CHIP CALLS IN THE WESTERN AND EASTERN WOOD-PEWEES

KONSHAU DUMAN, Animal Behavior Graduate Group, One Shields Avenue, Davis, California 95616; kduman@ucdavis.edu

ABSTRACT: The chip call of the Eastern Wood-Pewee (*Contopus virens*) is a frequently cited feature of that species' vocal repertoire, but similar calls of the Western Wood-Pewee (*C. sordidulus*) are usually overlooked. Differences in this call between the two species would aid in field identification of migrants, which rarely sing their diagnostic songs. Cross-correlations of audiospectrograms, comparisons of three audiospectrographic measures, and qualitative analysis of spectrograms show that most chip calls of the Eastern Wood-Pewee are not distinguishable from those of the Western Wood-Pewee, and Eastern chip calls are generally more variable than those of the Western. These analyses also show that the two wood-pewees are more similar to each other than they are to their respective sister taxa. This similarity raises questions about the role of chip calls in the behavior of *Contopus* species, especially as it relates to potentially shared functions and sources of selection in their nonbreeding ranges.

It is important to understand vocal differences between closely related species because field identification often depends on these differences, and songs and some calls are related to behavioral isolation between the species where they co-occur (Marler 1957). Vocal differences are especially important for recognition of species with similar or overlapping morphological traits and breeding ranges (Price 2008). One such example involves the Eastern Wood-Pewee (*Contopus virens*) and Western Wood-Pewee (*C. sordidulus*), two species often cited as being mainly or solely distinguishable from each other in the field by voice (Kaufman 1990). In morphological characteristics, the two species overlap partially, such that up to 15% of specimens cannot be identified by measurements alone, though all singing birds can be identified (Rising and Schueler 1980). The breeding ranges of the Eastern and Western Wood-Pewees overlap in a narrow area of sympatry in central Nebraska, where they have hybridized (Manthey and Robbins 2016), and their nonbreeding ranges overlap extensively (Bemis and Rising 2020). While the songs and song-like calls of these two species have major qualitative differences that are well described in most field-identification references, the call repertoires tend to be less clearly described. In particular, the "chip" call (also called "pip," "peep," or "plit") has been inaccurately cited as a distinguishing characteristic of the Eastern Wood-Pewee when it is in fact produced by both species. Various published descriptions of these two pewees' calls state that the chip call is produced by the Eastern without any mention of a similar call in the Western (Sibley 2000, Dunn and Alderfer 2017, Pieplow 2019, Lee and Birch 2023). Dunn and Garrett (1983) cautiously suggested that the call is distinctive of the Eastern. The sole published description of the Western Wood-Pewee's chip call (Bemis and Rising 2020) states that it "may be given by both sexes when alarmed," but in its discussion of field identification this work also incorrectly contrasts the chip call of the Eastern with the whistled calls of the Western. In this study I find that the Western Wood-Pewee regularly produces a chip call and assess differences between this call and the

better-known chip call of the Eastern Wood-Pewee, as well as with those of other closely related species of *Contopus*.

Although they have previously been referred to as sister species (Manthey and Robbins 2016, Bemis and Rising 2020) or even as potentially one species (Browning 1977), molecular phylogenetic work shows that the Eastern and Western Wood-Pewees are not each other's closest relatives. The Eastern is more closely related to the Cuban (*C. caribaeus*), Hispaniolan (*C. hispaniolensis*), and Lesser Antillean (*C. latirostris*) Pewees, while the Western is sister to the Northern Tropical Pewee (*C. bogotensis*); the Blackish (*C. nigrescens*), White-throated (*C. albogularis*), Southern Tropical (*C. cinereus*), and Tumbes (*C. punensis*) Pewees are also more closely related to the Western than the Western is to the Eastern (Fjeldså et al. 2018, Harvey et al. 2020, Ohlson et al. 2020). All these species also produce chip or pip calls that are similar to those of the two wood-pewees; the Lesser Antillean Pewee may be an exception, though few recordings of that species are available through the Macaulay Library (www.macaulaylibrary.org; ML) or https://xeno-canto.org. In several species, however, additional pip-like calls make it difficult to tell whether the chip is homologous in the group. The Cuban, Hispaniolan, and Tumbes Pewees make pip or peep calls that are longer, less sharply overslurred, more often repeated, and span a narrower range of frequencies than the wood-pewee-like chip calls those species also produce (www.macaulaylibrary.org, https://xeno-canto.org). Moreover, the chip calls of the Southern Tropical, Blackish, and White-throated Pewees are their most commonly recorded vocalizations and are often produced in consecutive series, suggesting that for these three this call may serve a function different from its function in the other seven species; those calls may not be homologous with the other species' chip calls.

METHODS

I observed and recorded the chip calls of four Western Wood-Pewees, one each in in Jefferson County, Oregon; Teton County, Wyoming; and Yolo and San Diego counties, California. In all four cases, I noted songs or song-like calls that were distinctive for the Western Wood-Pewee (Kaufman 1990), confirming their identity. In species like these in which vocalizations are innate, the sounds produced by hybrids are intermediate (Ivanitsky and Marova 2025, ML515859, ML390547891, ML69019781, ML447157451). To add to these four recordings, I surveyed for chip calls of the Western Wood-Pewee in 1029 recordings from Arizona, California, Colorado, Montana, Nevada, New Mexico, and Washington, publicly available in the Macaulay Library. I also searched the Macaulay Library for recordings of the chip calls of eight other species sharing the wood-pewees' most recent common ancestor (wood-pewee clade). For these additional species, I searched Xeno-canto for additional recordings because of the limited number available in the Macaulay Library. No chip calls of the Lesser Antillean Pewee are available, and the only two recordings of the Tumbes Pewee were of a quality insufficient for my analyses. I omitted the White-throated Pewee from further analyses because of the small number of recordings available relative to those of the Southern Tropical and Blackish Pewees, which are all equally related to the

Western Wood-Pewee. I then used Audacity (https://www.audacityteam.org; version 3.7.5) to convert all the files to a bit rate of 705 kilobytes per second, a sample rate of 44.1 kiloHertz (kHz), and 16-bit sample size. I trimmed the recordings down to a duration of 200 milliseconds roughly centered around the first available chip note in the recording that lacked conspicuous background noises. Next, I used RavenPro (https://www.ravensoundsoftware.com; version 1.6.5) to generate and compare spectrograms of the chip calls (Figure 1) and used RavenPro's batch-correlation tool to quantify the correlations of these chip notes between each pair of closely related species, with the options toggled for normalized spectrograms, linear power correlations, and a band-pass filter from 1.8 to 7 kHz. From each call, I also recorded three audiospectrographic measurements that often capture much of the inter-specific variation in bird calls and are minimally sensitive to differences in background noise: aggregate entropy, 90% frequency bandwidth, and frequency of peak amplitude ("peak frequency" in RavenPro). Following that, I conducted Mann–Whitney *U* tests on the aggregated cross correlations for each pair-wise species comparison of interest and between the audiospectrographic measurements for the wood-pewees and each of their related species in R (https://www.r-project.org/; version 4.3.2), using the function *wilcox.test*. I then represented the significant and nonsignificant differences in mean correlation in box plots (Figure 2).

The following recordings of chip calls were used in comparative analyses (ML, Macaulay Library; XC, Xeno-canto). Western Wood-Pewee: ML640846451, ML600922241, ML600422361, ML622267197, ML346031491, ML390237321. ML620765069, ML636858270, ML639778409, ML639814460, ML636489759, ML619966847, ML619633597, ML469855831, ML458352941, ML456312031, ML360736141, ML265013111, ML21402, ML21109, ML472510101, ML349632941, ML457823671, ML623759564, ML309699781, ML359998711, ML354739241, ML454827841, ML458550851, ML239223281, ML606732341, ML639533290, ML256400241, ML366064491, ML50560, ML197288641, ML348652251. Eastern Wood-Pewee: ML366457861, ML394566931, ML62976291, ML619703508, ML67071411, ML68384641, ML192209, ML29905581, ML394567911, ML624352875, ML622872757, ML115971841, ML261016981, ML67377981, ML622769897, ML623071005, ML625863696, ML485920341, ML479932111, ML371151811, ML38410. Cuban Pewee: ML613950894l, ML560032641, ML297467271, ML133256, ML287811351, ML33096820, XC48493. Hispaniolan Pewee: ML163114141, ML163112571, ML162708851, ML139297, XC97171. Southern Tropical Pewee: ML112726, ML250081051, ML224781211, ML243045961, ML456221351. ML636164983, XC11419, XC81522, XC221522, XC488983, XC729036, XC791414, XC996083. Northern Tropical Pewee: ML7356, ML459673331, ML300611501, ML83880151. Blackish Pewee: XC120599, XC120600, XC122878, XC208352, XC221531, XC221533, XC221537, XC249563, XC323872.

RESULTS

The Western Wood-Pewee may give the chip call infrequently, as appears to be the case in the Eastern Wood-Pewee, Cuban Pewee, Hispaniolan Pe-

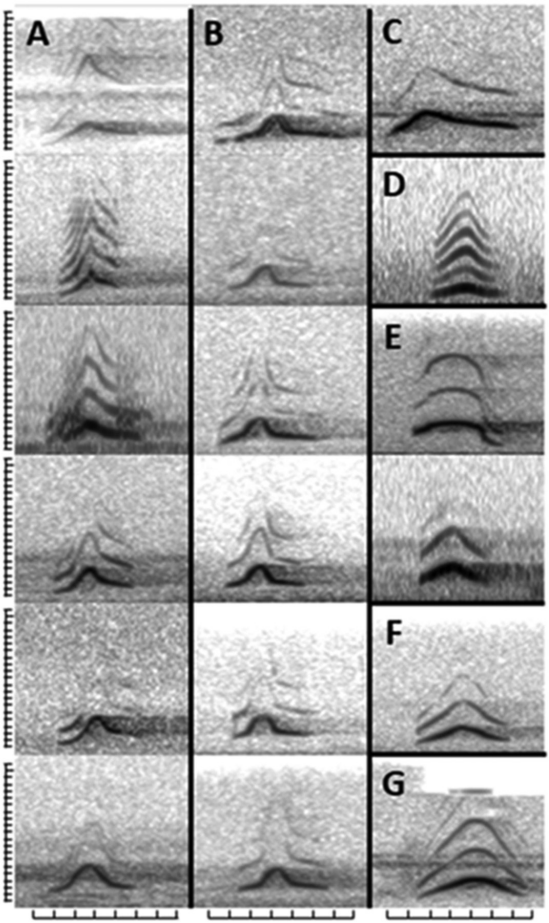

FIGURE 1. Western Wood-Pewee chip calls are more stereotyped than those of the Eastern Wood-Pewee, but the two overlap broadly. Eastern and Western chip calls are also more similar to each other than to more closely related species. (A) Six Eastern Wood-Pewee chip calls shown top to bottom; (B) six Western Wood-Pewee chip calls shown top to bottom; (C) Cuban Pewee chip, closely resembling all 8 available recordings; (D) Hispaniolan Pewee chip, closely resembling all 5 available recordings; (E) two Northern Tropical Pewee chips, the one below resembling most recordings; (F) Southern Topical Pewee, closely resembling most recordings; (G) Blackish Pewee, closely resembling most recordings.

wee, Tumbes Pewee, and Northern Tropical Pewee. In the Western, the call has been recorded rarely. Of the 1029 recordings I checked, only 19 had a separately delivered chip call that was not appended to the beginning of a *dzree* call or an interaction call (see Pieplow 2019). I heard these chip calls only infrequently during my field work in Western Wood-Pewee habitat,

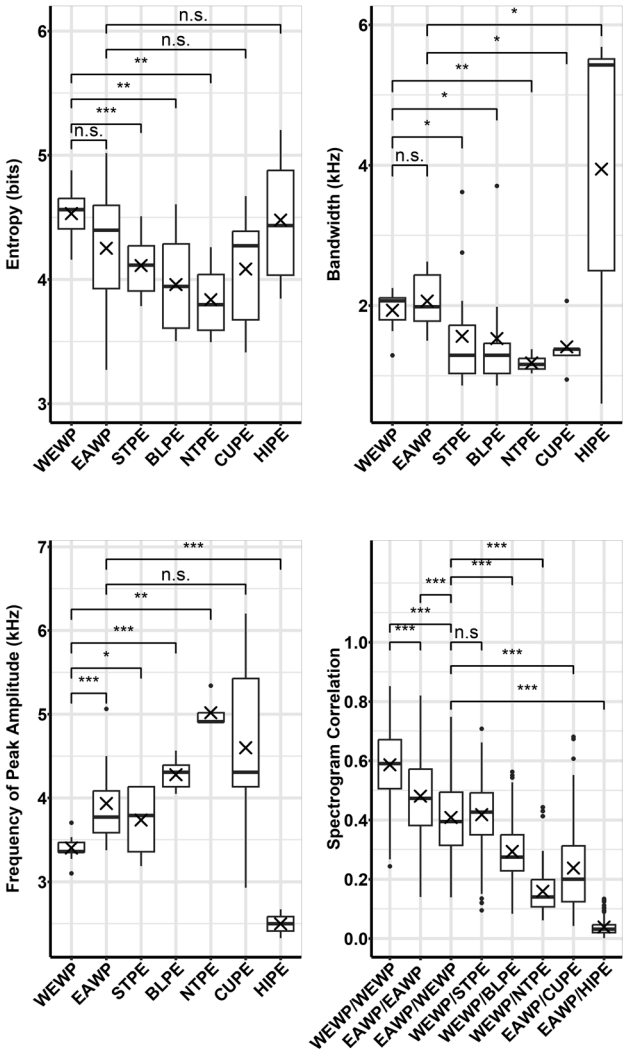

FIGURE 2. Western Wood-Pewee calls vary less intraspecifically than do Eastern Wood-Pewee calls, but individuals of both species resemble each other more on average than they resemble other species. Top left: Differences between species in entropy ("noisiness") of chip calls according to the aggregate entropy specified by RavenPro. Top right: Differences between species in bandwidth of chip calls as defined by 90% of the call's energy. Bottom left: Differences between species in peak frequency (frequency of the loudest part of the call) of chip calls. Bottom right: Correlations between the spectrograms of each pair of species being compared. Above the bars bracketing each pair of species is the level of significance of the difference according to a Mann–Whitney *U* test: three asterisks, $p < 0.0001$; two asterisks, $p < 0.001$; one asterisk, $p < 0.05$; n.s., $p > 0.05$. Sample sizes: Western Wood-Pewee (WEWP) 23; Eastern Wood-Pewee (EAWP), 18; Southern Tropical Pewee (STPE) 13; Blackish Pewee (BLPE), 9; Northern Tropical Pewee (NTPE), 4; Cuban Pewee (CUPE), 5; Hispaniolan Pewee (HIPE), 4.

noting them on only 4 of 22 occasions on which I observed the species in 2025 (recordings archived as ML637843433, ML637844077, ML640186014, ML640869555, ML637316631). However, the chip call might seem less common than the other calls only because it is much quieter than the song and songlike *dzree* calls. On all four occasions when I heard Western Wood-Pewee chip calls, they were produced by foraging birds when they landed back at a perch after sallying out for a flying insect. All four were near other Western Wood-Pewees, and one of them also produced the chip calls between aggressive interactions (during which it also produced interaction and *hee* calls) with another individual.

The chip calls of the Eastern and Western Wood-Pewees often show slight spectrographic differences, which result in a significantly higher average correlation among the calls of each species than between the calls of the two species (Figure 2). However, there is still extensive overlap, and many calls cannot be assigned to either species. Western Wood-Pewee chip calls are more stereotyped, while those of the Eastern Wood-Pewee are more variable. Eastern Wood-Pewees often produce calls that are apparently identical to Western Wood-Pewee calls, as well as additional variants that are apparently absent in the Western Wood-Pewee (Figure 1). These variants constitute at least 5 of the 19 recordings analyzed (some are intermediate) and result in significantly lower cross correlation among Eastern Wood-Pewee chip calls relative to Western Wood-Pewee and greater variance in all three acoustic characters measured (Figure 2). These Eastern-specific variants often include a sharper frequency peak creating a more angled inverted "V" profile on the spectrogram with the highest amplitudes of the call at the frequency peak in the center (Figure 1). In contrast, all Western Wood-Pewee chips and 14 of 19 Eastern Wood-Pewee chips analyzed show a peak in amplitude during the downslur in the second half of the call and a more gradual or rounded peak in frequency with a drop in amplitude at the peak relative to the upslur and downslur components (Figure 1). The Cuban Pewee appeared to have variants similar to the Eastern Wood-Pewee's, though the small sample size made it impossible to judge how common the different variants may be.

The Eastern and Western Wood-Pewees' chip calls are more similar to each other than to each of their closer relatives. Potentially homologous chip or pip calls are produced by at least 9 of the 10 species in the Wood-Pewee clade. The mean correlations of spectrograms of the Eastern Wood-Pewee with its sister species are significantly lower than with the Western Wood-Pewee (Figure 2). The Western Wood-Pewee's sister species is the Northern Tropical Pewee, and their spectrograms are significantly less correlated than those of the Eastern and Western Wood-Pewees (Figure 2). The spectrograms of the South American species that are more closely related to the Western Wood-Pewee are also less correlated with the Western's than the Eastern's are with the Western's, except that correlations between the Western Wood-Pewee and Southern Tropical Pewee are not significantly different from those between the Eastern and Western Wood-Pewees. The measurements of bandwidth, entropy, and frequency of peak amplitude mostly corroborated the cross-correlation findings: the Eastern and Western Wood-Pewees were more similar to each other than to most or all of their closer relatives despite some nonsignificant differences between the Eastern and its sister taxa (Cuban and Hispaniolan

Pewees), which could have been due to the very low sizes of samples of the sister taxa. The low variation in all three acoustic characters for the Western Wood-Pewee likely reflects the highly stereotyped nature of its chip calls (as shown in Figure 1) rather than simply being a product of the larger sample size.

DISCUSSION

The close similarity between Eastern and Western Wood-Pewee chip calls relative to their closer relatives is a somewhat unexpected finding, given that they are not sister species and calls tend to become different over time since divergence (Irwin et al. 2008). A homologous origin would require three independent changes (four if the unshared variants of the Eastern are considered) away from the inferred primitive call structure, while convergence would require only one or two independent changes toward the shared call, depending on whether one or both species converged toward the other. Any behavioral (e.g., shared alarm or aggression functions) or environmental (e.g., acoustic adaptation) factors that could have favored similarity, because of either homology or convergence, would most likely have been in their largely shared nonbreeding ranges. Under the acoustic adaptation hypothesis, similarity in nonbreeding calls can enhance the birds' fitness, as shared structural attributes of the habitat select for similar qualities of the vocalization, especially frequency of peak amplitude and bandwidth (McCracken and Sheldon 1997, Hardt and Benedict 2021). Similar nonbreeding calls can sometimes confer advantages in alarm calling, resulting in convergence (Ficken and Popp 1996). Past hybridization is a third possible hypothesis for this similarity, since there is substantial hybridization in the small current contact zone (Manthey and Robbins 2016), which could have been more extensive in the past. Careful observations of the chip calls of these two species throughout their annual cycles could help distinguish between these hypotheses in the future.

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