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# Differences in the male mating calls of co-occurring epauletted fruit bat species (Chiroptera, Pteropodidae, *Epomophorus wahlbergi* and *Epomophorus crypturus*) in Kruger National Park, South Africa

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## Abstract

**Background:** Almost nothing is known about the mating ecology and behavior of epauletted fruit bats (*Epomophorus* spp) of which eight species occur worldwide. Two species of epauletted fruits bats (*Epomophorus wahlbergi* and *Epomophorus crypturus*) overlap in their distributional ranges in Kruger National Park (KNP), South Africa. Morphologically, these two species are nearly identical to the human eye and field recognition is based upon the number and position of palatal rugae of captured individuals. In addition, the males of both species perform mating rituals during overlapping breeding seasons that appear quite similar and involve wing flapping and monotone vocalizations from calling stations in proximity to fruiting sycamore fig trees where females congregate to feed. The overlap in breeding seasons as well as physical and behavioral characteristics between these two species brings into question how species recognition occurs, and no research is available to understand how males are identified by the females of each species for mating purposes. We recorded vocalizations from calling males in local areas of KNP known to support both species and compared the sonograms to determine if the call structure of mating vocalizations between males of each species differs.

**Results:** We recorded 25 mating vocalizations from seven male epauletted fruit bats near the Shingwedzi Research Camp and 31 mating vocalizations from nine individuals along the Sabie River near Skukuza. Analysis of calls showed significant distinctiveness of male mating vocalizations between the two species in terms of mean fundamental frequency, mean high frequency, mean low frequency, mean bandwidth, and mean call slope at the two sites.

**Conclusions:** We hypothesize that differences in male mating vocalizations recorded at each of our study sites represent call structure differences that potentially may be used to avoid cross-mating between species.

**Keywords:** Epauletted fruit bats; Mating calls; Mating behavior; Kruger National Park; South Africa

## Background

Two species of epauletted fruit bats (*Epomophorus crypturus* and *Epomophorus wahlbergi*) co-occur in Kruger National Park (KNP), South Africa. Although the range of *E. wahlbergi* is quite extensive throughout Sub-Saharan Africa, *E. crypturus* is near-endemic to South Africa, occurring only marginally outside of South Africa in the

extreme south of Tanzania (Monadjem et al. 2010). Morphologically, the species are very similar to each other and are only told apart after capture by opening the oral cavity and counting the number of palatal ridges that reside behind the last upper molar (see 'Methods' section below); however, an analysis of museum specimens also revealed that maxillary width of the skull is significantly wider in *E. crypturus* than in *E. wahlbergi* (Taylor and Monadjem

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2008). Both species show sexual dimorphism with males being larger in body size than females (Bergmans 1988), and during the mating season, males of both species call from tree perches at night to attract females for mating (McCracken and Wilkinson 2000). Both *E. crypturus* and *E. wahlbergi* have a mating system in which year-round multi-male/multi-female groups copulate away from the roost (Wickler and Seibt 1976; McCracken and Wilkinson 2000). Although *E. wahlbergi* has a bimodal breeding season (December and May) in the southern part of its range (Monadjem and Reside 2012), the breeding cycle of *E. crypturus* has not been thoroughly documented.

The mating call of male *E. wahlbergi* is described as a loud, audible, repetitive, monotone call (Wickler and Seibt 1976; Acharya 1992; Fenton et al. 1985) and appears to serve two functions: a) to attract females and b) to space out male conspecifics calling in the same area (Kingdon 1974; Wickler and Seibt 1976; Adams and Snode 2013). Although the mating call of *E. wahlbergi* has been described, herein, we provide the first quantification of the male mating call of *E. crypturus*.

The detailed distribution of either species of epauletted fruit bat in Kruger National Park (KNP) is poorly known. Monadjem et al. (2010) reports no records for *E. crypturus* from the southern areas of KNP, but Bonaccorso et al. (2014) captured both species in southern and northern KNP between 2004 and 2007, but showed skewed population numbers with *E. crypturus* in higher abundance in the north and *E. wahlbergi* in higher abundance in the south. Fenton et al. (1985) captured and radio-tagged 10 male and 10 female *E. wahlbergi* near Pafuri, about 30 km north of Shingwedzi, where our study took place, thus showing that concentrations of this species can and do occur in the northern KNP. It also seems apparent that, although these species do occur in sympatry on a regional scale, one or the other appears to dominate at the local scale (Monadjem et al. 2010).

Seasonal movement patterns of either species are not well documented. However, a study on *E. wahlbergi* in the urbanized environment of Pietermaritzburg campus, University of KwaZulu-Natal, South Africa, showed that males and females had larger home ranges in winter compared to spring and that males on average were relatively sedentary throughout the year (having relatively small home ranges). Females, on average, made longer flights and had much larger home ranges (Rollinson et al. 2013). Our observations that both species mate within the same timeframe and that males of both species set up calling perches in proximity to fruiting fig trees in KNP resulted in us proposing the hypothesis that the males of each epauletted fruit bat species should show differences in mating calls to avoid cross-mating with the other species even though, to the human ear, little to no discernible differences are evident.

## Methods

### Study area

Our study sites were located in proximity to Skukuza in southern KNP and near Shingwedzi in Northern KNP (Figure 1). The habitat near Skukuza is diverse and includes mixed woodland with thorn thickets and Marula woodlands, whereas Shingwedzi is dominated by stunted Mopane woodlands and open savanna. There are riverine corridors near both Skukuza and Shingwedzi that are rich with sycamore fig trees (*Ficus sycomorus*) that fruit asynchronously and provide a major food supply for many vertebrate species in KNP, including epauletted fruit bats (Grant et al. 2001).

### Catching and identifying bats

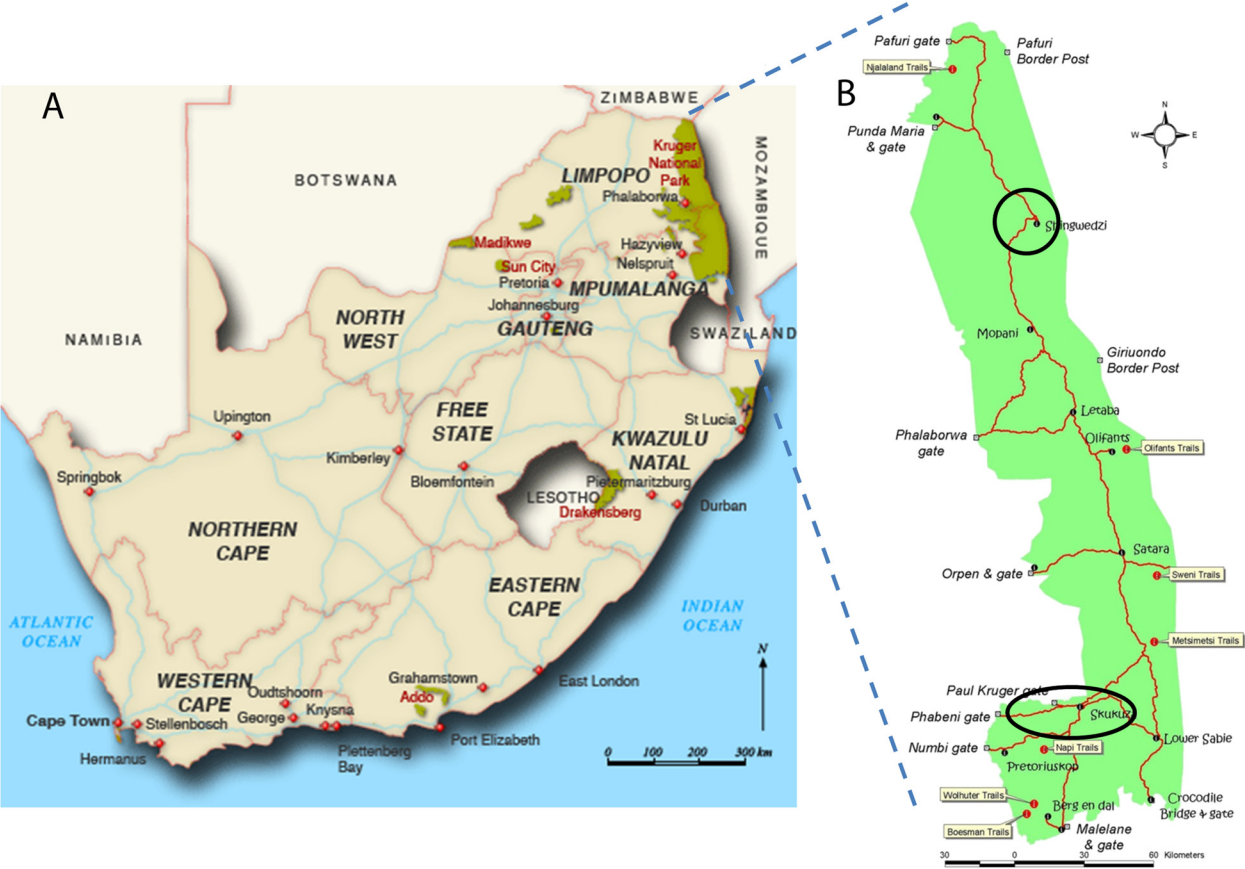
We used mist nets raised into the canopy of ripe fig trees (*F. sycomorus*) to capture epauletted fruit bats in May and June of 2007, 2008, and 2009. In two cases, we captured epauletted fruit bats while mist netting over water sources for insectivorous bats. We identified species using the position of palatal ridges in relation to the last cheek tooth in the upper tooth row (Figure 2) (Fenton et al. 1985). All individuals were released immediately after identifying to species, taking measurements of body mass and forearm length, and noting reproductive condition.

### Recording mating calls of male epauletted bats

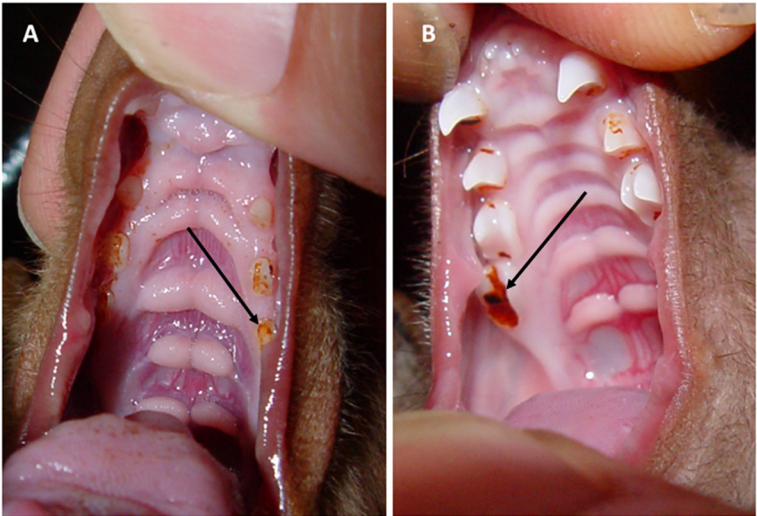
We recorded the male mating calls of epauletted bats in areas where our trapping indicated only one of each of the species was locally present. We used a Pettersson D240x bat detector (Pettersson Elektronik, Uppsala, Sweden) set to a 3.5-s recording time and attached to a digital recorder (Samson H2 Zoom, Samson Technologies, Hauppauge, New York, USA) to capture male calls in the vicinity of Shingwedzi in northern KNP and in the vicinity of Skukuza in southern KNP. We drove roads throughout each area at night and when we heard a male bat calling we approached in our vehicle slowly to a position that allowed clear recordings of the calls to be taken but far enough away to not cause that individual to move from its calling perch. All recordings in each area happened on the same night, and because we could hear any given male calling from its perch as we left the recording position, we are confident that we did not record the same male more than once.

### Data analysis and statistics

We analyzed call structure of male mating vocalizations using SonoBat 3.1 (Arcata, Oregon, USA) analysis software to determine the fundamental frequencies (first harmonic), high/low frequencies, bandwidths, and slope (downward or upward change in frequency from the initiation of the vocalization to the end of the vocalization) of each call. We compared means of call parameters of



**Figure 1** Map of survey areas. (A) South Africa showing the location of Kruger National Park and (B) Kruger National Park showing study areas where epauletted fruit bats were captured and sonar calls were recorded near Shingwedzi in the north and Skukuza in the south.



**Figure 2** Photographs showing palatal ridges. (A) *E. crypturus* having two post-dental palatal ridges and (B) *E. wahlbergi* having one post-dental palatal ridge behind the last molar in the tooth row indicated by arrows.

individuals recorded in the Skukuza area versus those recorded in the Shingwedzi area using a two-sample *T*-test (NCSS Statistical Software, Kaysville, Utah, USA) with the null hypothesis that there are no significant differences between mating calls gathered in each area. All *P* values were adjusted using the Bonferroni correction for multiple comparisons.

## Results

### Capture data

All individuals captured in and around the Skukuza tourist camp during the dry season in May and June in 2007 ( $N=5$ ), 2008 ( $N=9$ ), 2009 ( $N=3$ ), and during the wet season (December) in 2011 ( $N=1$ ) (total captures = 18) were identified as *E. wahlbergi*. All captures in the area of the Shingwedzi tourist camp were during the dry season in May and June in 2007 ( $N=8$ ), 2008 ( $N=5$ ), and 2009 ( $N=2$ ) (total captures = 15) and were identified as *E. crypturus*.

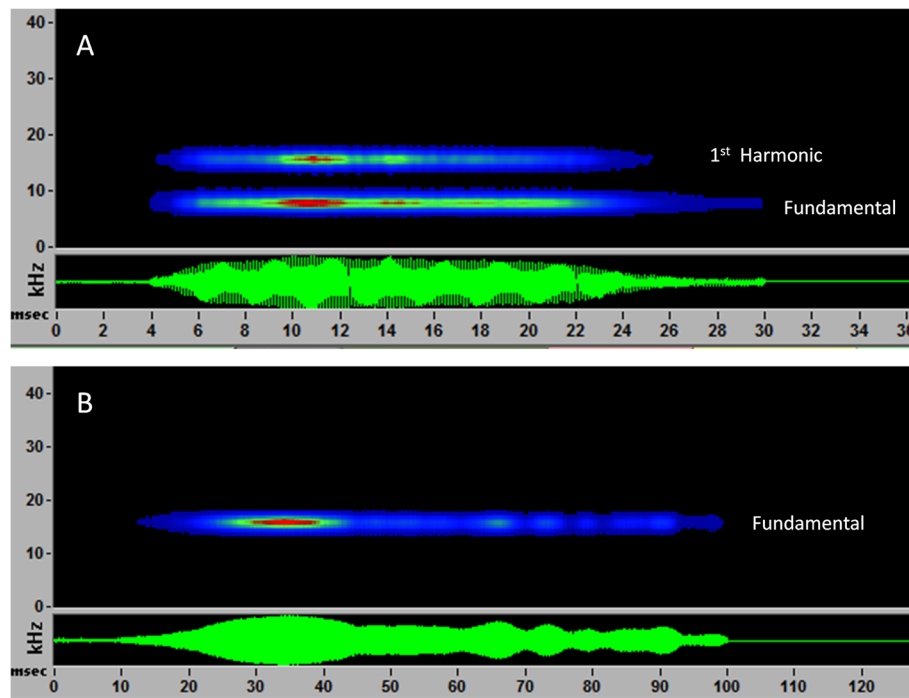
### Male mating calls

We recorded 25 mating vocalizations from seven male epauletted fruit bats (two to three calls per individual) near the Shingwedzi Research Camp on 22 June 2008 and 31 mating vocalizations from nine individuals (one to three calls per individual) along the Sabie River near Skukuza on 20 June 2009. If multiple calls were recorded from the same individual, we calculated mean values for

each call parameter for statistical analyses. Sonograms depicted by SonoBat of male mating calls recorded near Skukuza (Figure 3A) showed distinctive attributes from those recorded near Shingwedzi (Figure 3B). All calls recorded near Skukuza (Figure 4,  $N=31$ ) showed a mean fundamental frequency at 7.88 kHz (first harmonic, standard deviation = 0.11 kHz) followed by a second harmonic having a mean frequency of 15.71 kHz (SD = 0.23 kHz), whereas all male mating calls recorded near Shingwedzi (Figure 4,  $N=25$ ) showed a mean fundamental frequency of 15.71 kHz (SD = 0.07 kHz), and in only one case were multiple harmonics recorded and these were at 16, 48, 64, 96, and 112 kHz. The number of harmonics recorded from a vocalization is likely a product of the distance between our microphone and the individual vocalizing and also the level of power (dB) in the vocalization emitted by the bat itself. There were significant differences between the male calls from each area in fundamental frequency ( $t=2.04$ ,  $df=54$ ,  $P=0.0005$ ), high frequency ( $t=2.00$ ,  $df=54$ ,  $P=0.0005$ ), low frequency ( $t=2.04$ ,  $df=54$ ,  $P=0.0005$ ), bandwidth ( $t=2.00$ ,  $df=54$ ,  $P=0.0005$ ), and total slope ( $t=2.05$ ,  $df=54$ ,  $P=0.0005$ ) (Figure 4, Table 1).

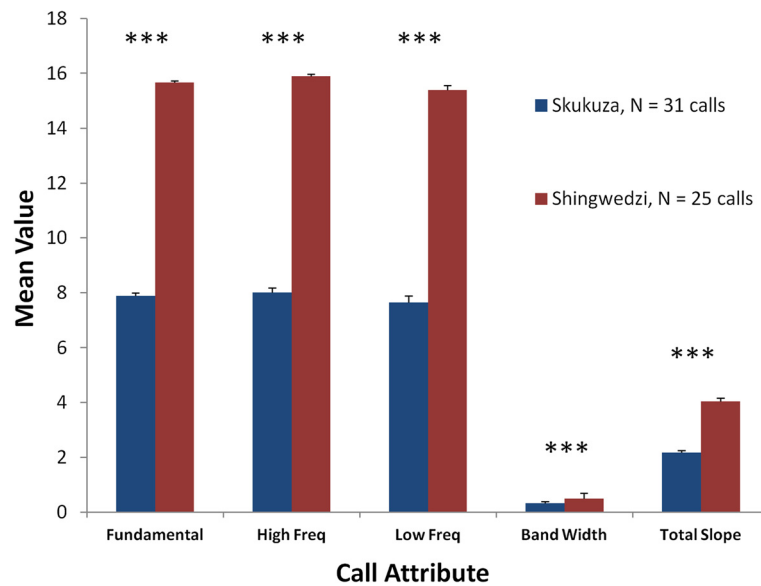
## Discussion

Analysis of mating calls of males recorded near Skukuza versus those calls gathered near Shingwedzi (separated



**Figure 3** Sonograms of male vocalizations. (A) Near Skukuza in southern KNP and (B) near Shingwedzi in northern KNP. X-axes are time in milliseconds, Y-axes are frequencies displayed in kilohertz.





**Figure 4** Comparative plot of mean values of five call attributes. Calls recorded near Skukuza (blue bars) versus calls recorded near Shingwedzi (red bars). Fundamental refers to the first harmonic where the highest energy occurred. Two-sample *T*-test determined that all four attributes differed significantly between sites after Bonferroni correction for multiple comparisons. \*\*\* $P = 0.0005$ .

by approximately 270 km) showed significant differences in basic call structure and thus supported our hypothesis. We found that the call structure of males around specific fruiting sycamore fig trees were consistent with single-species presence for males at a very localized scale. However, there is also range overlap between the species, and because the male mating calls travel at least 0.5 km from the calling perch near where females are feeding on figs (Wickler and Seibt 1976, personal observations), there is potential for females of each species in the area to approach calling males of the other species if there is not a discernible difference in call structure.

From our data, we conclude that the male mating calls we recorded from each area depicted *E. wahlbergi* from Skukuza and *E. crypturus* from Shingwedzi. As mentioned, the mating call of male epauletted bats appears to serve both the function of attracting females to their perch because male call rates increase as females

approach, but secondly, male calls appear to act as a deterrent to other conspecific males attempting to call from perches too close to other calling males (Wickler and Seibt 1976; Adams and Snode 2013). Although one could argue that because we could not definitively identify individuals to species from which calls were recorded, we could not make this determination. However, several factors help in corroborating our interpretation of results: a) there are unequivocal distinctions in the type of male mating calls recorded in different areas of KNP; b) the calls are consistently different in the two regions of KNP, with exceedingly small degrees of variation in each of the call parameters; c) our capture data, as well as data from other researchers (Bonaccorso et al. 2014), indicate that *E. wahlbergi* dominates the area around Skukuza, whereas *E. crypturus* dominates the area near Shingwedzi; d) capture data from other studies in KNP (Fenton et al. 1985), and other areas in Africa, show spatial separation between epauletted fruit bat species on both local (Wickler and Seibt 1976) and, in some cases, regional scales (Kingdon 1974); and e) there are no records of mixed-species feeding groups of epauletted fruit bats at the same fig trees, and radio-telemetry data indicate that female *E. wahlbergi* from a particular colony moved to the same feeding area of ripe fig trees nightly (Fenton et al. 1985).

An alternative hypothesis to ours would be that males of either *E. wahlbergi* or *E. crypturus* alter their call structure in different areas of KNP, and thus, we were recording the same species in both areas using calls that

**Table 1** Means and standard deviations (SD) among five call attributes by site

	Mean attributes		Mean attributes	
	Skukuza	SD	Shingwedzi	SD
Fundamental	7.88	0.11	15.66	0.07
High frequency	8	0.18	15.89	0.074
Low frequency	7.66	0.22	15.38	0.18
Bandwidth	0.33	0.071	0.5	0.2
Total slope	0.002	0.0008	0.004	0.0012

were geographically distinctive within species. Although we could not refute this hypothesis with our study, from a theoretical perspective, this seems unlikely, and we can think of no benefits of such mating behavior. In addition, the extreme lack of variation in call structure in the variables measured for this study suggests the possibility of stabilizing selection via mate choice that would not likely promote such strong regional differences in intraspecific mating calls. In fact, just the opposite would be expected (Ptacek 2000).

It should be noted that the call structure of male *E. wahlbergi* we recorded in KNP was substantially different from those recorded by Wickler and Seibt (1976) in Kenya. Our recordings contained only a fundamental and single second harmonic, whereas they found a fundamental with three harmonics (however, this could simply be the distance away from a perch where recording was taken). In addition, the fundamental frequency reported by Wickler and Seibt (1976) equated to 1.7 kHz, whereas our recordings show the fundamental at a much higher frequency of about 7 kHz. Although there are no published descriptions of *E. crypturus* calls available for comparison, it is also curious to note that *E. crypturus* calls in KNP correspond in frequency to the second harmonic of *E. wahlbergi* calls. Tonal differences in the calls of each species may be the product of differences in the slope of the calls. Although both species produce relatively flat calls, the total slope of the calls emitted in the Shingwedzi area was twice that of the calls we recorded in the Skukuza area on average. Alterations in call structure attributes presented herein represent a relatively simple measure by which males of co-occurring species of epauletted bats may use harmonic displacement to avoid call overlap with another similar species. The question of if species-specific differences in mating calls are learned or have inherent genetic components remains unanswered. However, our study raises the possibility that differences in mating calls between species of male epauletted fruit bats may serve to avoid hybridization between the two species of epauletted fruit bats.

## Conclusions

There are two species of epauletted fruit bats (*E. wahlbergi* and *E. crypturus*) that co-occur in Kruger National Park, South Africa. Males of each species position themselves at perches near feeding trees where females congregate, and males use mating vocalizations, as well as wing flapping, to attract females to their perch to mate. The two species have similar mating calls to the naked ear, but through structural analysis of call structure in two areas separated by 270 km, we provide evidence that the males of each species have distinctive calls. We hypothesize that the differences in the structure of calls from each area produce distinctions that are important to the mating success of each species.

## Competing interests

The authors declare that they have no competing interests.

## Authors' contribution

RAA designed the study, carried out part of the data collection, and statistically analyzed and interpreted the data. ERS carried out part of the data collection and edited the manuscript. Both authors have read and approved the final manuscript.

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