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Original investigation

Tracking the origin of the smearing behavior in long-nosed bats (*Leptonycteris* spp.)

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ABSTRACT

A unique and novel stereotypic 'smearing' behavior and the formation of an odoriferous dorsal patch have been recently described in two species of long-nosed bats, *Leptonycteris curasoae* and *L. yerbabuenae* (Glossophaginae: Phyllostomidae). It has been hypothesized that this structure represents a mechanism involved in female mate choice mediated through odor, and that it has only evolved within the genus *Leptonycteris*. No evidence has been published indicating whether the smearing behavior and the dorsal patch occur in *L. nivalis*, the third extant species within the genus. We reviewed the available data on the mating behavior of *L. nivalis* and conducted four surveys on the only mating colony known for this species at Cueva del Diablo, Tepoztlan, Morelos, Mexico, searching for evidence of both the smearing behavior and the dorsal patch in reproductive males of this species. Our findings indicate that *L. nivalis* does not display the smearing behavior or the dorsal patch, suggesting that this trait and its role in mate choice by females must have evolved from a common ancestor of *L. yerbabuenae* and *L. curasoae* after it separated from *L. nivalis*, between 1.0 and 0.5 million years ago. We propose a possible hypothetical scenario for the evolution of the smearing behavior, based on differential levels of ectoparasitic pressure acting on bat populations established at locations with markedly different environmental temperatures.

Introduction

In recent years, a unique and novel stereotypic 'smearing' behavior has been described in two species of long-nosed bats, *Leptonycteris curasoae* Miller and *L. yerbabuenae* Martínez and Villa-R. (Nassar et al., 2008; Muñoz-Romo and Kunz, 2009; Muñoz-Romo et al., 2011a). During the mating season, sexually mature male individuals deposit saliva, urogenital fluids, and anal secretions on their backs, creating an odoriferous dorsal patch (Fig. 1). Up to now, 19 compounds have been identified in the dorsal patch of *L. curasoae* (Muñoz-Romo et al., 2012), some of which have been reported as important in female attraction among other male mammals during their breeding season. Male individuals of *L. curasoae* and *L. yerbabuenae* with dorsal patches have larger testes, smaller body mass, lower body condition indices and fewer ectoparasites than males without patches (Muñoz-Romo and Kunz, 2009; Muñoz-Romo et al., 2011a; Rincón-Vargas et al., 2013). All together, the available evidence suggests that the formation of the dorsal patch in these bats is a mechanism involved in female mate choice mediated through odor (Nassar et al., 2008; Muñoz-Romo and Kunz, 2009; Muñoz-Romo et al., 2011a).

The smearing behavior observed in long-nosed bats has not been reported in any other species of bat, suggesting that this elaborated conduct has only evolved within this genus; however, we still do not know when it first appeared within this clade. To contribute to elucidate its origin, we needed to determine if males of *L. nivalis*, the other extant species within the genus, display the smearing behavior during the mating season or present a dorsal patch or an incipient version of it.

Up to now, two studies have examined the reproductive behavior of *L. nivalis* at Cueva del Diablo, the only known mating roost of this species in Mexico. Caballero-Martínez (2004) conducted observations and recordings with infrared cameras of the mating colony for two mating seasons, between September 2001 and December of 2002, and concluded that this species has a promiscuous mating system, conformed by multi-male and multi-female groups, finding no evidence of territoriality, harem, lek formation or courtship. In his description of the mating process, this author never mentioned the formation of a dorsal patch in reproductive males or evidence of new growing hair on the inter-scapular area after the mating season. Toledo-Gutiérrez (2009) also conducted a detailed study of

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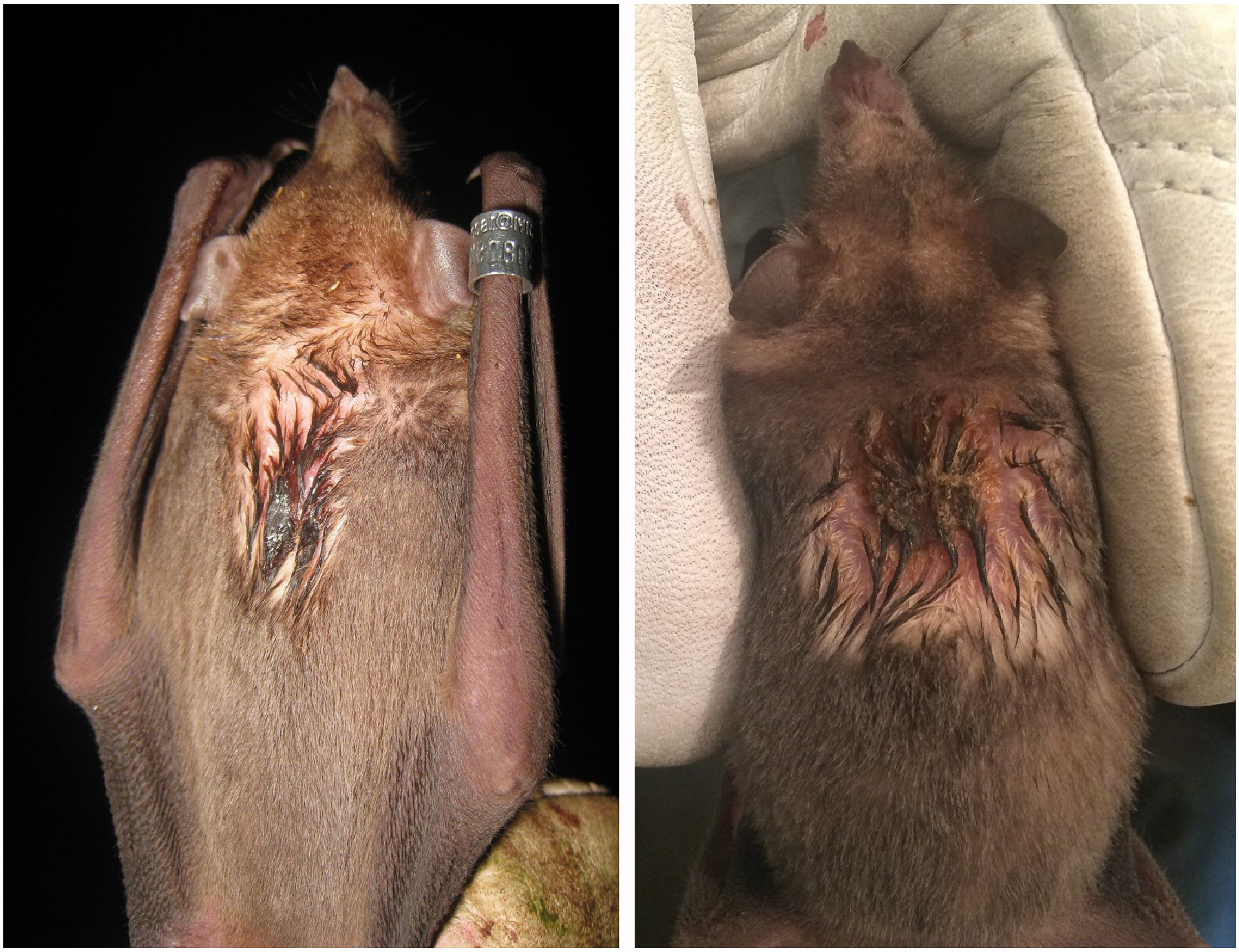

Fig. 1. Males of *Leptonycteris curasoae* from Spelonk Cave, Bonaire Island, Dutch Caribbean (left) and of *L. yerbabuenae* captured six months before without a dorsal patch in Gruta de Juxtlahuaca, Guerrero, Mexico, and kept in captivity in Mexico City where it developed the patch. The odoriferous dorsal patch develops during the mating season in both species, but not in *L. nivalis*.

the reproductive behavior of this species, capturing bats and using night vision cameras during two reproductive seasons (2005–2007) between September and February. This author did not observe the presence of a dorsal patch in the 291 adult males processed nor detected the smearing behavior during 87.6 h of videos recorded and analyzed.

In the present study, we combine the reported results on the mating behavior of *L. nivalis* with new data obtained from four additional sampling periods conducted on this species during the mating season at Cueva del Diablo. Further, we discuss one possible scenario in which the smearing behavior arose in an ancestral *Leptonycteris* species as a response of selective pressures associated with ectoparasite loads.

Material and methods

Study site

Cueva del Diablo (19°01′N, 99°04′W) is located near Tepoztlan, Morelos, Central Mexico (Hoffmann et al., 1986). The local climate is characterized as temperate subhumid, with average annual temperatures varying between 12 °C and 18 °C and average annual precipitation of 800 mm (Caballero-Martínez, 2004). The cave is of volcanic origin, composed of a system of chambers and tunnels with a total length of 1937 m (Téllez, 2001). It is located at the altitudinal limit (1883 m a.s.l.) of a tropical deciduous forest (Téllez, 2001). A full description of the cave was made by Hoffmann et al. (1986). It is the only known mating roost of *L. nivalis* in Mexico, also used by other species of bats, including *Pteronotus parnellii*, *Desmodus rotundus*, *Anoura geoffroyi*, *Artibeus jamaicensis*, and *Myotis velifer* (López-Segurajáuregui et al., 2006; Toledo-Gutiérrez, 2009).

Study species

The Mexican long-nosed bat, *Leptonycteris nivalis* (Saussure, 1860), is the largest Glossophagine (Phyllostomidae) bat (70–90 mm total length, 56–61 mm forearm; Reid, 1997; Hensley and Wilkins, 1988). *Leptonycteris nivalis* occurs at higher elevations and cooler sites than *L. yerbabuenae* (Arita, 1991). Although both species co-occur in the dry regions of Mexico, *L. nivalis* is mostly associated with the transition between pine-oak forest and tropical dry forest, as well as the Chihuahuan desert, while *L. yerbabuenae* is mostly found in tropical and subtropical dry forests and deserts, including the Sonoran desert, of South Western US, Mexico, Guatemala, El Salvador, and Honduras (Arita, 1991; U.S. Fish and Wildlife Service, 1994; Reid, 1997; Cole and Wilson, 2006). Both species have been captured in some locations at the same time (Villa-R., 1967; Wilson et al., 1985) and even sharing the same roost (Arita, 1991; Medellin, pers. obs.). The migratory behavior is reflected in its seasonal presence in the United States, northern, and central Mexico.

The species is gregarious, roosting in caves, tunnels, abandoned mines, and buildings (Hensley and Wilkins, 1988; Reid, 1997). It has a monoestrous reproductive pattern (Téllez, 2001). Maternity roosts occur in northern latitudes in Mexico and the U.S. (Moreno-Valdéz et al., 2004; Brown, 2008). Currently, this species is listed as Endangered by the IUCN (2016), as Endangered in the United States by the Endangered Species Act (U.S. Fish and Wildlife Species 1994) and as Threatened in the Mexican legislation (SEMARNAT, 2010) since 1991.

Bat sampling

We conducted mist netting sessions to capture individuals of *L. nivalis* at Cueva del Diablo during four reproductive periods: the first from September 2010 to February 2011 (Sep 5th, Oct 3rd, Nov 14th, Dec 4th, Dec 17th, Dec 29th, Jan 13th, Feb 2nd), the second from November to December 2011 (Nov 6th, Nov 17th, Dec 3rd), the third in December 2013 (Dec 27th, Dec 28th), and the fourth from December 2014 to February 2015 (Dec 19th, Jan 9th, Jan 30th, Jan 31st, Feb 20th). Mating frequency reaches peak values between November and December (Toledo-Gutiérrez, 2009). Each mist netting session consisted of one 6-m long × 2.6-m high mist net (38-mm mesh; Avinet Inc., Dryden, NY) set at the main entrance of the cave open for five consecutive hours (for capture periods 2010–2011 and 2011–2012, from 24:00 h to 05:00 h; for capture periods 2013 and 2014–2015, from 18:00 h to 23:00 h). Captured bats were temporally stored in cotton bags until processed. For each individual captured, we recorded gender, age, reproductive condition and forearm length. In the case of males during November and December, we also recorded testicle diameter. After processed, bats were released. We took special care examining the backs of males for any evidence of an oily dorsal patch as has been described for *L. curasoae* and *L. yerbabuenae* (Nassar et al., 2008; Muñoz-Romo and Kunz, 2009).

Results

We captured a total of 842 individuals of *Leptonycteris nivalis* between September 2010 and February 2015, from which 384 were females and 458 were males (Table 1). Sexually active males were recorded as follows: 48 out of 189 (2010–2011), 98 out of 130 (2011–2012), 49 out of 94 (2013–2014), and 15 out of 45 (2014–2015). Of the 458 male individuals captured, 210 were sexually active. Despite explicit and detailed examination, none presented the dorsal patch or any indication or even a hint of it. This sticky and odoriferous patch that has been described in the other two species of the genus (see Fig. 1) is evidently not formed in this species, the largest of the three. This species also differs from the other two in that it is virtually absent from tropical areas, inhabiting only mid to high elevations areas. Given that our data come from the single known mating colony of this species despite extensive searches for additional mating roosts (L. Torres, pers. comm. to R. Medellin), we are quite confident that *L. nivalis* indeed does not form the patch described for the other two species.

Discussion

Our observations of male *Leptonycteris nivalis* at Cueva del Diablo, in combination with results of previous studies evaluating mating activity of this species at the same cave, indicate that this species does not display the smearing behavior performed by the male of the other two species in the genus. This suggests that this stereotyped behavior must have evolved from a common ancestor to *L. yerbabuenae* and *L. curasoae* already differentiated from *L. nivalis* between 1.0 and 0.5 million years ago.

Over 400 adult males examined yielded negative results of a dorsal patch similar to the one formed in *L. yerbabuenae* and *L. curasoae* during their breeding seasons. The patch is easy to distinguish when processing individuals during handling or filming these bats. No reference exists documenting such patch despite the constant presence of research in the breeding season at the mating cave (e.g., Caballero-Martínez, 2004; Toledo-Gutiérrez, 2009). Our observations were intentionally conducted to search for the dorsal patch in *L. nivalis* males during four mating seasons, with the same results that in the previous monitoring sessions. Thus, based on the cumulative negative results obtained from all surveys conducted on this species at Cueva del Diablo during the mating season, we conclude that males of *L. nivalis* do not perform the smearing behavior as sexual conduct.

Wilkinson and Fleming (1996) inferred the evolutionary origin of the living species of long-nosed bats from a study examining the control region of mitochondrial DNA. They proposed that *L. nivalis* last had a common ancestor with *L. curasoae* and *L. yerbabuenae* about 1 million years ago, and that the latter two species separated about 0.54 million years ago. This historical scenario proposes that before the uplift of the Mexican plateau and its flanking Sierra Madres in the late Pliocene (about 2 million years ago, Axelrod, 1979), a single arid-adapted species of *Leptonycteris* existed, and its mating behavior must have been similar to the promiscuous multi-female multi-male system described for *L. nivalis* (Caballero-Martínez, 2004; Toledo-Gutiérrez, 2009). After the uplift, this ancestral species split into *L. nivalis* in the highlands and the ancestor of *L. yerbabuenae* and *L. curasoae* in the lowlands (from now on lowlands *Leptonycteris*). Between 1.0 and 0.5 million years ago, the smearing behavior must have evolved in the lowlands *Leptonycteris* as an odor-based signaling system, which helped females to choose mates. But, what selective pressures were responsible for the evolution of the dorsal patch in the lowlands *Leptonycteris* and not in *L. nivalis*?

The authors that described the dorsal patch in *L. curasoae* and *L. yerbabuenae* have postulated it as a temporal soft structure signaling mating readiness and male quality (Nassar et al., 2008; Muñoz-Romo and Kunz, 2009; Muñoz-Romo et al., 2011a); however, its precise function and what quality signals are being detected and evaluated by females to choose mate remain mostly unknown. One type of male quality signals barely examined in bats is represented by those expressing parasite resistance mediated through the immune system and behavioral attributes (Marshall 1982; Christe et al., 2000; ter Hofstede and Fenton 2005; Schad et al., 2012). Muñoz-Romo and Kunz (2009) and Muñoz-Romo et al. (2011b) demonstrated a suggestive relationship between presence and shape of the dorsal patch and ectoparasite load (streblid flies) in males of *L. curasoae* in a mating roost in Venezuela. Males with the patch had larger testes and significantly lower infestations of streblids than males without it, and parasite loads increased with greater asymmetry of the dorsal patch. Together, the available evidence indicates that this structure might function as a dual signal (odoriferous and visual) of mating readiness and resistance to ectoparasite infestation. If this is the primary function of the dorsal patch, then one possible evolutionary scenario determining the origin of this structure in the lowlands *Leptonycteris* and not in *L. nivalis* would be a marked difference in the level of ectoparasitic pressure on the bat colonies of both taxa.

The proposed difference in ectoparasitic pressure could be mediated by weather conditions surrounding the roosts used by both taxa, especially the mating roosts. Use of caves as roosts is a plesiomorphic common trait shared by all extant species of long-nosed bats. This roosting habit has been associated with high prevalence, abundance, and species richness of ectoparasites in bats (Patterson et al., 2007; Bordes et al., 2008; Tlapaya-Romero et al., 2015). On the other hand, climate can modulate the patterns

Table 1
Surveys of *Leptonycteris nivalis* at Cueva del Diablo during the mating season.

Reproductive season	# individuals captured	# males captured	# adult males captured	Source
2001–2002	207	173	173	Caballero-Martínez (2004)
2002–2003	65	46	46	Caballero-Martínez (2004)
2005–2006	167	101	94	Toledo-Gutiérrez (2009)
2006–2007	340	201	197	Toledo-Gutiérrez (2009)
2010–2011	376	189	124	This study
2011–2012	164	130	127	This study
2013–2014	152	94	92	This study
2014–2015	150	45	45	This study
Total	1621	979	898	

of ectoparasitism occurring in bird and bat populations (Marshall, 1982; Merino and Potti, 1996; Gray et al., 2009; Pilosof et al., 2012). Ectoparasite abundance was positively correlated to environmental temperatures in four species of Neotropical bats parasitized by highly host-specific bat flies (Pilosof et al., 2012). Bat ectoparasites can be directly affected by local climatic conditions. In temperate-zone cave-dwelling bats, roost temperatures below 11 °C inhibit reproductive activity of ectoparasites (Lourenço and Palmeirim, 2008). Thus, if temperature differences between roosting areas of the lowlands *Leptonycteris* and *L. nivalis* were sufficiently marked to determine a differential ectoparasitic pressure on their colonies, then the evolution of the dorsal patch as a structure contributing to show higher male quality in terms of parasite resistance could had been favored in the lowlands *Leptonycteris*, but not in *L. nivalis*.

Ecological segregation (altitude and vegetation type) between the lowlands *Leptonycteris* capable of performing the smearing behavior and *L. nivalis* must have been strong enough to allow them to reduce resource competition (Arita, 1991) and evolve separately. Recently, Ayala-Berdon et al. (2013) demonstrated that *L. nivalis* has a higher energy intake rate than *L. yerbabuenae*, an attribute that confers the former the capability to occupy cold environments. This spatial segregation probably also extended to the use of different roosts, including those used for mating and nursing. Two caves where Pleistocene fossil remains of *L. nivalis* have been found in north eastern Mexico did not contain fossil remains of *L. yerbabuenae* (Arroyo-Cabrales and Polaco, 2003). Co-occurrence of *L. yerbabuenae* and *L. nivalis* has been observed in seasons not comprising either mating or birthing periods and in localities far away from Cueva del Diablo (Medellin, pers. obs.). This cave remains as the only mating roost known for *L. nivalis* in the entire range, and no *L. yerbabuenae* has been reported in it (Caballero-Martínez, 2004; López-Segurajáuregui et al., 2006; Toledo-Gutiérrez, 2009). As indicated in the study site section of this article, the cave is located at 1883 m above sea level, the lowest environmental temperatures outside the cave are reached between November and January (annual mean temperature: 12–18 °C), and the temperature inside the cave is lower than 16 °C (Caballero-Martínez, 2004).

The use of different mating roosts must have played a key role in keeping the two lineages of long-nosed bats evolving apart, especially because their mating seasons probably overlapped in time, as it occurs at present between *L. nivalis* and the spring-birth populations of *L. yerbabuenae* (Ceballos et al., 1997; Stoner et al., 2003; López-Segurajáuregui et al., 2006). Once the smearing behavior evolved in the dry lowlands of Mexico, this behavioral trait probably contributed to increase reproductive isolation between the lowlands *Leptonycteris* and *L. nivalis*. Then, the lowlands *Leptonycteris* carried this sexual trait with it to northern South America through semi-arid corridors during Pleistocene glacial advances, with time speciating into *L. yerbabuenae* in North and Central America and *L. curasoae* in South America (Wilkinson and Fleming, 1996). The smearing behavior has been maintained in northern South America. Presence of this trait in *L. yerbabuenae* and *L. curasoae* at present suggests that these sister species could interbreed if entering in contact through Central America.

One possibility to test the ectoparasitic pressure hypothesis would be to examine and compare prevalence, abundance, and species richness of ectoparasites in both males and females of the three living species of long-nosed bats. Ectoparasite evaluation should consider both the bats' mating season and the birth and lactation season. Newborns of *L. curasoae* can present considerably high numbers of streblids (>100 per individual; Nassar, pers. obs.), probably acting as a negative selective pressure at an early stage in life for these organisms. Under this hypothesis, we should expect to find comparatively lower ectoparasite pressure in *L. nivalis* during its entire life cycle; however, we should keep in mind that environmental temperatures that characterized the roosts and surrounding habitats of *L. nivalis* at early stages during its speciation could be substantially different than temperatures at present. What these interactions between reproductive behavior and parasite load mean for population dynamics and survival is still very much up in the air and should serve as the focus for future studies.

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