song type I, i.e., it does not include the combination *pip* + IPV in its singing performances (Smith 1969, 1970a; pers. obs.). The Eastern does retain the IPV as a call (Figure 2b) but uses it rarely (Smith 1969, 1970b; pers. obs.).

It may have been the superficial similarity of the Eastern's IPV (Figure 2b) to Say's song type I (Figure 1a), presented side by side in Smith's (1970a) figure 2, that led him to characterize the latter as an IPV rather than an RRV (i.e., a song type). As we have shown, however, these “pipped IPV's” are not just analogous but homologous to all other sounds used by the phoebes in their singing performances at dawn, in that they are constructed according to the rule “species-specific *pip* + phrase I, II, or III.” The appropriate comparison among IPV's appears in Figure 2.

At least in the Black and Say's Phoebes, IPV, unlike the song types, constitutes a spectrum of vocal displays; it could be considered a continuum of variability with modal peaks (e.g., Gardali and Ballard 2000). These modal peaks were classified by Smith (1969, 1970a, b) as subtypes of the IPV—e.g., the “high-tailed” IPV (htIPV) and the “chevron-peaked” IPV (cpIPV)—that tend to be deployed in different behavioral contexts. In the Black Phoebe, the htIPV, without an introductory *pip*, is inserted occasionally in dawn singing performances and is associated with brief pauses (Smith 1970a:80). The cpIPV, on the other hand, occurs with a *pip* during bouts of singing, as the

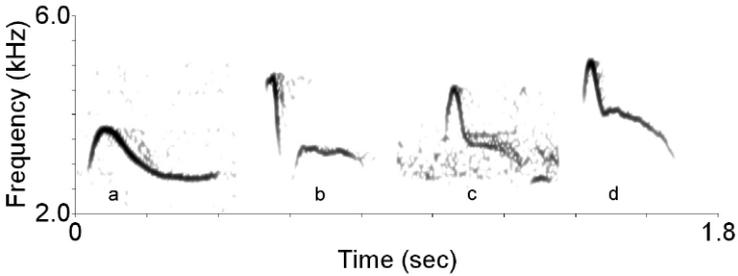


Figure 2. Initially peaked vocalizations (IPV) (Smith 1970a) of (a) Say's, (b) Eastern, (c) the Eastern  $\times$  Black hybrid (Pieplow et al. 2008), and (d) Black Phoebes. Figure 2d is the "chevron-peak" (cp) variant of Smith. Recordings: (a) Wasco Co., Oregon, by McCallum; (b) Warren Co., Virginia, by McCallum; (c) Larimer Co., Colorado, by Pieplow; (4) Clark Co., Nevada, by Pieplow.

terminal song phrase of song type I, in both the Black and Say's Phoebes. A string of *pipless* IPVs sometimes precedes dawn bouts as well.

In addition, calling Black and Say's Phoebes commonly utter the *pipless* cpIPV after dawn (Smith 1969, 1970b; pers. obs.). These species also give extended performances, i.e., "sing" (Smith 1991), with cpIPV alone (Smith 1970a). We would say, alternatively, that they sing by day with *pipless* song type I, although Say's often retains *pips* in its daytime singing (pers. obs.). These performances are often interrupted for self-maintenance activity, as the Eastern's daytime singing is with RR1 (song type II) (Smith 1970a). Smith (1970a) surmised that in the Say's and Black Phoebes, cpIPV had replaced the RR1 of Eastern in these contexts. Our reconstruction of homology suggests that the reverse is more likely true, i.e., that the Eastern has adopted the pipped song type II (RR1) in contexts reserved for cpIPV (*pipless* song type I) in the other two species. The near loss of IPV in the Eastern, and the absence of an IPV-like song type (i.e., song type I) in its repertoire, exemplify its more derived repertoire (Smith 1970b:86).

The hybrid included in its songs a phrase that, with a few exceptions, lacked a *pip* prefix (Figure 1f), was much shorter than any other song type in *Sayornis*, and had a much smaller bandwidth and lower maximum frequency than the hybrid's other two song types (Table 1). If its frequency-modulated tail were smoothed, the frequency contour of this phrase would most resemble the htIPV of the Black Phoebe (Pieplow et al. 2008), although that call occupies a higher band of the frequency spectrum. The frequency-modulated tail may be an "acoustic overlay" contributed by the Eastern parent. Modulation of both frequency and amplitude of otherwise similar sounds often distinguishes the vocalizations of closely related species (McCallum pers. obs.).

Given the homologies we have hypothesized (Figure 1), this third song type should closely resemble the Black's song type I because the Eastern lacks song type I. That is the complementary pattern seen with song type II. An alternative prediction is for the hybrid's song phrase I to resemble its cpIPV, as do song type I of the Black and Say's. Both the absence of a *pip* and the structure of the song-phrase are therefore enigmatic. A third

possibility, that this sound is the hybrid's version of htIPV, would solve the previous two problems but produce another: the frequency of use of this sound in dawn bouts (Table 2) does not agree with any of the three species' use of an IPV. We must reserve judgment, therefore, on the exact homology of this sound, but we refer to it operationally as song type I, for the sake of assessing the hybrid's syntax.

The hybrid also produced sounds (Figure 2c) nearly identical to the Black Phoebe's cpIPV (Figure 2d), in typical cpIPV contexts (e.g., in homogeneous strings near the beginning and end of dawn singing). These sounds resemble the Black's cpIPV in shape but are intermediate in frequency between the IPVs of the two parental species (Figure 2). The emergence of an apparently distinct htIPV and cpIPV in the hybrid may support the hypothesis that these different forms of the vocalization have separate evolutionary histories, further underscoring the independent inheritance of many features of a repertoire.

In summary, we hypothesize that Say's has retained the ancestral phoebe's repertoire of three song phrases, and that the Eastern and Black, with two phrase types each, have lost types I and III, respectively. Either the ancestral repertoire of three phrase types has been reconstituted in the hybrid, because the two parental species each contributed a phrase type missing in the other, or the htIPV was inherited from Black and is used in place of phrase type I.

#### Syntax of Dawn Singing

Dawn singing is highly stereotyped in all three species of *Sayornis* and can be described by simple combination rules applied to two or three highly stereotyped song types (Table 2). Daytime singing is much more variable (Smith 1969, 1970a, b; pers. obs.), as birds communicate at this time of day about, for example, their openness for interaction at close quarters. A daytime singer may give a long string of a single song type, such as RR1 (our song type II) in the Eastern, IPV (*pipless* song type I) in Say's, and cpIPV (also *pipless* song type I) in the Black. Two interacting birds may interleave various call types (Smith 1970b). Vigorous interactions are accompanied, as in most flycatchers, by rapid-fire strings of sounds that include recognizable repertoire elements and others that are not used alone but do have the general acoustic quality of flycatcher sounds (pers. obs.).

Our interest is interspecific comparison, so we focus on the most stereotyped behaviors, which are more likely to carry a phylogenetic signal. We agree with Smith (1969, 1970a, b) that during dawn song the Eastern and Black alternate their two song types in roughly equal measure (Table 2). Smith referred to each species' two song types with identical designators, "RR1" and "RR2." According to our reconstruction of homology, however, RR1 and RR2 in these two species cannot be homologous. RR1 of the Black is our song type I, while RR1 of the Eastern is our song type II. Although the homology of the Black's song type II (Figure 1j) is somewhat conjectural, it would be far-fetched to consider Figure 1d and Figure 1i homologues, given their great similarity to Figure 1b and 1a, respectively. By our terminology, the Eastern sings by alternating song types II and III, the Black by alternating I and II.

REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

**Table 2** Syntax of Dawn Singing in Phoebes<sup>a</sup>

Species	Song type	Relative abundance <sup>b</sup>	Following song type	Probability <sup>c</sup>	Modal lag <sup>d</sup>
Say's	I	0.799	I	0.743	1.2
			II	<b>0.108</b>	1.2
			III	<b>0.150</b>	1.4
Eastern	II	0.082	I	<b>0.982</b>	1.8
			III	0.119	1.2
			II	0.465	2.6
Black	III	0.533	II	<b>0.933</b>	1.6
			III	<b>0.812</b>	1.6
			III	0.187 <sup>e</sup>	2.8
Hybrid	I	0.487	I	0.082	2.2
			II	<b>0.918</b>	1.2
			II	0.122	1.0
Hybrid	II	0.564	I	0.389	1.0
			II	0.106	1.0
			III	<b>0.505</b>	1.0
Hybrid	III	0.104	I	<b>0.783</b>	2.0
			II	0.050	2.0
			III	0.167	2.1
Hybrid	III	0.307	I	<b>0.834</b>	1.4
			II	<b>0.126</b>	1.0
			III	0.04	2.8

<sup>a</sup>Statistics pertain to continuous series of songs only; the very small number of calls inserted in these dawn performances were omitted, as were the transitions to and from them. Final songs were not scored, i.e., there are no transitions to "stop."

<sup>b</sup>Relative abundances of song types pooled over all dawn performances examined for the species. May differ slightly from the species totals obtained from the Appendix because of omission of calls and final songs.

<sup>c</sup>Probability is the relative frequency of the following song type when the preceding song type is the one listed in the song-type column. A following song type is omitted from this table if it has a relative frequency <0.02. Transition probabilities greater than expected by chance are in bold. For each species, the result of a test for independence of the contingency table was highly significant.

<sup>d</sup>Distributions of lag times are highly skewed to the right, with essentially no tail on the left, so the mode seems to capture the minimal "syntactical" lag.

<sup>e</sup>The 0.187 probability of repetition of song type III in the Eastern Phoebe is due almost entirely to a single bird (see Appendix).

In both species the tendency to alternate is highly nonrandom, i.e., they repeat one song type consecutively far less frequently than would be expected if song types were drawn from the repertoire randomly (Table 2). When in these species repetition does occur, the interval between songs is >50% greater than between unlike song types (Table 2). In fact, these intervals are almost great enough to allow insertion of the other song type without breaking the typical cadence when song types are alternated. In the hybrid, this pattern is also true of repetitions of song type III, which are separated by a gap long enough for

insertion of song type I. The sole exception to this tendency to pause when repeating is with song type II in the Black, which is repeated slightly more quickly than the alternation of song types. These patterns of tempo suggest that, at least at dawn, syntax is highly conserved, even if communication demands that one song type be emphasized. The restriction of our sample to dawn song is perhaps responsible, also, for our not finding pauses after song type III in the Eastern, as reported by Kroodsma (1985, 2005).

Say's Phoebe, on the other hand, deploys its three song types in unequal proportions (Table 2). Song type I is by far the most frequent, and II is typically but not always least frequent. Song types II and III are so seldom repeated or follow each other (Table 2) that the few exceptions are likely aberrations. Despite the abundance of song type I, repetitions of it are underrepresented, showing again that the phoebes' songs are constructed according to rules. There is a brief pause after each song type II, suggesting that it marks the end of a syntactical subunit.

Like Say's Phoebe, but unlike both parental species, the hybrid Eastern × Black sang with three song types rather than two (Figure 1). One of these song phrases (III) is essentially identical to the Eastern parent's, one (II) is nicely intermediate between the Eastern's and Black's versions, and one (I) is somewhat enigmatic but appears to be part of the song type I–IPV complex (Figure 1). Most of the songs in a dawn performance were of type I (Table 2), and hence, with a reconstituted repertoire of three song types, this bird, a hybrid of the Black and Eastern Phoebes, sang in the manner of the only extant species with three song types, Say's Phoebe.

In summary, the nonrandomness of the song types' order (Table 2) indicates that some form of syntax does exist and directs the assembly of a performance. In dawn song, the consistency of song-type ratios from individual to individual (Appendix) suggests that at least at that time of day the innate species-specific syntax is on display and perhaps is concerned more with communicating fitness (e.g., Murphy et al. 2008) than openness to interaction (e.g., Smith 1969, 1970a, 2008).

As to homology of syntax across species, the predominant [I–II] pattern of the Black, where the brackets enclose minimum repeatable units, seems different from the [II–III] of the Eastern. It may be, however, that rules for combining unit elements can be homologous even when the unit elements are not. The general pattern of dawn singing in both the Eastern and the Black is [AB], where A and B represent the two song types in the species' repertoires. We suggest that they follow an identical, homologous syntax that operates on whatever it “finds” in the repertoire.

The initially surprising behavior of the hybrid supports our interpretation. Like Say's Phoebe, it sang [(I) II (I) III], with the caveat that neither II nor III occurred in every iteration of this pattern. One would expect the bird to have inherited the syntax of one parent or the other, or a blend of the two. That its singing did not meet this expectation does not necessarily mean it inherited the syntax of Say's; it may mean that all three species share a syntax that operates one way, [AB], with a two-song repertoire, and another, [(I) II (I) III], with three songs. In this event the syntax of all three species would be homologous. These combination rules, then, are not predicted by

the content of the song types they organize. They are instead higher-order operators that appear to be inherited and neurally organized independently of the acoustic tokens they combine into a performance.

## CONCLUSIONS AND RECOMMENDATIONS

Every song type used for dawn singing in *Sayornis* consists of a species-specific prefix and a terminal phrase type that is shared with at least one other species. Thus all song types are homologous in architecture, the prefixes are homologous, and their shared phrase types are homologous as well.

The rules for combining song types into dawn performances appear to be identical in the sister species the Black and the Eastern, even though the repertoire elements combined by this syntax differ partially. Moreover, song type I is not as dominant in the Black, with two song types, as it is in Say's, with three. Say's Phoebe uses three rather than two song types, and, unlike its congeners, does not use them with equal frequency. Rather, types II and III are embedded in a matrix of type I songs. Unequal usage of song types may be "different" syntax or it may not. We emphasize that it is a species-specific characteristic, not a variable result of a varying context of intraspecific communication, as in the daytime singing of the Eastern Phoebe (Smith 1969) and the Eastern Wood-Pewee (Smith 1988). In *Contopus* and *Empidonax* as well, species vary much more in the syntax of dawn singing than do individuals within a species, i.e., these differences are evolved rather than situational. On the usual criterion of reduced uncertainty (entropy) (Shannon 1948, Hailman et al. 1985) as well as the greater number of song types, Say's Phoebe's performances are more complex (contra Wolf 1997) than those of the Eastern and Black.

It is apparent from our independent assessment of homology that the labels (e.g., "RR1") Smith used to indicate "apparently homologous displays" (Smith 1970b:105) need revision. Possibly Smith's RRV phrases are homologues under Remane's first criterion, similarity of position, but we find similarities in special quality and intermediacy more compelling. It is important, in our view, not to assume that Smith's designators encode homology. We recommend instead the usage of our homologue designators I, II, and III in future interspecific comparisons of the singing behavior of the phoebes.

Further comparisons are warranted. We have examined three recordings of Black Phoebes from the eastern slopes of the Andes in Bolivia and northern Argentina. These birds used two song types that do not closely resemble those of Black Phoebes in the United States. One song type resembles type II of the Black  $\times$  Eastern hybrid (Pieplow et al. 2008); the other, while clearly consistent with other song types of the other phoebes, is unique. The pacing of the South American birds' singing resembles that of the Eastern Phoebe. Like the hybrid's, their *pips* are highly variable. Southern populations clearly deserve more study, as the limited material we have reviewed suggests that southern Andean populations (*S. n. latirostris*) represent a species distinct from *S. n. semiatra* of western North America, as represented by our sample (Appendix). This putative species may not, however, be equivalent to the "*latirostris* group" (American Ornithologists' Union 1998), also known as the "White-winged Phoebe," which comprises also subspecies *S. n. angu-*

## REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

*stirostris* and occurs in South America and central and eastern Panama. The spectrogram presented as Figure 2b by Smith (1970a) is equivalent to one of the two song types sung by southernmost Black Phoebes, but Smith's cited recording location, Cerro Punta, is in westernmost Panama, in the range of subspecies *S. n. amnicola* of the North American *nigricans* group of subspecies (American Ornithologists' Union 1998).

Finally, the hybrid turned out to be very helpful in confirming and clarifying the song-type homologies we hypothesized on the basis of special quality. The significance of even single hybrids to understanding repertoire organization and evolution in an entire genus is underscored by the apparent atavism in the hybrid's arrangement of elements in its dawn performances. This surprising outcome suggests that the syntax of dawn song is contingent on repertoire organization and hence that any phoebe equipped with three song types will sing in the manner of Say's Phoebe, [I] II [I] III. If the Black and Eastern Phoebes continue to hybridize as their ranges expand, following the predictions of Pieplow et al. (2008), more recordings of hybrid phoebes should be sought. Replicate data will not only permit a test of our specific prediction about hybrids' syntax, they may clarify the mode of inheritance of phoebe syntax, which currently appears to be independent of the apparent quantitative inheritance of the acoustic characteristics of the sounds on which that syntax operates.

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REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

**Appendix.** Samples Used for Quantitative Analysis of Acoustic Variation and Syntax<sup>a</sup>

Species	Locality	Time	Date	Sample <sup>b</sup>	Song type		
					I <sup>c</sup>	II <sup>c</sup>	III <sup>c</sup>
Black × Eastern	Loveland, Larimer Co., Colorado	08:00	24 Apr 2007	NDP2007-12-01	1	5	4
	Loveland, Larimer Co., Colorado	08:15	24 Apr 2007	NDP2007-12-03	10	8	15
	Loveland, Larimer Co., Colorado	05:30	2 May 2007	NDP2007-15-01	169	24	70
	Loveland, Larimer Co., Colorado	05:15	6 May 2007	NDP2007-16-01	150	23	93
Black	Sec. 34, T13N, R13W, McKinley Co., New Mexico	05:00–06:00	11 Jun 2000	DAM0016b	22	24	0
	Sec. 34, T13N, R13W, McKinley Co., New Mexico	05:00–06:00	11 Jun 2000	DAM0016b	31	43	0
	Paradise, Cochise Co., Arizona	06:39	19 Jun 2000	DAM0019a	7	5	0
	Red Bluff, Tehama Co., California	06:20	30 Mar 2008	DAM0808a	40	42	0
	Red Bluff, Tehama Co., California	06:40	30 Mar 2008	DAM0808a	54	73	0
	Lower Table Rock, Jackson Co., Oregon	05:10	25 Jun 2009	DAM0930a	22	22	0
	Cosumnes Reserve, Sacramento Co., California <sup>d</sup>	10:00	5 Apr 2003	DAMdv0324	7	2	0
	Kern NWR, Kern Co., California	06:14	26 Feb 2004	DAMdv0401	22	20	0
	American Canyon Campground, San Luis Obispo Co., California	05:54	18 May 1990	ML50171	26	30	0
	Cave Creek Canyon, Cochise Co., Arizona	05:01	26 May 1999	ML109083	37	37	0

(continued)

REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

**Appendix (continued)**

Species	Locality	Time	Date	Sample <sup>b</sup>	Song type		
					I <sup>c</sup>	II <sup>c</sup>	III <sup>c</sup>
Eastern	Portal, Cochise Co., Arizona	06:05	23 May 1977	ML20890	31	15	0
	Davidson, Mecklenburg Co., North Carolina	06:25	21 Apr 2007	DAM0704a	0	60	61
	Montreat, Buncombe Co., North Carolina	06:39	28 Apr 2008	DAM0811b	0	8	12
	Montreat, Buncombe Co., North Carolina	06:40	29 Apr 2008	DAM0811b	0	5	6
	Montreat, Buncombe Co., North Carolina	06:41	28 Apr 2008	DAM0811b	0	7	8
	Montreat, Buncombe Co., North Carolina	06:50	30 Apr 2008	DAM0812a	0	26	25
	James Island, Charleston Co., South Carolina <sup>d</sup>	09:43	26 Mar 2003	DAMdv0319	0	37	32
	Nobleboro, Lincoln Co., Maine <sup>d</sup>	10:35	8 Jul 1962	BLB6054	0	11	10
	Lancaster, Fairfield Co., Ohio <sup>d</sup>	08:21	28 May 1965	BLB7621	0	20	21
	Blendon Township, Franklin Co., Ohio <sup>d</sup>	07:36	10 May 1975	BLB13454	0	21	20
	Lakewood, Oconto Co., Wisconsin	04:30	4 Jun 1988	BLB16915	0	27	26
	Georgesville, Franklin Co., Ohio	06:50	21 Apr 1973	BLB12067	0	3	14
	Georgesville, Franklin Co., Ohio	06:53	21 Apr 1973	BLB12095 <sup>e</sup>	0	4	24
	Zaleski, Vinton Co., Ohio	05:47	12 Jun 1987	BLB16657	0	20	21
	Zaleski, Vinton Co., Ohio	05:48	12 Jun 1987	BLB16705 <sup>e</sup>	0	7	7

REASSESSMENT OF HOMOLOGIES IN VOCAL REPERTOIRES OF PHOEBES

**Appendix (continued)**

Species	Locality	Time	Date	Sample <sup>b</sup>	Song type			
					I <sup>e</sup>	II <sup>c</sup>	III <sup>c</sup>	
Say's								
	Sec. 34, T13N, R13W, McKinley Co., New Mexico	05:47	09 Jun 2000	DAM0016b	41	8	9	
	Sec. 34, T13N, R13W, McKinley Co., New Mexico	05:00–06:00	11 Jun 2000	DAM0016b	9	1	2	
	Sec. 34, T13N, R13W, McKinley Co., New Mexico	05:26	30 Jun 2006	DAMdv0624	85	4	21	
	Arizona	—	April	ML61892	13	6	2	
	Longlake NWR, Moffit Co., North Dakota	dawn	01 Jun 1988	ML42215	94	10	15	
	Malheur NWR, Harney Co., Oregon	07:00	28 Sep 1994	ML107605	34	2	3	
	Eureka, Juab Co., Utah	06:00	26 Apr 1996	BLB28738	93	1	0	
	Taylor Hwy., SE of Fairbanks, Alaska	06:00	11 Jun 1972	ML49907	24	5	1	
	Tijuana NWR, San Diego Co., California	05:45	2 May 2002	ML120202	48	16	8	
	Sheldon NWR, Humboldt Co., Nevada	05:08	3 Jun 1990	ML50502	131	12	25	

<sup>a</sup>Each line represents a different individual except where indicated.

<sup>b</sup>BLB and ML accession numbers, analogue cassette tape numbers from McCallum's personal collection, or digital track numbers from Pieplow's personal collection.

<sup>c</sup>Number of songs of this type measured from this cut. Some long cuts were not completely assayed.

<sup>d</sup>Sample does not represent dawn singing and is not included in Table 2.

<sup>e</sup>Same individual and recording session as in line above.