Novel odorous crust on the forearm of reproductive male fringe-lipped bats (*Trachops cirrhosus*)

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Olfactory cues are especially important for nocturnal mammals such as bats and can communicate an individual's condition and facilitate mate choice. Here, we introduce a novel odorous substance found on the forearm of reproductive male fringe-lipped bats (*Trachops cirrhosus*), which we term "forearm crust." We continuously captured bats over a 3-year period to determine the prevalence and possible seasonal distribution of this forearm crust. We evaluated males to elucidate whether forearm crust was associated with specific morphological characteristics. Males with forearm crust were captured throughout the year, but we found an increase in captures of males with a forearm crust from September to December, prior to peak female pregnancy in March. All males with a forearm crust had enlarged chest glands and testes. Males with a forearm crust had significantly higher body condition indices than males without a forearm crust. We observed males in their natural roosts and in captivity, and describe a novel stereotyped behavior in which males scratch the body dorsally and ventrally, insert a claw into their mouth, and then lick their forearm repeatedly. Males with a forearm crust licked their forearm significantly more than males without a forearm crust. Together, these data suggest that this novel odorous forearm crust is a male reproductive trait. Further investigation is needed to understand its role in reproduction.

Las señales olfativas son especialmente importantes para los mamíferos nocturnos, como los murciélagos, dado que pueden comunicar la condición de un individuo y facilitar la selección de pareja. Este estudio presenta una nueva sustancia olorosa ubicada en el antebrazo de los machos reproductivos del murciélago de labios verrugosos (*Trachops cirrhosus*), que denominamos "costra del antebrazo." Capturamos murciélagos durante un período de 3 años para determinar la prevalencia y posible distribución estacional de la costra. También evaluamos a los machos para determinar si la costra se asocia a características morfológicas. Los machos con costra se capturaron durante todo el año, pero se encontraron un mayor número de machos con costra desde septiembre hasta diciembre, antes de la captura de hembras preñadas en marzo. Todos los machos con costra tuvieron la glándula de pecho y los testículos agrandados. Los machos con costra mostraron un índice de condición corporal significativamente mayor que los machos sin costra. Además, observamos machos en sus refugios naturales y en cautiverio y hemos descrito un nuevo comportamiento en donde los machos se rascan todo el cuerpo con una garra, luego colocan la garra en la boca y después lamen un antebrazo repetidamente. Los machos con costra lamieron su antebrazo significativamente más que los machos sin costra. Nuestros datos sugieren que la costra del antebrazo está relacionada a la reproducción o apareamiento de esta especie. Proponemos más investigaciones como ésta para comprender el rol de la costra en la reproducción de *T. cirrhosus*.

Key words: behavior, chemical communication, fringe-lipped bat, odor, Phyllostomidae, sexual selection, *Trachops cirrhosus*

In small mammals, olfactory signals can play a role similar to visually conspicuous, sexually selected traits in larger species, such as body size, weapons, or ornaments (Blaustein 1981). Odorous signals tend to be sexually dimorphic, with males producing a wider repertoire of odors and scent marking more frequently than females (Andersson 1994; Gosling and Roberts 2001). Odors can play important roles in sex recognition (Ferkin and Johnston 1995) and mate attraction (Johnston 1974), and

Fig. 1.—Image of a reproductive male fringe-lipped bat (*Trachops cirrhosus*) with forearm crust circled.

also are effective indicators of an individual's health and condition (Penn and Potts 1998; Zala et al. 2004). For example, female mice (*Mus musculus domesticus*) discriminate between parasitized and nonparasitized males based on the odor of urine and associated odorous secretions (Kavaliers and Colwell 1995). Furthermore, olfactory cues are thought to be a crucial part of mammalian mate choice through the major histocompatibility complex, communicating genetic diversity among individuals (Santos et al. 2016). Given their nocturnal habits and social lifestyles, bats are ideal candidates to study the use and function of secondary sexual odorous traits (Dechmann and Safi 2005).

Many bats produce species-specific odors that result from a combination of glandular secretions, diet, and bacterial fermentation (Quay 1970; Schmidt 1985; Scully et al. 2000). For example, some Neotropical bat species perform complex behaviors to create odorous cocktails. Among the family of leaf-nosed bats (Phyllostomidae), male long-nosed bats (*Leptonycteris curasoae*) combine fluids from the mouth, penis, and anus to produce an odorous "dorsal patch" during the mating season (Muñoz-Romo and Kunz 2009). The dorsal patch is thought to be a sexually selected trait as it is only present in reproductive adult males (Muñoz-Romo and Kunz 2009) and females prefer the odor of males with a dorsal patch more than the odor of males without it (Muñoz-Romo et al. 2011). While male long-nosed bats apply their scent mixture to their fur, male greater sac-winged bats (*Saccopteryx bilineata*) transfer genital and chest gland secretions into specialized wing sacs near their forearms to create odorous cocktails, which they then waft toward females in their territory (Voigt and von Helversen 1999; Voigt et al. 2008).

Our study was prompted by the capture of several wild male fringe-lipped bats (*Trachops cirrhosus*) with a conspicuous substance characterized by a pungent odor on the forearm, which we termed "forearm crust" (Fig. 1). Upon a review of the literature, we found that this forearm crust had never been described. Since we only found the forearm crust in reproductive adult males, we postulated that it played a role in reproduction. To better understand the function of the forearm crust, we investigated the following questions: first, we asked if the forearm crust signals readiness for mating. If so, we expected the forearm crust to coincide with the female reproductive season and to be correlated with the presence of sexually dimorphic structures (e.g., enlarged chest glands; Fig. 2) and other traits involved in reproduction (e.g., enlarged testes). Second, we asked whether the forearm crust reflects male condition. We hypothesized that males would exhibit differences in body condition in relation to forearm crust presence or absence. We predicted that males with a higher body condition index would exhibit a forearm crust. Our third goal was to determine how this forearm crust is produced. Preliminary analyses of 4 adult *T. cirrhosus* specimens (2 females and 2 males) using a scanning electron microscope showed no evidence of a forearm gland. Given this observation, we predicted that, similar to other bat species, males create this odorous cocktail via complex stereotypical behaviors. Finally, we studied museum specimens to determine the seasonal and geographic distribution of the crust.

Materials and Methods

Study species.—Fringe-lipped bats range from southern Mexico to Brazil and Bolivia (Cramer et al. 2001) and are found in lowland forest (< 500 m) where they roost in hollow trees, culverts, buildings, and caves (Kalko et al. 1999). Fringe-lipped bats are

Fig. 2.—Ventral view of adult fringe-lipped bats (*Trachops cirrhosus*). A) Female *T. cirrhosus* with rudimentary chest gland (barely visible). B) Male *T. cirrhosus* with a forearm crust with chest gland enlarged.

considered omnivorous, eating insects, lizards, and frogs (Cramer et al. 2001). The mating system has only been described for ~8% of phyllostomid species (McCracken and Wilkinson 2000) and is not known for *T. cirrhosus*. There is no sexual dimorphism in size (Willig 1983). Females give birth to 1 offspring at a time and the gestation length is unknown (Cramer et al. 2001).

Study site.—We conducted fieldwork in Soberanía National Park (9°07′N, 79°65′W), Panama from 1 February 2014 to 5 May 2017. This tropical lowland forest is characterized by seasonal rainfall (average 2,612 mm annually), with a January to April dry season followed by a May to December rainy season (Windsor 1990). Additionally, we conducted behavioral observations in the field and in captivity at the Smithsonian Tropical Research Institute's (STRI) Gamboa field station.

Bat sampling.—Bats were captured with 6-m-long, 4-shelf, 38-mm-mesh mist nets (Avinet, Dryden, New York) set along trails and streams and at the exit of culverts and other structures where we found *T. cirrhosus* roosting. We recorded age, sex, and reproductive stage, as well as morphological metrics, such as body mass and forearm length. We identified juveniles by the presence of epiphyseal gaps in the phalanges (Brunet-Rossini and Wilkinson 2009). Females were classified as nonreproductive or pregnant. Pregnancy was determined by gentle palpation of the abdomen (Racey 2009). Males were determined to be reproductively active by the scrotal position and enlarged size of the testes (Racey 2009). Length of forearm was measured to the nearest 0.1 mm using a dial caliper (Swiss Precision Instruments, Garden Grove, California). Body mass was recorded using a 100-g scale (Pesola, Schindellegi, Switzerland). We also noted the condition of the chest gland (Fig. 2) and classified the gland as not enlarged (barely visible, not secreting any substance; Fig. 2A), semi-enlarged (visible, and secreting substance), or enlarged (prominently visible and secreting substance; Fig. 2B). We marked each bat with a passive integrated transponder tag (Biomark, Boise, Idaho). We released bats at their capture site. All sampling protocols followed guidelines approved by the American Society of Mammalogists for capture, handling, and care of mammals (Sikes et al. 2016) and were conducted in accordance with the standards of the STRI Institutional Animal Care and Use Committee (IACUC# 2014-1001-2017) and the University of Chicago (IACUC# 72356). All research was licensed and approved by the

government of Panama (SC/A-45-16; SE/A-89-14; SE/A-9-14; SE/A-86-14; SE/A 69-15; SE/AH-2-16).

Forearm crust and male condition.—Because portions of the forearm crust flaked off during capture in the mist nets and subsequent handling, we could not accurately measure the total forearm crust area. We thus scored crust as a binary trait: present or absent. Observation of crust application behavior in captivity (see below) reinforced this classification system. Males with forearm crust frequently reapplied the crust to their forearms; the amount of the forearm covered at any one moment in time varied. We calculated body condition index by dividing body mass (g) by forearm length (mm). This index is commonly used to assess body condition in bats (Reynolds and Korine 2009), and has been validated as the best predictor for the amount of lipid present in big brown bats (*Eptesicus fuscus*—Pearce et al. 2008).

Other bat studies have found a negative relationship between ectoparasite load and bat body condition (the higher the ectoparasite load, the lower the body condition: e.g., Lourenço and Palmeirim 2007). Thus, as another indicator of condition, we quantified ectoparasites on adult males. We categorized an individual bat's ectoparasite load as low (0–5), medium (6–10), or high (10+).

Behavioral observations.—We recorded the behavior of males at their day roosts in the field with a video camera (DCR-SR45; Sony Corp., Tokyo, Japan) supplemented with infrared lights (CMVision-IR100, Houston, Texas). Observations took place in November 2014, July 2015, and September 2015 using an ad libitum sampling protocol (Altmann 1974). Additionally, we recorded the behavior of bats in an outdoor flight cage (5 × 5 × 2.5 m) under ambient temperature and humidity, illuminated by a 25-W red light bulb. We conducted observations from September to February between 2015 and 2017 using a video recorder (DCR-SR45; Sony Corp., Tokyo, Japan) supplemented with infrared lights (CMVision-IR200, Houston, Texas). Each captive bat was observed once between 1700 and 1900 h using an ad libitum sampling protocol (Altmann 1974).

Museum specimens.—We examined dry specimens of *T. cirrhosus* at the American Museum of Natural History (New York, New York), the Field Museum of Natural History (Chicago, Illinois), and the National Museum of Natural History (Washington, D.C.). We investigated whether specimens had a

forearm crust present, whether there was a seasonal distribution of this forearm crust, and whether there was variation in the geographic range of individuals exhibiting this forearm crust.

Statistical analyses.—Data were checked for normality using the Shapiro–Wilk test. We tested for a correlation between the percent of males with a forearm crust and the percent of females pregnant using a Kendall's rank correlation (τ). We analyzed whether males with a forearm crust differed in body condition index from males without a forearm crust using mixed-effect ANOVAs fit in the R packages lme4 and car package (Fox and Weisberg 2011; Bates et al. 2015). We first used a linear mixed model to predict body condition index with forearm crust presence, sampling year, and their interaction as fixed effects. Since we recaptured individuals during different years, we included individual bats as a random effect. Additionally, we analyzed differences in body condition index among the same individuals in different conditions using a paired *t*-test. We evaluated differences in ectoparasite load between males with a forearm crust and without a forearm crust using a chi-square test. Differences in forearm licking behavior between males with and without a forearm crust were analyzed using *t*-tests. We performed all statistical tests in R (R Development Core Team 2013) using $\alpha = 0.05$.

RESULTS

Bat sampling.—We captured a total of 473 bats (2014, $n = 91$; 2015, $n = 126$; 2016, $n = 194$; 2017, $n = 62$). After accounting for recaptures ($n = 237$), 236 individual bats (males, $n = 142$; females, $n = 94$) were examined. We analyzed juveniles ($n = 57$) separately. Over 80% of juveniles were captured in June ($n = 15$), July ($n = 18$), and August ($n = 14$). Pregnant females ($n = 35$) were captured from December to May with the majority (74%) captured in March ($n = 14$) and April ($n = 12$; Fig. 3A). Additionally, we captured 4 females with pups attached to their nipples in May 2014 ($n = 1$), June 2016 ($n = 2$), and May 2017 ($n = 1$).

Forearm crust.—We captured a total of 211 adult male *T. cirrhosus* (2014, $n = 47$; 2015, $n = 47$; 2016, $n = 85$; 2017, $n = 32$). After considering recaptures and missing data on forearm crust presence or absence ($n = 107$), we included the first capture of each individual male ($n = 104$) and 46% of adult males captured had a forearm crust present. All males with a forearm crust present
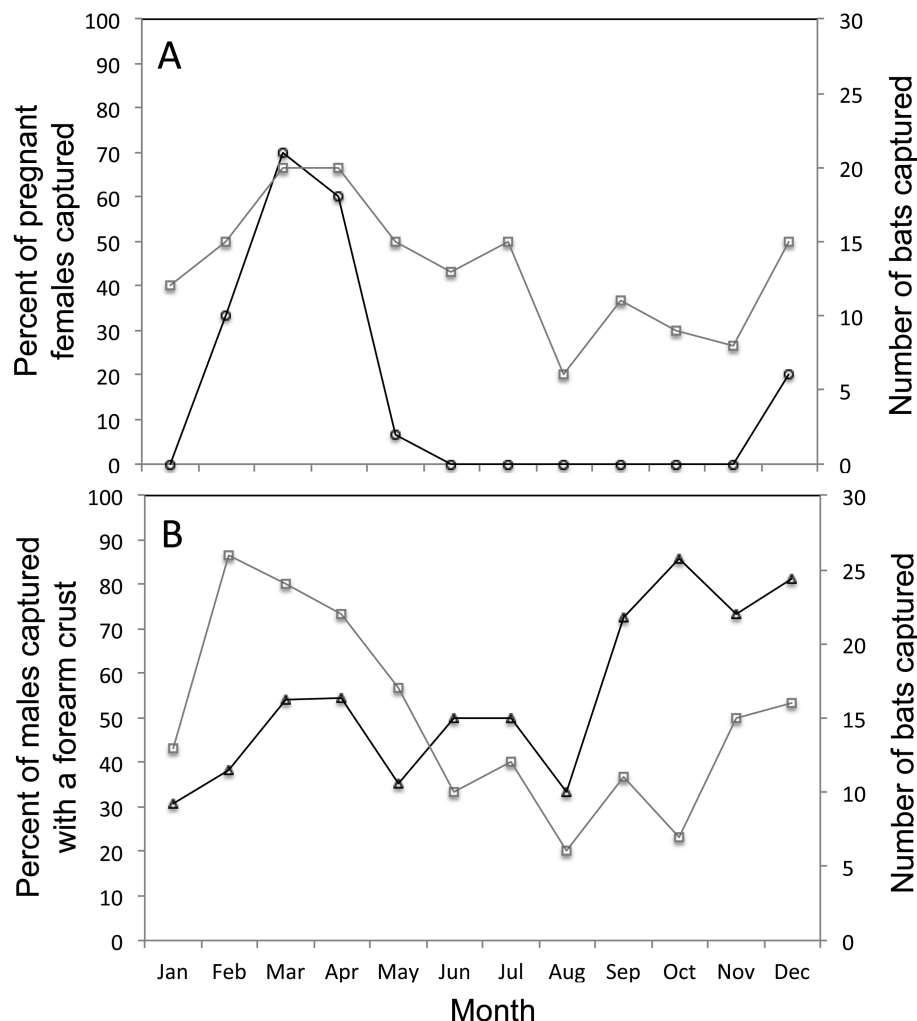

Fig. 3.—Reproductive patterns of fringe-lipped bats (*Trachops cirrhosus*). A) Total number of adult females captured per month (gray line and open square) and percent of pregnant females captured per month (black line and open circle). B) Total number of adult males captured per month (gray line and open square) and percent of males captured with a forearm crust (black line and open triangle).

had enlarged testes. Although some males with an absent forearm crust had enlarged testes, the majority of males without a forearm crust (77%) did not have enlarged testes. None of the juveniles had enlarged testes or a forearm crust. None of the females examined had a forearm crust present. Although forearm crusts were found throughout the year, there was an increase in the percent of bats captured with a crust from September to December (Fig. 3B). The percent of males with a forearm crust was not correlated with the percent of pregnant females ($\tau = 0.05$, $P = 0.82$).

Chest gland.—We classified chest gland status for 160 individuals. Juveniles had either chest glands that were not enlarged ($n = 25$) or semi-enlarged ($n = 6$). Likewise, adult females that were not reproductive had chest glands that were not enlarged ($n = 19$) or semi-enlarged ($n = 10$). All adult females in reproductive condition had chest glands that were not enlarged ($n = 24$) and barely visible (Fig. 2A). The chest glands of adult reproductive females did not produce any secretions. Nonreproductive adult males had chest glands that were enlarged ($n = 10$), semi-enlarged ($n = 6$), and not enlarged glands ($n = 3$). Adult males with enlarged testes had enlarged chest glands, irrespective of forearm crust presence ($n = 48$) (Fig. 2B) or absence ($n = 9$).

Male condition.—After accounting for missing measurements (absence of body mass or forearm length), 104 individual adult male bats were included in our analyses. Bats with a forearm crust had higher body condition indices than bats without a forearm crust ($F_{1,124.8} = 34.12$, $P < 0.0001$; Fig. 4). We recaptured 8 bats with a forearm crust absent in the first capture and then present in the second capture. In 7 of these bats (87.5%), body condition index increased, although not significantly ($t_7 = -1.88$, $P = 0.10$).

We classified ectoparasite load for 78 adult males bats ($n = 46$ with forearm crust, $n = 32$ without forearm crust). The main

ectoparasites found were bat flies (Diptera); however, 4 bats also had ticks. Although most males with a forearm crust had few ectoparasites, the difference in ectoparasite load between males with and without a forearm crust was not significant ($\chi^2_2 = 2.65$, $P = 0.27$; Fig. 5).

Behavioral observations.—We recorded 3 males with a forearm crust in their natural culvert roost for a total of 3.6 h ($\bar{X} = 1.22 \pm 0.8$ h SD). Grooming, which consisted of scratching the head and body with one hind claw, licking the body and the wing membranes, then inserting the claw used to groom into the mouth accounted for between 2% and 32% of total observation time. During grooming, we noted a stereotyped behavioral sequence focused on the forearm, which we termed "forearm licking behavior" (Fig. 6; Supplementary Data SD1). Male bats scratched their body (dorsally and ventrally) with one of the hind claws, inserted this hind claw into the mouth, licked and nibbled the claw, and then licked one of the forearms repeatedly. During this sequence, males also appeared to occasionally scratch the chest gland with the hind claw. While licking the forearm, males continued to scratch the body and insert the claw into their mouth. They also flicked the tongue repeatedly. Each stereotypical forearm licking bout ranged from 21 to 62 s ($\bar{X} = 46 \pm 21.9$ s SD) with 7 to 17 ($\bar{X} = 12 \pm 5$ SD) discrete forearm licks per bout. Forearm licking bouts accounted for ~1% of the time each individual was observed.

In addition to our field observations, we recorded the behavior of 21 adult bats (11 males with a forearm crust, 6 males without a forearm crust, and 4 females) in captivity, which allowed us to compare behaviors across individuals. Eleven bats were observed alone, whereas the remaining observations occurred in groups (from 2 to 5 individuals per group). We observed a total of 33.97 h ($\bar{X} = 1.62 \pm 0.22$ h SD, $n = 21$). All individuals spent a large percentage of time inactive (42–99%). The most prevalent behavior was grooming: females groomed 0–44% of the observation period, whereas males grooming bouts ranged between 4.4% and 53.5% of the observation period.
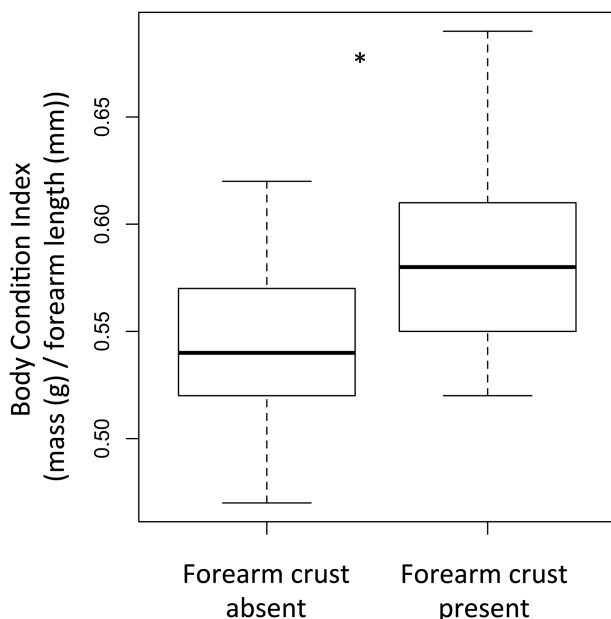

Fig. 4.—Body condition index (body mass (g)/forearm length (mm)) of male fringe-lipped bats (*Trachops cirrhosus*) with and without a forearm crust. Males with a forearm crust present had significantly higher body indices than males with an absent forearm crust.
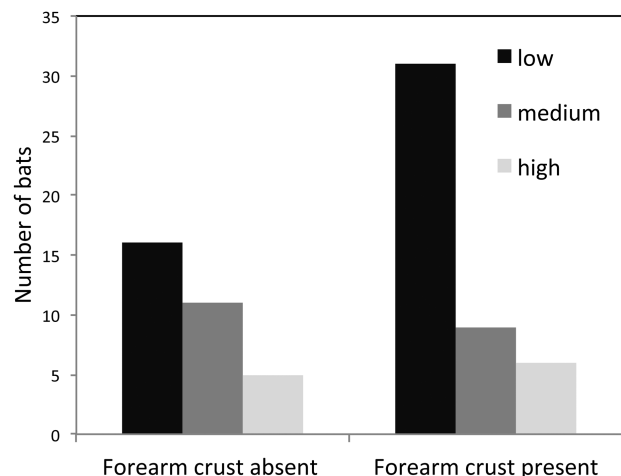

Fig. 5.—Estimated ectoparasite load in adult male fringe-lipped bats (*Trachops cirrhosus*) with and without a forearm crust. Ectoparasite load classified as low (0–5), medium (6–10), or high (10+).
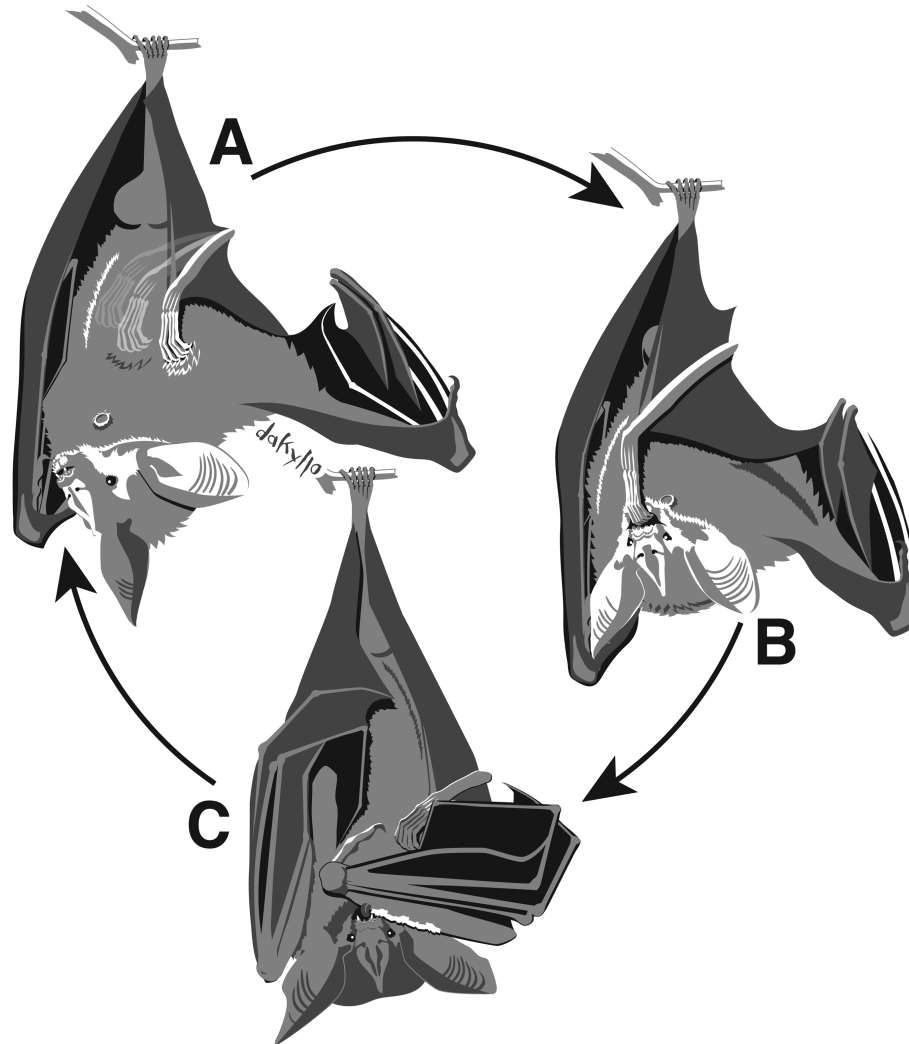
Fig. 6.—Illustration of male fringe-lipped bats (*Trachops cirrhosus*) performing the stereotyped forearm licking behavior. A) Males scratch body (dorsally and ventrally). B) Males insert one claw into mouth. C) Males repeatedly lick forearm. Arrow indicates the cycle which male *T. cirrhosus* repeat several times per bout. Illustration by Damond Kyllo.

We never observed forearm licking behavior in females. Both males with forearm crust (Supplementary Data SD2) and without forearm crust performed this behavior. Males without a forearm crust performed only 1 of these stereotyped behavioral bouts per observation ($\bar{X} = 35.8$ s ± 32.6 *SD*, $n = 6$) licking their forearm between 1 and 10 times per observation. In contrast, males with a forearm crust performed between 1 and 3 forearm licking behavioral sequences per observation period, with bouts ranging from 37 to 93 s ($\bar{X} = 62.62$ s ± 15.89 *SD*, $n = 21$), and licked their forearms between 4 and 30 times per observation period ($\bar{X} = 16.9 \pm 6.55$ *SD*). Males with a forearm crust performed significantly more numbers of licks to the forearm per bout than males without a crust ($t_{14.13} = 5.73$, $P < 0.001$); however, the overall time males spent forearm licking did not differ ($t_{5.69} = 1.95$, $P = 0.10$). In several of the observations of males with a forearm crust, a strand of liquid could be seen from the mouth to the forearm. After the behavior observation males were captured and males with a forearm crust had an amber colored thick liquid on their forearm (Supplementary Data SD2) that was not present prior to our behavior observations. Forearm licking and crust production

was not related to variation in diet among individuals as all bats were fed a uniform diet of fish (Characidae) in captivity.

Forearm licking sequences accounted for 0.59% to 3.23% of total time for males with a forearm crust and for 0.01% to 0.72% for males without a forearm crust. In both males and females, the remainder of the observation period was devoted to other behaviors (urinating, defecating, yawning, and flying), which accounted for less than 2% for all individuals of the observation period.

Several of our observations of males with a forearm crust, in natural roosts ($n = 2$) and in captivity ($n = 4$), were with conspecifics. In these, we never observed the male with a forearm crust mark the territory or roost members. Furthermore, males with a crust did not display toward females and we found no evidence that other males prevented each other from forearm licking.

Museum specimens.—We examined 70 dry specimens of *T. cirrhosus* (25 males and 45 females, specimen age not specified) at the American Museum of Natural History, 60 dry specimens of *T. cirrhosus* (22 adult males, 1 juvenile male, and 37 adult females) at the Field Museum of Natural History, and 363 dry specimens of *T. cirrhosus* (171 adult males, 17 juvenile

males, 161 adult females, and 14 juvenile females) at the National Museum of Natural History. In total, we found 12 specimens collected from 1948 to 1972 with a forearm crust present. These were captured in Panama ($n = 9$), Mexico ($n = 2$), and Guatemala ($n = 1$) in March ($n = 5$), April ($n = 1$), May ($n = 1$), September ($n = 1$), October ($n = 3$), and December ($n = 1$). We did not find forearm crust present in female specimens. Our findings are likely conservative as the forearm crust likely flaked off or was removed during specimen preparation. Additionally, field notes from the "BCI Bat Project," an extensive mist netting operation spanning nearly a decade on Barro Colorado Island, Panama (Handley et al. 1991; Kalko et al. 1996), document 3 adult male *T. cirrhosus* that had "sticky substance on both forearms," had a "strong odor," and were "strong smelling" captured January 1980, October 1981, and September 1984, respectively (C. O. Handley, Jr. field notes).

DISCUSSION

Overall, our captures suggest a seasonal pattern to reproduction in *T. cirrhosus*. We found a peak in juvenile captures at the beginning of the wet season (June, July, and August). Our results also show that females were mostly pregnant during the dry season (April and May). Since lactation is the most costly period for females and weaning is the most critical period for pups (Kurta et al. 1989), it appears that pregnancy is timed to coincide with the beginning of the wet season, when prey species, especially frogs, are abundant. Our results are consistent with findings (Durant et al. 2013) that document a single peak in pregnancy during the dry season for gleaning animalivores, such as *T. cirrhosus*.

Although the gestation length of *T. cirrhosus* is unknown, by comparing our observations to reproductive patterns of other leaf-nosed bats (Altringham 1996; Rasweiler and Badwaik 1997), we can infer that gestation is approximately 4 to 6 months in length. If males were creating a forearm crust solely to court females or to compete with other males for access to females, we would expect an increase in captures of males with a forearm crust from October to November. Although males with a forearm crust were found throughout the year, we did find an increase in the percent of males captured with a crust from September to December. Our finding that mature males can display this odorous forearm crust throughout the year (both in our captures and museum observations) is similar to observations in other bats. Male buffy flower bats (*Erophylla sezekorni*) produce a garlic-scented supraorbital secretion and then perform aerial displays to females. This secretion is present in all mature males, regardless of whether they are displaying to females (Murray and Fleming 2008). Similar results have been found in *S. bilineata* where males court females year-round, irrespective of female reproductive state (Knörnschild et al. 2016).

The fact that the forearm crust was only present in adult males suggests that it is involved in reproduction. Additionally, the finding that all males with a forearm crust also had enlarged testes indicates a strong association with sexual maturity and possibly to signal readiness for mating. It is unclear, however,

why some males with enlarged testes did not have a forearm crust. Perhaps these males are younger. The condition and size of the epididymides in males with a forearm crust and males without a forearm crust needs to be examined to determine whether both are storing active sperm. Our results are similar to those found in *L. curasoae* (Muñoz-Romo and Kunz 2009), in which some males have enlarged testes but do not display an odorous dorsal patch, but all males that displayed a dorsal patch had enlarged testes.

Our observation that all males with a forearm crust had enlarged chest glands (Fig. 2B) further suggests the forearm crust is involved in reproduction. For the most part the glands that have been described in bats are sexually dimorphic, with adult males having enlarged glands (Quay 1970; Schmidt 1985; Scully et al. 2000). In contrast to other species (Valdivieso and Tamsitt 1964), the chest gland in *T. cirrhosus* is only sexually dimorphic after reproductive maturity. Active chest glands in both female and male *T. cirrhosus* secrete a white oily odorless exudate. However, after maturation, all reproductive females had rudimentary glands that were barely visible and did not produce any secretions. In contrast to other bats, the secretion of the chest gland in *T. cirrhosus* is not odorous (Valdivieso and Tamsitt 1964). The differences found in gland size invite further study into the role that hormones play in determining the size and production of secretions.

In this study, we demonstrate that males with a forearm crust had a significantly higher body condition index than males without a forearm crust (Fig. 4). These results suggest that the forearm crust could communicate the condition of an individual to conspecifics. Chemical signals are particularly suited to mate choice because they include by-products of everyday life and are thereby honest indicators of an individuals' condition (Voigt 2013). For example, male and female meadow voles (*Microtus pennsylvanicus*) prefer the scents of conspecifics on a higher protein diet (Ferkin et al. 1997). Furthermore, in mammals, odors can honestly convey an individual's condition since the production of chemical signals is linked to hormone levels; once an individual's immunity is suppressed androgens are costly to produce (Zahavi 1975; Wingfield et al. 1990; Wyatt 2014). The fact that males with a forearm crust had significantly higher body condition indices suggests that only males in good condition are able to produce a forearm crust. Finally, odorous signals can play an important role in mate choice because chemical profiles can communicate information about individual heterozygosity and genetic distance (Charpentier et al. 2008; Santos et al. 2016). Further investigation is warranted to elucidate whether this forearm crust is involved in female mate choice.

The forearm licking crust application behavior described here is a novel behavior that, to our knowledge, is exclusively found in *T. cirrhosus*. Preliminary analyses found no glands on the forearm of male fringe-lipped bats; hence, the odorous forearm crust is likely created through a combination of substances from elsewhere. Although several species exhibit self-anointing behaviors through which they spread substances over their body (Brockie 1976; Alfaro et al. 2012), the forearm

licking behavior was only observed in males and is therefore sexually dimorphic. Although there are cases in which male mammals rub secretions from glands onto their body to attract females (Gosling 1987), bats appear to be unique in creating odorous cocktails by combining several bodily secretions. Even though we observed bats urinating in many of our observations, this never occurred immediately prior to the crust application behavior. Additionally, we did not observe a urine uptake behavior as described in *S. bilineata* (Voigt 2002). This suggests that urine might not be one of the compounds in the forearm crust. Although male bats did scratch the chest gland area, it was difficult to determine whether they were explicitly collecting secretions from the chest gland to create the forearm crust. Our observations demonstrate that males did flick their tongues repeatedly, which suggests that males are using saliva to create this odorous forearm crust. Several studies indicate that saliva can act as a chemical signal in mammals (Block et al. 1981; Gray et al. 1984). Further studies describing the chemical profile of the forearm crust are needed to determine the exact composition of this odorous forearm crust.

The forearm licking behavior we described is similar to the behavior found in *L. curasoae* where males use their claws to collect bodily fluids and transfer them to their dorsal side (Muñoz-Romo and Kunz 2009) and to the perfume blending behavior of *S. bilineata* (Voigt and von Helversen 1999). However, the perfume blending of *S. bilineata* is restricted to afternoons (Voigt 2013), whereas our roost observations demonstrated that forearm licking occurs throughout the day. Furthermore, each forearm licking bout was shorter in *T. cirrhosus*, lasting only 37 to 93 s, in comparison to *S. bilineata*, which perfume blend for an average of 7 min (Voigt 2002).

Similar to sac-winged bats, the position of this forearm crust odorous patch on the forearm suggests that males might be wafting this odor toward individuals during flight. However, in our observations at the roost and in groups in captivity, we never observed males performing courtship displays to females or scent marking roostmates. It is possible that males are courting females outside of the roost. Females would be able to locate males faster while they are foraging if the forearm crust odors are being spread while in flight. Brooke and Decker (1996) found that male greater fishing bats (*Noctilio leporinus*) were broadcasting their odor during flight. Chemical cues are ideal signals for Neotropical bats because odors have extended ranges compared to visual signals and also can travel farther through cluttered environments, such as tropical forests. Furthermore, it has been suggested that smaller organisms cannot produce the lower-frequency sound signals that travel further than higher-frequency signals (Dusenbery 1992).

Olfaction is a dominant sense for most mammals and in turn heavily influences their behavior (Wyatt 2014). Odors play an especially important role in the lives of bats. For example, many fruit eating bats (e.g., *Dermanura watsoni*, *Vampyressa pusilla*, *Carollia perspicillata*, *C. castanea*) use olfactory cues when foraging (Thies et al. 1998; Korine and Kalko 2005). Some bat species also use species-specific scents to mark their territories or colony members (Brooke 1997). Furthermore,

bats can discriminate among roost mates and individuals from a different colony based on odor (De Fanis and Jones 1995; Safi and Kerth 2003). The crucial role that odors play in leaf-nosed bats (Phyllostomidae) was recently highlighted (Yohe et al. 2017). Whereas most families of bats have lost their vomeronasal organ, phyllostomids are a major exception where the vomeronasal organ has persisted. These results suggest that vomeronasal olfaction plays an important role in the lives of phyllostomids.

In conclusion, this study provides new information on an odorous substance found on the forearm of adult male *T. cirrhosus*. We propose that this odor is involved in signaling readiness for mating and communicating male condition. Additionally, we have described a novel behavior performed by males of this species to create this odorous forearm crust. Further studies determining whether the forearm crust is involved in female choice or male–male competition are warranted.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Group of fringe-lipped bats (*Trachops cirrhosus*) roosting in a culvert in Soberanía National Park, Panama. A second group of *T. cirrhosus* can been seen roosting deeper within the culvert in late afternoon. The 4 *T. cirrhosus* in the foreground are grooming. The bat on the far right is the reproductive male and is the only bat in the group that additionally exhibits the forearm licking behavior.

Supplementary Data SD2.—Reproductive male fringe-lipped bat (*Trachops cirrhosus*) in a flight cage, performing the forearm licking behavior on left forearm.

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