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Resting posture drives the evolution of agonistic displays in bats

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Abstract

Agonistic displays are one of the most diverse social behaviors that have important functions in animal's life history. However, their origin and driving factors have largely been unexplored. Here, we evaluated agonistic displays of 71 bat species across 10 families and classified these displays into two categories: (a) *boxing displays* where a bat attacks its opponent with its wrist and thumb and (b) *pushing displays* where a bat uses its head or body to hit a rival. We estimated the strength of the phylogenetic signal of the agonistic displays, revealed their origin, and tested the potential evolutionary relationships between agonistic behaviors and body size or resting posture (free hanging vs. contact hanging where the bat is in contact with some surface). We found that agonistic displays were phylogenetically conserved and that boxing displays are the ancestral state. Moreover, we found that bats with a free-hanging resting posture were more likely to exhibit boxing displays than pushing displays. In addition, bats with longer forearms do not have a higher propensity for boxing displays. This study expands our limited knowledge of the evolution of agonistic displays and highlights the importance of resting posture as a driving force in the diversity of agonistic displays.

Keywords: agonistic displays, Chiroptera, ancestral state, posture

Introduction

Agonistic displays are common in the animal kingdom. They can be defined as any behaviors associated with conflict or competition, including fighting, threat, defense, flight, freezing, and avoidance (Hardy & Briffa, 2013). Agonistic displays fulfill various functions such as territorial or mate defense or food competition (Scott, 1971). Agonistic displays also have important implications for fighting strategies. Agonistic displays can contain information about the fight ability of the signalers or can impart measurable costs on competitors. These displays should therefore enable competitors to assess a rival's competitive ability or to assess their own energetic thresholds conditional on an agonistic interaction, and thus allow the contestants to utilize adaptive assessment strategies (Arnott & Elwood, 2009). Therefore, the knowledge of how agonistic displays evolve and how they are evolutionarily maintained in animals is important for understanding game theoretic consequences of agonistic interactions.

Phylogenetic constraints are potentially important in understanding the direction and rate of evolution of behavioral traits (Harvey & Pagel, 1991). A weak or absent phylogenetic signal indicates the presence of traits that are evolutionary labile.

Similar traits shared among closely related species result in high phylogenetic signal (Blomberg et al., 2003; Pagel, 1999). There is a widespread belief that behavioral traits are usually more labile, and they exhibit lower phylogenetic signals than other types of traits such as morphological traits (Blomberg et al., 2003). There were two main possibilities that might explain this pattern: (a) behavioral plasticity: behavioral traits can be modified in response to environmental cues and this plasticity allows individuals to adjust their behavior based on changing conditions, resulting in greater variability and a lower phylogenetic signal (Van Buskirk, 2002). (b) cultural transmission: since some behavior traits are learned and transmitted through social interactions, these learned behaviors can change quickly within populations without genetic changes, leading to higher lability and lower phylogenetic signal (Beans, 2017). However, not all behavioral traits exhibit high lability and lower phylogenetic signal, as some traits may have a relatively strong genetic basis and thereby exhibit more stability across species or populations (Arato & Fitch, 2021). In addition to understanding the direction and rate of behavioral trait evolution, it is also important to uncover the origin of behavioral traits because the variation

in behavior within and between lineages can provide clues to both its functions and underlying mechanisms (Hernández et al., 2021). Unfortunately, we know little about the phylogenetic signals and ancestral characters of agonistic displays.

The evolution of behavioral traits can be associated with the evolution of correlated traits such as body size and resting posture. Body size has been suggested as a main driver of the evolution of behavioral traits in many animals (Jenkins & Breck, 1998; Kang et al., 2017; Zhang et al., 2022). This is probably because large body size is generally related to higher resource-holding potential (Parker, 1974). Additionally, the resting posture of shorebirds, for example, has been shown to affect their alert and escape behaviors (Timmis et al., 2022). However, no studies have systematically investigated how traits influence the agonistic displays of animals on an evolutionary scale nor has there been a systematic analysis of phylogenetic signals and ancestral character states of agonistic displays.

Bats (Mammalia: Chiroptera) are an ideal taxon for understanding the origin of agonistic displays and the potential factors contributing to their evolution. They represent a taxon that has one of the highest diversities of agonistic displays among vertebrates, ranging from short and relatively simple actions, such as baring of teeth, pushing at conspecifics, or defensive posturing (Gadziola et al., 2012; Lin et al., 2015; Zhao et al., 2018), to long and elaborate ritualized agonistic displays, resulting in a succession of behavioral stages from low levels of aggression (bared teeth, slightly pulled up body and/or wings) to high levels of aggression (rapidly flapping wings, boxing, biting or wrestling; Clement & Kanwal, 2012; Fernandez et al., 2014; Sun et al., 2019). Among the agonistic displays by bat species, two types of agonistic displays are particularly common: *pushing displays* and *boxing displays*. The pushing display occurs when one individual approaches another and uses its body or head to try to move and displace its opponent (Figure 1A; Supplementary Video S1). The boxing display occurs when one bat approaches another and swings its forearm at the other bat, making contact with its wrist and thumb (Figure 1B; Supplementary Video S2). It is relatively easy to differentiate pushing displays from boxing displays, but differentiating nonphysical agonistic displays can be more challenging. Although pushing and boxing displays are physical combat, they can also represent aggressive or agonistic communications if the posture itself provides information about further moves by the aggressor. The complex information processing from aggressive signals and from the costs inflicted by the rival during physical combat can influence animals' adoption of different fighting strategies (Mesterton-Gibbons & Heap, 2014).

Some bat species only show pushing displays; some species only have boxing displays; other species show both pushing and boxing displays (C. Sun, personal observation). This diversity provides a unique chance to study the evolution of agonistic displays using the comparative method. Additionally, bats exhibit a specific upside-down resting posture. The resting posture of bats can be classified into two categories: (a) *free hanging* is where the bat's two feet hang from the roof of the cave or from a branch, with both forearms naturally drooping without touching anything (Figure 1B) and (b) *contact hanging* is where the bat hangs with 2 feet but also contacts a vertical surface using both forearms (Figure 1A; Kunz & Fenton, 2005). The specific resting posture might be an important trait associated with the evolution of agonistic displays, considering that the agonistic interactions occur frequently when bats are roosting and the specific posture itself will constrain the type of agonistic interaction that can occur between opponents.

In this study, we use data on agonistic displays in 71 bat species from 10 families to address the following three specific questions in a phylogenetic comparative framework: First, do agonistic displays have a phylogenetic signal? Our hypothesis was that agonistic displays in bats would suffer phylogenetic constraints because agonistic displays play a crucial role in determining social rank, survival, or reproductive success, and therefore, they may be influenced by genetic factors that regulate social interactions and social status. Therefore, we predicted that there would be a high phylogenetic signal in agonistic displays.

Second, which agonistic displays appeared earlier in evolutionary history? We hypothesized that boxing displays would
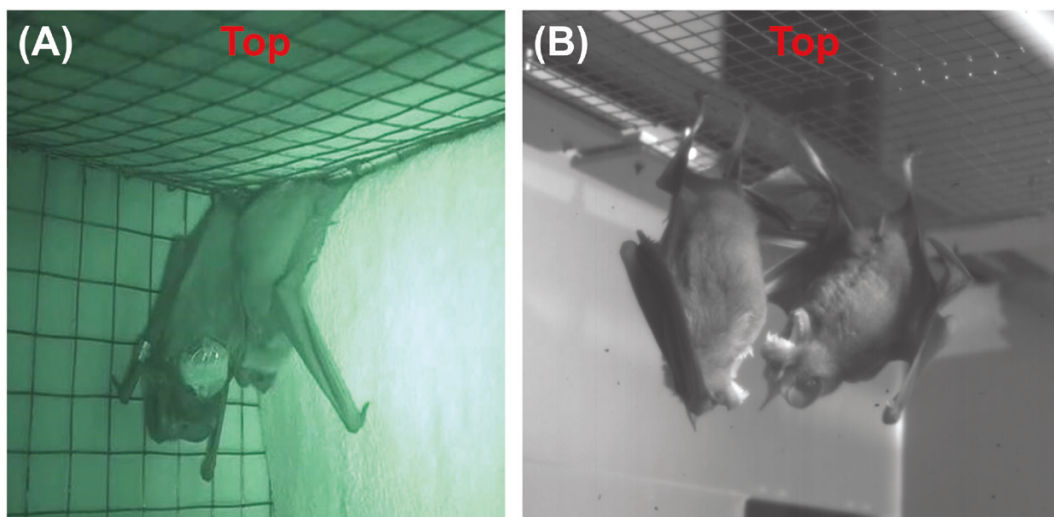
Figure 1. Typical examples of agonistic displays in bat species. (A) Two Asian particolored bats (*Vespertilio sinensis*) perform pushing displays by hitting the opponent with their head or body. (B) Two great Himalayan leaf-nosed bats (*Hipposideros armiger*) conduct boxing displays by knocking the opponent with their wrist and thumb.

be the ancestral state because boxing displays may be a more efficient means of conflict resolution in physical contests with a more rapid assessment of their opponent's fighting ability and lower energy expenditures than pushing displays. Thus boxing displays should help reduce fighting costs by decreasing the number of agonistic interactions or the time and energy spent on a contest. Therefore, we predicted that the reconstructed ancestral node would be boxing displays.

Third, how are forearm length and resting posture associated with agonistic displays? Our hypothesis was that (a) forearm length and (b) resting posture would influence the evolution of agonistic displays. We assume that (a) larger species may be better at tolerating other bats and thus should require a more potent aggression to initiate a fight and (b) species with a free-hanging resting posture may prefer to use their free forearms to fight each other, while species with a contact-hanging resting posture may tend to fight each other using the head or body. This leads to the prediction that species with (a) longer forearm length and (b) a free-hanging resting posture would be more likely to exhibit boxing displays than pushing displays.

Materials and methods

Database of bat agonistic displays

Datasets on fighting behavior of bat species came from three sources: (a) literature search using the Web of Science database and Google Scholar by searching with the following terms: ("bats" + "aggressive behaviour" or "agonistic behaviour" or "fighting" or "aggression") or personal communication with the author of the literature; (b) agonistic display videos from YouTube obtained by searching with the keywords "bats" + "aggressive behaviour" or "agonistic behaviour" or "fighting" or "aggression"; and (c) fighting behavior videos from our own recordings (see Supplementary Materials for detailed recording process). See Supplementary Table S1 for a list of sample sizes and references for each species. Bats were classified into the following three categories according to their agonistic displays: (a) *pushing displays*, (b) *boxing displays*, and (c) *both pushing and boxing displays*. In total, we obtained information on agonistic displays of 71 bat species (Supplementary Table S1).

Phylogenetic signal

To test the phylogenetic signals in fighting behaviors, we used the time-calibrated mammal supertree (Faurby & Svenning, 2015), which integrated 1,146 bat species within the order Chiroptera. To reduce the impact of phylogenetic uncertainty on our analyses, we randomly chose and employed 100 trees from the set. The phylogenetic signal was tested using the δ-approach of Borges et al. (2019). A high positive δ-value indicates a higher phylogenetic signal (Borges et al., 2019). The significance of the δ-value was determined based on 100 iterations. The phylogenetic signal was calculated using the "delta" function of the "ape" package (Paradis & Schliep, 2019).

Ancestral character reconstruction

We reconstructed ancestral character states at internal nodes of the tree using the "ace" function in the R package "ape" (Paradis & Schliep, 2019). Specifically, we adopted three different models to reconstruct the ancestral characters of agonistic displays: (a) the equal rate (ER) model assumes

that transitions between any pair of characters occur at the same rate, (b) the symmetric rate (SYM) model assumes that transitions between any pair of characters occur at the same rate regardless of direction, but that the rate of change differs among states, and (c) the all rates different (ARD) model assumes that all transitions between pairs of characters can occur at different rates (Keating, 2023). We used the "fitDiscrete" function in the R package "geiger" (Harmon et al., 2008) to compare these three models and chose the model with the lowest corrected Akaike information criterion (AICc) value.

Species traits correlation

We collected data on bat forearm length and resting posture from the published literature (Supplementary Table S1). The forearm length is a better indicator of body size than body mass because the adult bat forearm length does not vary much across seasons or with variations in food intake rate (Bogdanowicz et al., 1999). Resting postures of bats were separated into two categories: free hanging and contact hanging (as defined above).

Statistical analysis

There are three aggressive display strategies: boxing only, pushing only, and both boxing and pushing. Our phylogenetic analyses included all three strategies, although only five species showed both types of displays.

We used multivariate phylogenetic generalized linear mixed models (PGLMMs) to assess the effects of predictor factors on agonistic displays. We focused on boxing-only and pushing-only species for these analyses, which allowed us to look at species-level comparisons of these two strategies. We excluded the both boxing and pushing species for analyses because only (7%) of our species showed this trait, providing low confidence in the patterns associated with this species category. Setting 1 for pushing displays and 0 for boxing displays, we ran PGLMMs with a binomial distribution with 100 randomly chosen phylogenetic trees using the R packages "phyr" and "ape" (Harmon et al., 2008; Ives et al., 2020). We considered forearm length and resting posture (free- vs. contact-hanging) as predictors. In addition, to test the effect of each trait and for interactions between phylogenetic signal and traits, we also conducted single-variable PGLMMs.

Results

Phylogenetic signals of agonistic displays

In total, we collected data from 71 bat species in 10 families (Supplementary Table S1), including Vespertilionidae ($N = 20$), Miniopteridae ($N = 1$), Rhinolophidae ($N = 10$), Hipposideridae ($N = 7$), Phyllostomidae ($N = 10$), Pteropodidae ($N = 10$), Molossidae ($N = 4$), Mormoopidae ($N = 1$), Megadermatidae ($N = 3$), and Emballonuridae ($N = 5$). The studies were performed on East Asian, Western European, and American bats (Figure 2A).

There was a strong phylogenetic signal of agonistic displays ($\delta = 8.53$, $P < 0.001$; Figure 2B). All species of Pteropodidae, Rhinolophidae, and Hipposideridae showed boxing displays. All species of Molossidae had both pushing and boxing displays. Most species of Vespertilionidae had pushing displays, except for one species (*Myotis myotis*) with boxing displays. Most species of Phyllostomidae showed boxing displays, except for one species (*Phyllostomus discolor*) with both
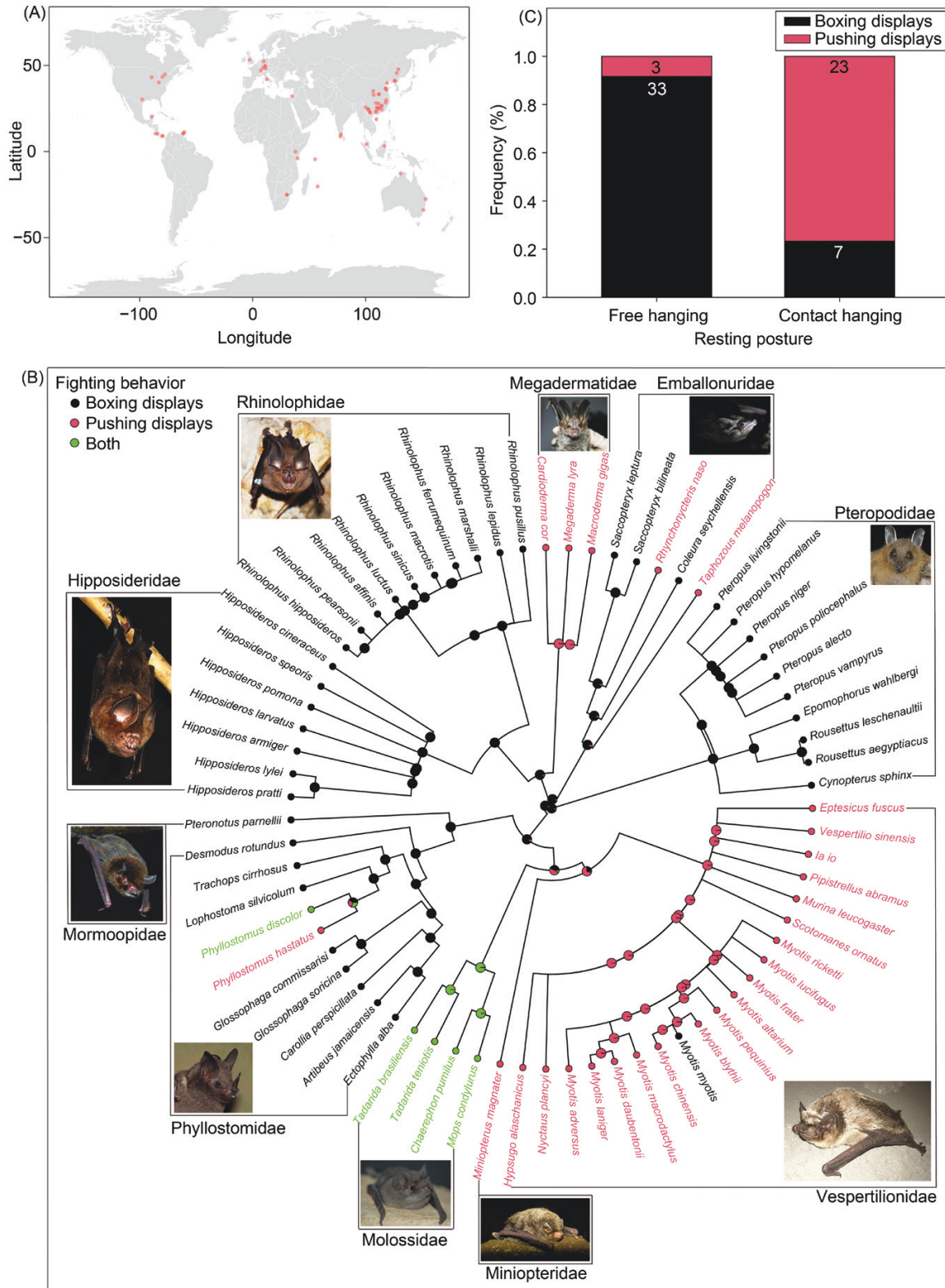
Figure 2. (A) The study locations (red dots), (B) phylogenetic tree of bat species (*N* = 71 species) with the reconstructed ancestral state. For internal models in the tree, the posterior probability of agonistic displays reconstructed using the "ace" function from the R package "ape" is shown. Pie colors indicate three states (i.e., "Boxing" = black, "Pushing" = red, and 'Both' = green). Small dots (with three colors) at each tip of the tree indicate three categories of agonistic displays of species. Images of the periphery of the phylogenetic tree represent ten bat families. (C) The association of resting posture with the probability of boxing or pushing behavior. The values in each histogram indicate the number of bat species. Photograph credits: Huang Xiaobin (Rhinolophidae: *Rhinolophus ferrumequinum*; Pteropodidae: *Cynopterus sphinx*), Burton Lim (Mormoopidae: *Pteronotus parnellii*), Sun Congnan (Hipposideridae: *Hipposideros armiger*; Miniopteridae: *Miniopterus magnater*), Maël Dewynter (Phyllostomidae: *Carollia perspicillata*), Dan Neubaum (Molossidae: *Tadarida brasiliensis*), Zhao Xin (Vespertilionidae: *Vespertilio sinensis*), Lin Aiqing (Emballonuridae: *Taphozous melanopogon*), Shi Biye (Megadermatidae: *Megaderma lyra*).

pushing and boxing displays and one species (*P. hastatus*) with pushing displays.

The ancestral character of agonistic displays

We analyzed three models (i.e., "ARD," "ER," and 'SYM' models) to reconstruct the ancestral character of agonistic displays and found that the ER model was the best-fit model (logLik$_{ER}$ = –31.71, AICc = 65.48) compared with the ARD model (logLik$_{ARD}$ = –29.16, AICc = 71.63) and the SYM model (logLik$_{SYM}$ = –30.42, AICc = 67.20). This "ER" model showed that boxing displays were most likely the ancestral state (Figure 2B).

Trait correlations

In multivariate and single-variable models, the PGLMM showed that bats with longer forearm length did not have a higher propensity for boxing displays compared with those with relatively short forearm length (Table 1), but the bats with a free-hanging resting posture had a larger propensity for boxing displays than those with a contact-hanging resting posture (Table 1; Figure 2C). All 100 random phylogenetic trees led to the same results, which indicates that the effects of the resting posture are robust.

Discussion

We found that agonistic displays were phylogenetically conserved, which supported our first hypothesis that agonistic displays in bats were not random across phylogenies. Moreover, we found that boxing display was the basal state, which supported the second hypothesis that boxing display was the ancestral behavior. Finally, we found that resting posture but not forearm length was correlated with agonistic displays, which supported the fourth hypothesis that resting posture would be influential in shaping the aggressive behavior but did not support the third hypothesis that body size would affect the evolution of agonistic displays.

We found a strong phylogenetic signal for agonistic displays in bats, indicating phylogenetic constraints for agonistic displays. Thus, closely related bat species are more likely to have similar agonistic displays than distantly related taxa. This tendency of similar behavioral design between closely related species is common in other taxa, ranging from insects (Vidal-García et al., 2020), amphibians (Carvajal-Castro et al., 2020), birds (Remeš et al., 2015), and mammals (Zhang et al., 2022). Why do the agonistic displays of bats have such high phylogenetic signal? One possible interpretation is that from a mechanistic point of view, phylogenetic constraints of behaviors can result from genetic inheritance of behaviors across generations, and eventually across species (Dugatkin et al., 2020). Similar phenomena may be showing up in bats and birds, which possess some genetic signatures in their vocal behaviors (Arato & Fitch, 2021; Luo et al., 2017).

Our data showed that boxing displays are likely to be the ancestral state, whereas pushing displays and the both pushing and boxing displays have multiple independent origins (Figure 2B). Our data also show that roosting behavior is an important driver of agonistic displays. Roosting postures have also been proposed to affect a number of behavioral traits (Timmis et al., 2022). Our data show that families at the base of the bat phylogenetic tree fall within the category of boxing displays and the resting posture of these bats is a free-hanging posture. Subsequently, this ancestral state evolved toward two alternative agonistic displays with a change of resting posture, either to pushing displays or to both pushing and boxing displays. Resting postural changes could have affected the use of different body parts during aggressive interactions and thus bats' agonistic displays, indicating that roosting posture might be a main driving force of agonistic display evolution (see below).

To our knowledge, this is the first study that identifies the relationships between resting posture and agonistic displays in animals. We found that bats with a free-hanging resting posture, rather than those with a contact-hanging resting posture, tend to perform boxing displays. This pattern is significant irrespective of whether or not phylogeny was controlled for. The reasons behind these relationships have not been explored. Agonistic interactions of bats usually occur when bats are roosting. Bats that use a free-hanging resting posture generally hang upside down suspended from above with their two forearms naturally drooping without touching anything. This may allow bats to fight each other using their idle forearms. In contrast, bats with a contact-hanging resting posture generally contact surfaces with both feet and forearms. As such, it appears more efficient for these bats to aggress each other using the head or body to push each other compared to using forearms. A similar phenomenon has been documented in several taxa. For example, nonhuman primates and marsupials, which have unencumbered forelimbs, tend to fight with their hands, while some ungulates that use their forelimbs for walking or for supporting their bodies tend to fight with their head or body (Hardy & Briffa, 2013).

In contrast to previous studies (Jenkins & Breck, 1998; Kang et al., 2017; Zhang et al., 2022), we found that there was no significant association between forearm length and agonistic displays, suggesting that a size-related morphological constraint did not affect the evolution of agonistic displays in bats. The decoupling of body size and behavioral displays has been documented in Qinghai toad-headed agamas, *Phrynocephalus vlangalii* (Peters et al., 2016), salamanders (Vági et al., 2022), and praying mantises (Vidal-García et al., 2020). One possible interpretation of this phenomenon is that

Table 1. Effects of predictor variables on bats' fighting behavior based on phylogenetic generalized linear mixed models (PGLMM).

Statistics method	Predictors	Estimate	*Z* value	*P* value
PGLMM	Single-variable model			
	Forearm length	–0.006	–0.275	0.783
	Resting posture	3.223	2.130	**0.033**
PGLMM	Multivariable model			
	Forearm length	0.003	0.123	0.902
	Resting posture	3.293	2.039	**0.041**

body size does not fully affect the type and transmission distance of dynamic visual cues in bat species because agonistic interactions usually occur in dark environments and bats may also use other sensory modes such as scent or sound to communicate.

In addition to resting posture, we believe that the evolution of agonistic displays in bats may be shaped by many other driving forces. For example, brain size drives the evolution of animals' behaviors because it is related to animals' cognition (Liao et al., 2022; Lindsay et al., 2015; Zhang et al., 2022). Habitat structure has been indicated as an environmental factor in shaping gestural displays in birds because it can influence the effectiveness of signal transmission (Menezes & Santos, 2020; Mikula et al., 2022). Moreover, group size, the number of sympatric species, or social organization have been suggested as social factors in driving the evolution of more complex gestural displays at least because individual discrimination is more difficult when an increasing number of individuals need to be differentiated (Fichtel & Kappeler, 2022; Nelson et al., 2022). However, we cannot test these hypotheses with our data set because there are few data for the above factors in bats. Thus, the accumulation of physiological, environmental, and social data of many abundant species will help reveal a more complete picture of the evolution of fighting behaviors in bats.

A limitation of our study needs to be considered. The potential for available data to be biased may affect our results. We have data on 71 species from 10 families (Vespertilionidae, Miniopteridae, Rhinolophidae, Hipposideridae, Phyllostomidae, Pteropodidae, Molossidae, Mormoopidae, Megadermatidae, and Emballonuridae), which suggests a taxonomic bias of studies of agonistic behaviors. This bias may result from a preference to study abundant species. Therefore, more behavioral data from less abundant bat species will provide a more comprehensive picture of the evolution of agonistic behaviors in bats.

In conclusion, our study demonstrated that the evolution of boxing displays and pushing displays in bats is a conserved trait, and resting posture is critical in shaping these agonistic displays. Boxing displays appear to be the ancestral state, and pushing displays and pushing + boxing displays appear to have evolved multiple times independently. These results offer significant cues for understanding the evolution of different agonistic behaviors in animals. We also call for exploring the agonistic displays of more taxa and using more advanced technology like the pose estimation tool DeepLabCut for elaborate behavior tracking and quantifying descriptions of multiple display components in future studies (Wiltshire et al., 2023).

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

The data supporting the results of the article are available as Supplementary Material.

Author contributions

C.M.Z. and C.N.S. participated in study design, analyzed the data, and wrote the manuscript. L.G.J. and Z.J.L. collected

the data and assisted with data analysis. J.R.L., J.F., and T.L.J. revised the manuscript. All authors have read and agreed to the published version of the manuscript.

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