



# Olfactory cues of mate quality in mammals: inflammatory response is higher in males of long-nosed bats with odorous dorsal patch

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## Abstract

Bats use olfactory signals to provide information of species and individual identity and quality. Males of two species of long-nosed bats, *Leptonycteris curasoae* and *L. yerbabuena*, display an odoriferous dorsal patch during the mating season that is involved in mate choice. The dorsal patch is documented to serve as an indicator of male quality; for instance, males with dorsal patch present larger testes and lower ectoparasite loads. We evaluated the role of the dorsal patch in males of *L. curasoae* and *L. yerbabuena* as an indicator of inflammatory response 6 and 12 h after being injected with phytohemagglutinin (PHA). We found that the inflammatory response of males of both species was not different between reproductively active bats with or without dorsal patch 6 h after PHA injection, but the response was higher in bats with dorsal patch 12 h after the injection. Our study adds to the evidence that the dorsal patch exhibited by males of long-nosed bats indicates their immune quality for mating females. Further work including other branches of the immune system and the potential role of microbiota in the strength of the inflammatory response is warranted.

**Keywords** Bats · Immune response · Mate choice · Nectarivorous bats · Phytohemagglutinin

Olfactory signals are essential in bat communication, providing information of species identity, sex, age, individual identity, group membership, territory, social status, sexual

receptiveness, and health status (Chaverri et al. 2018; Muñoz-Romo et al. 2021; Zhang et al. 2022). Olfactory communication is arguably the most important source of information that bats use during mate choice (Voigt 2014; Muñoz-Romo et al. 2021). For instance, males of the sac-winged bat, *Saccopteryx bilineata*, produce odors that have an important function during courtship (Voigt et al. 2008), males of the greater spear-nosed bat (*Phyllostomus hastatus*) that roost with groups of females have significantly different chemical profiles than males roosting with other males (Adams et al. 2018), and the size of the odorous crust of male fringe-lipped bats (*Trachops cirrhosis*) indicates testosterone plasma levels and testicle size (Muñoz-Romo et al. 2020).

Males of two species of long-nosed bats, *Leptonycteris curasoae* and *L. yerbabuena*, transfer fluids collected from different parts of their body onto the interscapular region, followed by the formation of an odoriferous dorsal patch during the mating season (Nassar et al. 2008; Muñoz-Romo and Kunz 2009). Odor released from this soft structure is involved in mate choice, as indicated by experimental evidence showing that females of *L. curasoae* prefer the odor collected from the dorsal patch than the odor from males with no patch (Muñoz-Romo et al. 2011a). The dorsal patch appears to serve as an indicator of male quality because males with presence of the dorsal patch have larger testes,

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**Fig. 1** Males of *Leptonycteris curasoae* presenting a fresh dorsal patch (A) and a dry dorsal patch (B). Fresh dorsal patches have a humid aspect and an intense odor, suggesting their recent appearance in the individual (photographs: J. M. Nassar).

smaller body masses, lower body condition indices, and lower ectoparasite loads than males without dorsal patches (Muñoz-Romo and Kunz 2009; Rincón-Vargas et al. 2013).

We evaluated the role of the dorsal patch as an indicator of immune quality of males of *L. curasoae* and *L. yerbabuena* in Venezuela and Mexico, respectively. We measured the inflammatory response against phytohemagglutinin (PHA) in reproductively active males with or without the dorsal patch. PHA injection is widely used in vertebrate immunology (Vinkler and Albrecht 2011, Merlo et al. 2014, Bilková et al. 2015, Plasman et al. 2015, Otálora-Ardila et al. 2016), and it measures the strength of the individual's innate immune response (Vinkler et al. 2010, 2014). We tested the hypothesis that the presence of the dorsal patch functions as an indicator of the quality of the individual's innate immune response. We predicted that males with the dorsal patch would express a higher inflammatory response to the PHA challenge because males without the patch have higher ectoparasite load (Muñoz-Romo and Kunz 2009), and an inverse relationship between inflammatory response to PHA and ectoparasite load has been reported in bats (Christe et al. 2000).

## Methods

### Bat captures

Adult males of *L. curasoae* were trapped with mist nets at the exit of Piedra Honda Cave (11°55'N, 70°2'W) in the Paraguaná Peninsula, Falcón State, Venezuela in November 2012. Adult males of *L. yerbabuena* were trapped with mist nets in Mexico in Zapotitlán de las Salinas, Puebla (18°19'N, 97°27'W) in May 2012 and with a hand net in a cave in Tlilapan, Veracruz (18°51'N, 97°05'W) in June 2012. Bat sampling procedures followed ASM guidelines (Sikes et al. 2011) and were approved by the Bioethics Commission of the Venezuelan Institute of Scientific Research, Venezuela, and the General Directorate of Wildlife, Mexico. Bats were placed in individual cloth bags and transported to a nearby facility to conduct the experiment within 2 h after being captured. We recorded weight, forearm length, and reproductive condition (males with inguinal or scrotal testicles) and presence of a fresh dorsal patch (Fig. 1). Fresh dorsal patches have a humid aspect and an intense odor, suggesting their recent appearance in the individuals (Fig. 1A). We captured individuals bearing patches with a dry appearance (Fig. 1B) and inguinal testicles but we did not include them in the study. Because bats with and without the patch might differ in body



condition (Muñoz-Romo and Kunz 2009), we estimated the body condition index ( $BC_i$ ) for each individual as body mass (g)/forearm length (mm). We estimated the diameter of fresh dorsal patches as the average of two perpendicular measurements in all males of *L. curasoae* and in a reduced number of individuals of *L. yerbabuena*. Bats of both species were fed with a sugar solution every six hours during the experimental period. We hand-fed the bats with the sugar solution before they were released near their capture sites after the experiment concluded (~24 h after PHA injection). We anticipated no negative consequences of PHA administration, because a previous work with captive bats shows that this process does not affect their well-being (Otálora-Ardila et al. 2016).

## Immune challenge

We injected 50  $\mu$ L (Otálora-Ardila et al. 2016) of a 3 mg/mL solution of PHA (PHA-P, no. L8754, Sigma-Aldrich) in phosphate-buffered saline (PBS; Allen et al. 2009) in the right footpad of each individual. As a control, 50  $\mu$ L de PBS were injected in the left footpad. Average thickness (from three measures) of both footpads was measured with a digital caliper (Mitotoyo, Japan, 0.01 mm) 10 min before and 6 and 12 h after PHA or PBS injection. PHA response was evaluated as the swelling index 6 ( $SI_6$ ) and 12 h ( $SI_{12}$ ) after the injection as.

$SI = (THtPHA - THoPHA) - (THtPBS - THoPBS)$ , where THt is the footpad thickness 6 or 12 h after the injection and THo is the footpad thickness before the injection of PHA or PBS (Smits et al. 1999). A SI value of 0 occurs when swelling in the PHA-injected foot is equal to that in the PBS-injected foot and indicates no or low immune response.

## Data analyses

$SI_6$ ,  $SI_{12}$ ,  $BC_i$ , and patch diameter were normally distributed for both bat species. We used separate one-way analyses of covariance (ANCOVA) for each bat species to compare

$SI_6$  and  $SI_{12}$  between males with scrotal testicles with and without fresh dorsal patches. We included  $BC_i$  as a covariate. The assumption of independence of the covariate and the treatment effect (Miller and Chapman 2001) was met since  $BC_i$  did not differ between male categories in any species. When the effect of the covariate was significant, we tested if SI and  $BC_i$  were significantly correlated with linear regression analysis. Finally, we tested if the diameter of the patch in males of *L. curasoae* was significantly correlated with  $SI_6$  and  $SI_{12}$  with linear regression analyses. All the analyses were conducted in STATISTICA (StatSoft, Inc. 2011).

## Results

### Presence of the dorsal patch

We captured 44 males of *L. curasoae* with scrotal testicles, of which 19 presented a dorsal patch and 25 did not (Table 1 and Fig. 1). We captured a total of 14 males of *L. yerbabuena*, of which 6 presented a fresh dorsal patch and 8 did not present patch (Table 1 and Fig. 1).

### Inflammatory response and the dorsal patch

There was no significant difference in the inflammatory response of males of *L. curasoae* between bats with scrotal testicles with or without dorsal patch 6 h after PHA injection ( $F_{1,41} = 1.95$ ,  $p = 0.17$ ; Fig. 2A), but the response 12 h after the injection was significantly higher in bats with dorsal patch ( $F_{1,41} = 5.21$ ,  $p = 0.02$ ; Fig. 2A). There was no significant difference in inflammatory response of males of *L. yerbabuena* with scrotal testicles with or without dorsal patch 6 h after PHA injection ( $F_{1,11} = 0.05$ ,  $p = 0.82$ ; Fig. 2B), but males with dorsal patch had a significantly higher response 12 h after the injection ( $F_{1,11} = 6.92$ ,  $p = 0.02$ ; Fig. 2B). The effect of the covariate was significant for the comparison of  $SI_{12}$  in *L. curasoae* ( $F_{1,42} = 4.76$ ,  $p = 0.03$ ), but not for any other comparison ( $p \geq 0.36$ ). There was a nearly significant

**Table 1** Presence of fresh dorsal patch and testicle condition in males of *Leptonycteris curasoae* and *L. yerbabuena*. Males of *L. curasoae* were captured in Venezuela in November 2012 and males of *L. yerbabuena* were captured in Mexico in May–June 2012

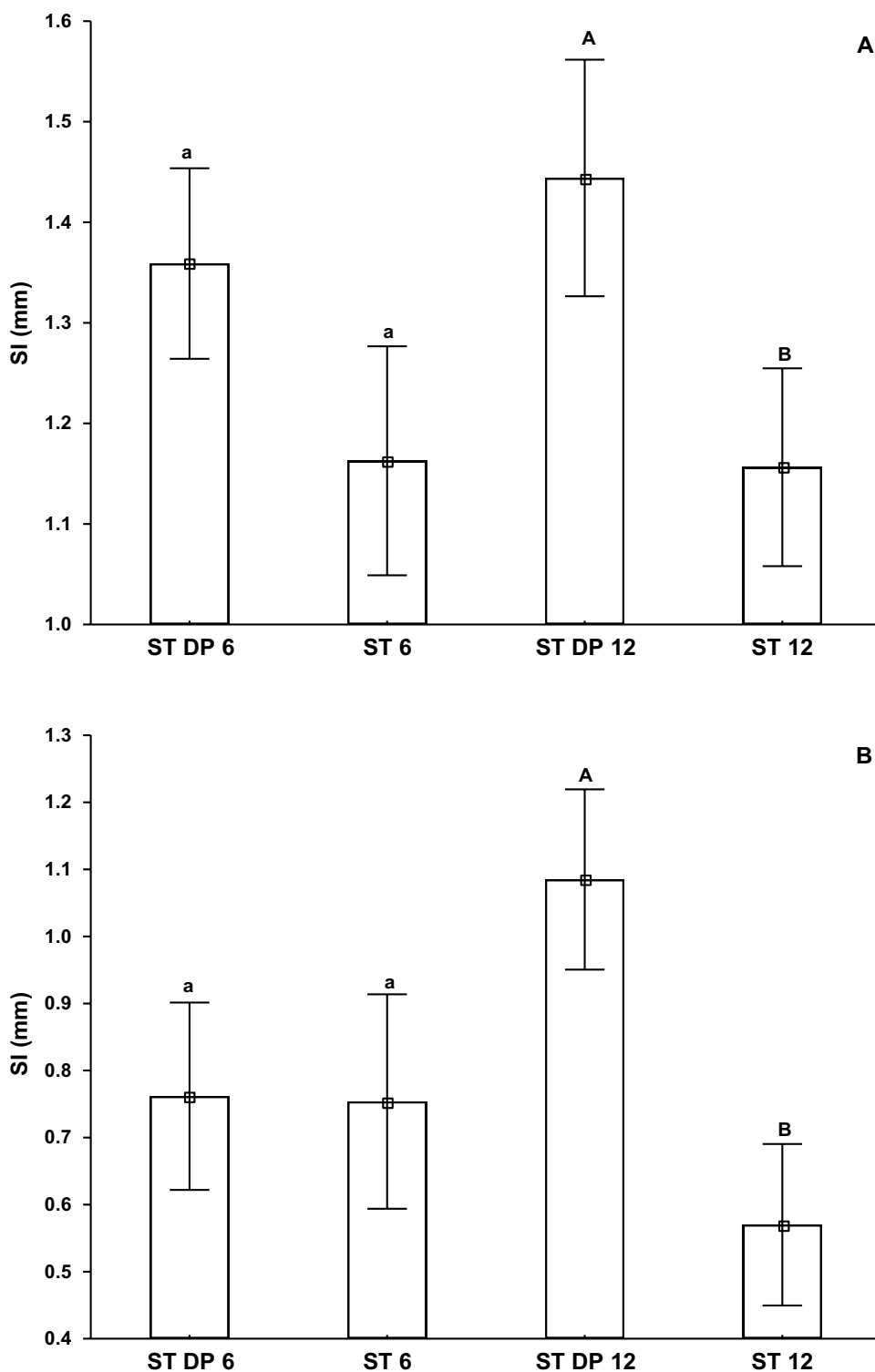
| Species              | Status                                    | BM (g)           | FAL (mm)         | BC (g/mm)       | PD (mm)           | n  |
|----------------------|---|------------------|------------------|-----------------|-------------------|----|
| <i>L. curasoae</i>   | Scrotal testicles with fresh dorsal patch | 27.47 $\pm$ 1.13 | 53.47 $\pm$ 0.20 | 0.51 $\pm$ 0.02 | 16.91 $\pm$ 0.96  | 19 |
|                      | Scrotal testicles without dorsal patch    | 28.90 $\pm$ 0.85 | 53.32 $\pm$ 0.01 | 0.54 $\pm$ 0.01 |                   | 25 |
| <i>L. yerbabuena</i> | Scrotal testicles with fresh dorsal patch | 31.18 $\pm$ 2.54 | 54.80 $\pm$ 0.49 | 0.56 $\pm$ 0.04 | 13.02 $\pm$ 1.56* | 6  |
|                      | Scrotal testicles without dorsal patch    | 29.01 $\pm$ 1.04 | 54.35 $\pm$ 0.26 | 0.53 $\pm$ 0.02 |                   | 8  |

BM, body mass; FAL, forearm length; BC, body condition (BM/FAL); PD, dorsal patch diameter; n, sample size

Values are mean  $\pm$  SE

\*Dorsal patch was measured only in four individuals

**Fig. 2** Swelling index (mean  $\pm$  SE) 6 ( $SI_6$ ) and 12 h ( $SI_{12}$ ) after the injection of phytohemagglutinin in males of *Leptonycteris curasoae* (A) and *L. yerbabuena* (B) presenting scrotal testicles with fresh dorsal patch (ST DP) or without dorsal patch (ST). Significant differences between ST DP and ST were found in  $SI_{12}$  values (uppercase letters) in both species but not in  $SI_6$  values (lowercase letters)



positive relationship between  $SI_{12}$  and  $BC_i$  in *L. curasoae* ( $F_{1, 43} = 3.12$ ,  $p = 0.08$ ,  $r = 0.26$ ), but no significant relationship between patch diameter and any inflammatory indices ( $SI_6$ :  $F_{1, 17} = 0.03$ ,  $p = 0.85$ ,  $r = 0.04$ ;  $SI_{12}$ :  $F_{1, 17} = 1.67$ ,  $p = 0.21$ ,  $r = 0.29$ ).

## Discussion

We found support to our hypothesis that the dorsal patch in males of *L. curasoae* and *L. yerbabuena* could function as a signal of the strength of the individual's innate immune response.

In our comparison, we were careful to consider only males with external signs of reproductive activity (scrotal testicles), because inflammatory response to PHA might vary between reproductive and non-reproductive males (Greenman et al. 2005). As predicted, inflammatory response to PHA was stronger in reproductive males with dorsal patch than in males with no patch. The mean response of males with dorsal patch was ~20 and ~15% higher than that of males of *L. curasoae* and *L. yerbabuena* with no patch, respectively. Inflammation is a key component of innate immune defense because pro-inflammatory cytokines activate immune sentinel cells that protect from pathogens (van der Veerdonck et al. 2011). A stronger inflammatory response might confer advantage to males of long-nosed bats during the mating season, when population density increases (Galindo et al. 2004; Rincón-Vargas et al. 2013), expanding the risk of transmission of pathogenic microorganisms (Nunn et al. 2000). A previous work with birds shows that a higher inflammatory response is positively correlated with the abundance of lymphocytes and neutrophils at the site of PHA injection (Martin et al. 2006). The functional significance of PHA-induced swelling in bats has been examined only in Brazilian free-tailed bats (*Tadarida brasiliensis*). Although PHA injection increases the presence of leukocytes, the magnitude of swelling has a marginally positive correlation with basophil abundance and no correlation with the abundance of other leukocytes (lymphocytes, neutrophils, macrophages, and eosinophils; Turmelle et al. 2010). Therefore, further work should examine if a higher inflammatory response among males of long-nosed bats is accompanied by a higher recruitment of specific types of leucocytes or rather by an increase of total leukocytes.

Our findings are concurrent with previous work conducted with other vertebrates that also found a positive relationship between the strength of PHA inflammatory response and the expression of sexual secondary traits. With some exceptions (Garvin et al. 2008; Vinkler et al. 2012; Merrill et al. 2014), the inflammatory response to PHA injection is stronger in males showing more attractive secondary sexual traits in birds (Blount et al. 2003; Faivre et al. 2003; Mougeot et al. 2009; Trigo and Mota 2015; York et al. 2016), reptiles (Martín and López 2010; Vroonen et al. 2013; Plasman et al. 2015), and amphibians (Iglesias-Carrasco et al. 2016). To the best of our knowledge, our work is the first study testing this relationship in mammals.

It is unknown what determines that reproductive males of long-nosed bats present or not the dorsal patch. The dorsal patch develops in males of *L. curasoae* and *L. yerbabuena* after the deposition on their interscapular region of fluids collected from different parts of their body (the mouth, head, penis, and anus; Nassar et al. 2008; Muñoz-Romo and Kunz 2009). It is possible that males that do not develop the dorsal patch do not show this behavior. Alternatively, even if bats engage on this behavior, the development of the patch might be contingent on the composition of the microbiota contained in

the body fluids transferred. Fermentative bacteria are reported in the dorsal patch of *L. yerbabuena* (Gaona et al. 2019), and the activity of these microorganisms might be responsible for the production of some chemical compounds identified in dorsal patches (Muñoz-Romo et al. 2012). However, there is no information of the microbiota in the interscapular region of males that do not develop the patch, nor of the microbiota present in the body parts contacted by males to form the dorsal patch. There is evidence that microbiota composition determines the expression of the innate immune response of bats (Ingala et al. 2019). Accordingly, a stronger inflammatory response in males that develop a dorsal patch might be related to the individual's microbiota composition, which probably determines the development and chemical composition of the patch. Further work should fill these gaps to test the hypothesis that the presence of the dorsal patch and the strength of the inflammatory response might be indirectly related via the individual's microbiota composition of male long-nosed bats.

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**Author contribution** Study conception and design was performed by L. Gerardo Herrera M. and J. M. Nassar. Material preparation and data collection were performed by all authors; data analyses were performed by L. Gerardo Herrera M. The first draft of the manuscript was written by L. Gerardo Herrera M., and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data Availability** Data is readily available under request to correspondent authors.

## Declarations

**Ethical approval** The study followed the considerations for the welfare of the study animals stated in the permits for scientific work provided by the Ministerio del Poder Popular para el Ambiente (#0966) and by the Dirección General de Vida Silvestre (#02082/12) in Venezuela and Mexico, respectively.

**Competing interest** The authors declare no competing interest.

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