Behavioral Ecology and Sociobiology (2019) 73: 45
https://doi.org/10.1007/s00265-019-2657-0

ORIGINAL ARTICLE

Self-assessment strategy during contest decisions between male Great Himalayan leaf-nosed bats

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Received: 18 June 2018 / Revised: 28 February 2019 / Accepted: 8 March 2019 / Published online: 16 March 2019

Abstract

Agonistic interactions in animals are often settled based on the rules of an assessment strategy. We tested the predictions of evolutionary game theory models (including two models based on self-assessment: (a) the energetic war of attrition model, (b) the cumulative assessment model, and a third model (c) based on mutual assessment model) during contests between males of the Great Himalayan leaf-nosed bat *Hipposideros armiger*. We also studied the potential proxies of resource holding potential (RHP: body mass and forearm length) and their relationship to contest duration and the level of escalation. Overall, heavier males won more contests than lighter males, and they had an advantage in physical fights. In physical contests, the contest duration was positively correlated with the body mass of the loser but not the body mass of the winner. These results supported the prediction that males make decisions based on their own RHP (self-assessment: the energetic war of attrition model) rather than on RHP of their opponent (mutual assessment). Contest duration was not related to the forearm length of the winner or the loser. No relationship between body size (i.e., body mass and forearm length) and contest duration was observed for non-physical contests. This did not support any of the predictions applying to the energetic war of attrition model, the cumulative assessment model, and the mutual assessment model, indicating that no assessment occurred during non-physical contests. This study provides the first empirical evidence that bats make decisions based on their own RHP during agonistic interactions.

Significance statement

This study provides empirical evidence supporting the hypothesis that during physical contests bats make decisions based on estimates of their own ability (self-assessment) rather than on a process of mutual assessment. This finding will facilitate comparative studies of fighting strategy across bat species.

Keywords Agonistic behavior · Agonistic interaction · *Hipposideros armiger* · Mutual assessment · Self-assessment

Introduction

Competition for limited resources, such as mates, food, shelters, or territories is common in most animal species (Bradbury and Vehrencamp 2011). This competition can involve physical fighting that involves injury risk and energy expenditure, and may result in death (Enquist and Leimar 1990; Briffa and Elwood 2004; deCarvalho et al. 2004). Thus, most animals are usually interested in resolving combat before escalating to costly physical contests (Bradbury and Vehrencamp 2011). Game theory models are beneficial in understanding how and why contests are resolved (Maynard Smith 1982; Briffa 2015). Game theory provides three main fighting strategy models to explain how contestants acquire information about resource holding potential (RHP, defined as "fighting ability"; Parker 1974) to permit them to decide to

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Communicated by M. Knörnschild

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-019-2657-0) contains supplementary material, which is available to authorized users.

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quit or persist in a contest. These assessment models are the energetic war of attrition model (E-WOA), cumulative assessment (CAM), and mutual assessment (Arnott and Elwood 2009). The E-WOA and CAM are considered to be self-assessment models (Taylor and Elwood 2003). Animals can adopt a single assessment strategy during a contest or use different assessment strategies during different phases of an agonistic interaction (Morrell et al. 2005; Hsu et al. 2008; Arnott and Elwood 2009).

The energetic war of attrition (E-WOA; Payne and Pagel 1996, 1997) model assumes that decision-making is based only on individual energetic thresholds. The model predicts that fight duration and intensity should be strongly positively related to the loser's RHP but there should be a weaker or even insignificant positive relationship with the winner's RHP (Taylor and Elwood 2003). This is because weaker contestants tend to reach their limits and give up first (Taylor and Elwood 2003). In the amphipod *Gammarus pulex*, males have been shown to follow E-WOA during contest resolution; contest duration was positively related to the body mass of the loser but not the body mass of the winner (Prenter et al. 2006).

The cumulative assessment model (CAM) (Payne 1998) shows that decision-making is based on a combination of individual energetic thresholds and costs inflicted by the rival. The CAM predicts a significant positive relationship between the loser's RHP and contest duration and intensity, but a significant negative relationship between the winner's RHP and contest duration and intensity (Arnott and Elwood 2009). In the fiddler crab *Uca mjoebergi*, males apparently adopted a CAM strategy, because contest duration increased with both the loser's claw size and the average competitor's claw size, and decreased, but to a lesser extent, with the winner's claw size (Morrell et al. 2005). This fighting strategy is adopted by many animals such as the Wellington tree weta *Hemideina crassidens* (Kelly 2006), the house cricket *Acheta domesticus* (Briffa 2008), the cyprinodont fish *Aphyosemion striatum* (Payne 1998), and the cape dwarf chameleon *Bradypodion pumilum* (Stuart-Fox 2006).

Mutual assessment models, such as the sequential assessment model (SAM; Enquist and Leimar 1983; Enquist et al. 1990), suggest that decisions are based on the assessment of their opponent's RHP relative to their own RHP. SAM predicts a significant positive relationship between the RHP of the loser and contest duration and intensity, and a significant negative relationship between the RHP of the winner and contest duration and intensity (Taylor and Elwood 2003). In the mantis shrimp *Neogonodactylus bredini*, individuals apparently fight using an SAM strategy, because contest duration increased with increasing mass of the loser, decreased with increasing mass of the winner, but was unaffected by average competitor mass (Green and Patek 2018). Other examples of SAM are found in animals such as the wasp *Hemipepsis ustulata* (Kemp et al. 2006), the sand fiddler crab *Uca pugilator* (Pratt et al. 2003), and the cichlid fish *Nannacara anomala* (Enquist et al. 1990).

Individual resource holding potential (RHP) is usually positively related to body size (Stamps and Krishnan 1994; Draud and Lynch 2002) or weapon size (Barki et al. 1997; Sneddon et al. 1997) because larger combatants are normally more successful in escalated physical contests (e.g., Wells 1988; Briffa 2008; Hsu et al. 2008; Rudin and Briffa 2011). E-WOA can be distinguished from CAM and SAM based on the relationship between contest duration/intensity and the winner's RHP (E-WOA positive and CAM/SAM negative; Taylor and Elwood 2003; Arnott and Elwood 2009). CAM can be differentiated from SAM based on the relationship between contest duration/intensity and the mean RHP between closely RHP-matched pairings (CAM positive relationship and SAM no relationship; Arnott and Elwood 2009).

Agonistic behavior and fighting strategies have been investigated in animals such as crickets (Briffa 2008), spiders (Bridge et al. 2000), fishes (Enquist et al. 1990; Payne 1998; Hsu et al. 2008), anurans (Reichert and Gerhardt 2011), chameleons (Stuart-Fox 2006), deer (Jennings et al. 2004), and monkeys (Benítez et al. 2017). In bats, however, studies on agonistic behavior are rare because they live in dark environments (Bastian and Schmidt 2008; Clement and Kanwal 2012; Gadziola et al. 2012; Fernandez et al. 2014; Luo et al. 2017). It is unclear whether bats make contest decisions according to their own RHP (self-assessment) or to their opponent's RHP relative to their own (mutual assessment) during agonistic interactions.

The Great Himalayan leaf-nosed bat, *Hipposideros armiger*, has a wide distribution range in mainland East Asia (Bates et al. 2008). *H. armiger* is a suitable model for studying agonistic interactions because individuals are daily involved in agonistic encounters. Our preliminary observations in the field and in the laboratory found that *H. armiger* in diurnal roosts usually maintains a 10–15 cm minimum spacing between individuals (see Supplementary Material, Fig. S1) and both sexes are daily involved in agonistic displays to defend their day-roost territory (i.e., broadband calls, teeth baring, wing flapping, boxing, or wrestling) (CS, pers. observ.). Agonistic interactions occur within and between the sexes (CS, pers. observ.). Since *H. armiger* has a harem mating system and forms groups including one male and several females (Yang 2011), it is possible that males defend a territory against other males and that females defend their perching space against other females within one male's territory during the entire day, especially when returning from foraging (CS, pers. observ.). Similar behaviors are found in the bat species *Saccopteryx billineata*, *Saccopteryx leptura*, and *Rhynchonycteris naso* (Bradbury and Emmons 1974).

We hypothesized that males of *H. armiger* with either large body mass and/or longer forearm length would be more successful in fights compared to those with relatively small body mass/forearm length. This hypothesis is based on two observations. First, body size of an individual is associated with fighting success in many taxa including bats (Williams 1986; McWilliam 1988; Archer 1998; Arnott and Elwood 2009). Second, we can assume that in the dark, forearm length and body mass are used as proxies for self-assessment of RHP since mutual assessment is more difficult without physical contest. As a test of this hypothesis, we made the following three predictions: (1) if a positive relationship between the loser's body size and contest duration is detected, and a weaker or an insignificant positive relationship between the winner's body size and contest duration also is observed, opponents are using self-assessment, and E-WOA would be the most appropriate model; (2) if a strong positive relationship between loser's body size and contest duration, and a strong negative relationship between winner's body size and contest duration, then the contestants are adopting mutual assessment or CAM. In order to distinguish CAM from mutual assessment, we further predicted (3) if a positive relationship between mean body size of size-matched opponents and contest duration is detected, opponents are adopting CAM. If no such relationship is detected, opponents are adopting SAM.

Methods

Acquisition and maintenance of animals

Since it was necessary to test alternative assessment models using a large sample size (Hsu et al. 2008; Reichert and Gerhardt 2011), in August–November 2017, we captured 230 adult males of *H. armiger* by mist nets from 3 localities in south China, including individuals from Hanzhong (96 males), Puer (88 males), and Hekou (46 males). The maximum and minimum distances between localities were 1297 km and 329 km, respectively. *H. armiger* bats from those sites may be not likely to encounter one another in the wild. Males were considered adult (> 1-year-old) if they had epididymides or enlarged testes (or both), a sealed epiphyseal gap, brown fur, and worn canine cusps (Cheng and Lee 2002). Captured adults were housed in two rooms (5 m × 3 m × 3 m each). Each room was equipped with an outdoor mosquito net (2 m × 1.8 m × 1.9 m) at a relative humidity around 65% and an ambient temperature between 22 and 25 °C. The bats in the mosquito net were separated individually by cloth but could move freely. There were eight, or fewer, adult male *H. armiger* in each mosquito net. Males captured at the same site were housed separately to assure that males encountering each other in fights were unfamiliar to each other. We captured adult males every 1–2 days. There was a turnover of bats every 1–2 days. Captured males were housed for at least 24 h in a flight cage before being used in an experiment. On the second day, males were used in behavioral experiments and the two males that engaged in the agonistic interaction were transferred back to the mosquito net they used to be before trial. On the third day, individuals that engaged in combat were released into the wild, and we captured other adult male. In order to avoid recapturing the tested bats, we marked individuals with odorless and nontoxic nail polish applied to the lower back before releasing them. This marking procedure has previously been used in bat studies (Kunz and Weise 2009) and has no apparent effect on the normal behavior of *H. armiger* (CS, pers. observ.). All of the bats were fed with *Zophobas morio* larvae and had water ad libitum.

Morphological measurements

We measured the body mass, to the nearest 0.01 g, of each individual using a portable electronic balance (DH-I2000, Diheng Ltd., Shenzhen, China) and the length of the right forearm was measured, to the nearest 0.01 mm, using an electronic vernier caliper (111-101V-10G, Guanglu Ltd., Shenzhen, China) at the end of the agonistic interaction. The body mass and forearm length of every male were measured three times, and their mean was used for the analysis. In addition, following the criterion of closely size-matched individuals proposed by Morrell et al. (2005), we defined closely mass-matched individuals as 0.9 < winner's mass/loser's mass < 1.1. We did not define closely forearm length-matched individuals as 0.9 < winner's forearm length/loser's forearm length < 1.1 because the number of contests ($N = 109$ contests) that fit the standard was close to the number of total contests ($N = 111$ contests).

Experimental design

In order to recognize individual identity, we marked bats with 4.2-mm numbered aluminum alloy bands (Porzana Ltd., East Sussex, UK) on their left forearm or right forearm. The bands weighed 0.12 g, which was less than 0.28% of the bat's body mass. We ensured that the bands could slide freely along the forearm but could not cut into the forearm. Based on our recent study (Jiang et al. 2017), the bands did not change the normal behavior of the bats.

On the days before each trial, we first transferred each experimental bat from its mosquito net to the test cage where experiments were carried out (0.5 m × 0.5 m × 0.5 m) for 15 min to minimize the potential impacts of examination in a strange environment. The testing cage was located in a third room (5 m × 3 m × 3 m). We observed agonistic interactions at night including the period of maximal social vocal activity, from 10 p.m. to 8 a.m. Agonistic interactions only occurred when males were in close proximity (less than 15 cm apart; CS, pers. observ.). Preliminary tests in a testing wire mesh cage demonstrated that if there were less than seven bats in the cage, they rarely contested because the distance between them was more than 15 cm. In theory, more bats in a testing wire mesh cage should lead to more agonistic interactions between individuals. However, it is difficult to distinguish individuals by a frame-by-frame video analysis if there are more than eight individuals in the cage. Thus, to stimulate males to spontaneously contest, we selected eight experimental bats at random and introduced them into the testing cage. These bats were separated individually by cloth in the testing cage. When they calmed down, i.e., started self-grooming or remained motionless, we removed the cloth so that bats could interact freely. A contest started from the first wing flap or boxing move given by either male. Interactions were terminated once a clear winner was determined or when we were unable to identify a clear winner and loser after 15 min. We stopped the behavioral experiments immediately after the completion of the first agonistic interaction between two of the eight males in the cage. We considered one agonistic interaction as a contest and there was only one agonistic interaction occurrence within each trial. After the trials, males were returned to their mosquito net and were used in subsequent trials. To reduce the potential effect of odors on the next contest, we cleaned the testing cage with 90% alcohol after each trial. After the trials, the six bats that did not engage in the aggressive interaction were returned to their mosquito net, and then were used for another trial until they engaged in combat with another bat. The two males who engaged in the agonistic interaction were removed. In many animal species, individual recognition plays an important role in influencing aggressive behavior (Reichert and Quinn 2017). Thus, we controlled the potential effect of recognition and learning between familiar individuals during fights. Eight males from the same location were included in the first trial (Fig. 1). The second trial consisted of six new individuals plus two from the preceding (first) trial after eliminating the pair engaging in agonistic interactions. Each successive trial consisted of a set of five new individuals with inclusion of one individual from the first trial and two from the immediately preceding trial after exclusion of the pair engaged in agonistic interactions. Each male was included three times at maximum in trials if the male did not engage in an agonistic interaction in the previous two trials. This procedure helped ensure that a bat would fight with a random individual within each trial. Individuals that engaged in combat, however, were not used in the following trials.

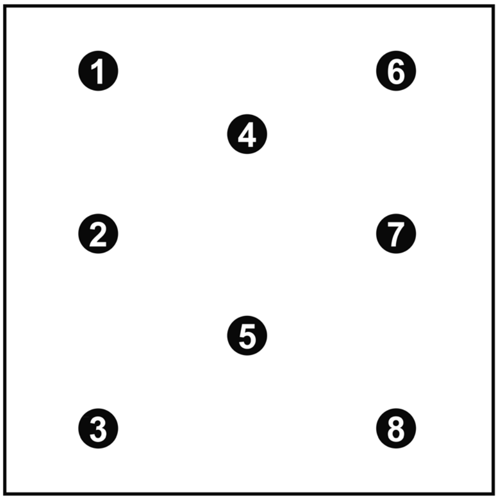

Fig. 1 Scheme of the experimental design. Closed circles represent bats. The numbers in the closed circle represent different individuals

We used a night-shot camcorder (HDR-CX 760E, Sony Corp., Tokyo, Japan) to monitor all of the agonistic interactions. The camcorder was positioned 1 m in front of the testing cage. The experimenter remained quiet in the testing room during the tests, ca. 2 m from the testing cage.

Behavioral analysis

We used a QvodPlayer with a resolution of 25 frames/s (Version 5.0.80, Shenzhen Qvod Technology Co., Ltd., Guangdong, China) to perform a frame-by-frame video analysis of 115 dyadic agonistic interactions and to describe male agonistic displays. We defined mutual displays as contests involving fighting behaviors by both opponents. Separate displays were defined as contests involving fighting behavior by one of the opponents. We defined a physical fight as one in which any physical contact occurred during an agonistic interaction (i.e., contests involving boxing or wrestling behavior). A non-physical fight was defined as one in which no physical contact occurred during an agonistic interaction (e.g., contests involving wing flap behavior). We defined two different kinds of agonistic contests (I, II). The first kind (I) includes non-physical contests in which bats escalate from being calm and motionless to showing aggressive display behavior (i.e., engaged in aggressive displays). The second kind (II) involves contests in which bats can escalate to a physical level (involving touching the opponent) either right from the start of a contest or from a non-physical level to a physical one. We defined contest duration as the difference in time between the first and last wing flap or boxing move given by either male. Contest interactions were terminated when we defined a clear winner during an interaction. We defined the winner as the bat remaining at the location of interaction after retreat of the loser. We defined the loser as the bat leaving the interaction location apparently as a consequence of opponent agonistic activity, and not performing any agonistic behaviors and social vocalizations after retreat for at least 20 s. Our pilot laboratory experiments showed that 20 s was a sufficient time interval, because the loser did not return to the interaction location to show retaliation or re-engage in agonistic interactions with another individual for at least 10 min. We calculated the number of wing flaps and the number of boxing movements and were used as a measure of contest intensity.

Wing flapping and boxing movements were assumed to express aggression or a threat toward a rival. Wing flapping was recorded when an up-and-down flapping cycle occurred. A boxing movement was recorded when a bat punched with its wrist toward an opponent. To minimize observer bias, a blinded method was used when all the bats' behavioral data were recorded and analyzed.

Statistical analyses

Kolmogorov-Smirnov tests were used to test the normality of the data. We used parametric tests for all variables, with the exception of forearm length ($N = 250$) and contest intensity (number of wing flaps and number of boxing moves) of smaller individuals and larger individuals.

Fisher's exact test was used to compare the differences in behavioral patterns of the three populations. Exact binomial probability tests were performed to test whether contests tended to be won by the individual that was heavier or longer, to determine whether contests tended to be induced by the male that was heavier or longer, and to examine whether contests tended to be escalated by the male that was heavier or longer. Binary logistic regressions were used to determine whether the level of escalation of contests was related to body size (forearm length and body mass). An independent sample t test was used to determine whether individuals that had longer forearms tended to be involved in physical contests. Wilcoxon signed-rank tests were used to determine whether there were differences in contest intensity (number of wing flaps and number of boxing moves) between the smaller individuals and larger individuals. To examine the predictions of different assessment models, we used multiple linear regression analyses to estimate the relationship between contest duration and body size (three variables of body mass: the mass of the winner, the mass of the loser and mean mass between closely mass-matched individuals; or two variables of forearm length: the forearm length of the winner and the forearm length of the loser). Spearman rank correlation was performed to assess the relationship between forearm length and body mass.

Results

Description of agonistic interactions

Among the 111 agonistic interactions, there were 5 main behavioral displays (Table 1, description of behavioral terms following Clement et al. 2006). Of the 111 contests, 8 (7%) escalated to the wing flapping stage (non-physical contests) and 103 (93%) escalated to the boxing/wrestling stage (physical contests). There was no significant difference in the probability of occurrence of each of the behavioral patterns described in Table 1 among the three populations (Fisher's exact test: $\chi^2 = 1.839$, $P = 0.781$). The sequence of behavioral phases of male *H. armiger* during agonistic interactions is displayed in Fig. 2. The contest duration and general agonistic behaviors of male *H. armiger* are displayed in Table 2. The heavier opponents of the dyad initiated 76 of 111 fights (binomial test: $P = 0.000125$). The bats with longer forearms in the dyad induced 48 of 111 fights (binomial test: $P = 0.184$). The heavier opponents of the dyad usually escalated to the physical level (92 of 111 fights; binomial test: $P < 0.0001$). The bats with the longer forearm in the dyad escalated, but not significantly so, to the physical level (64 of 111 fights; binomial test: $P = 0.128$).

Of the 111 interactions, 69 (62%) involved aggressive displays by both opponents (mutual displays). In the other 42 (38%) interactions, only 1 opponent displayed (separate displays) and the other withdrew. Among the 69 fights with mutual displays, 6 (9%) escalated to the wing flapping stage (non-physical contests) and 63 (91%) escalated to the boxing stage/wrestling stage (physical contests).

Table 1 Description of fighting behaviors of male *Hipposideros armiger*

Behavior	Description
Ear movements	Ears move around to detect the opponent; often accompanied by echolocation. There is no physical contact.
Head raise/turn	Contestants raise and/or turn heads by bending their neck backward toward the interactive bat. There is no physical contact.
Crouching, unfolding wings	Opponents perform an upside-down crouch, stretch necks and initiate rapid wing flapping toward the interactive bat. Sometimes one of them walks toward the other. Often one or both contestants start to emit social calls. There is no physical contact between opponents although sometimes the distance between contestants is less a wing length.
Boxing	Boxing is an escalating and physical fight between two males. Each of them uses the carpal joint to knock each other vigorously until one of them retreats.
Wrestling	Bats briefly holding on to each other with either their forearms or semi-extended wings.

Influence of body size on contest success

When we combine the two levels of escalation (non-physical and physical contests; $N = 111$ fights), the heavier opponents of the dyads were more likely to win (Table 3; $N = 81$, binomial test: $P < 0.0001$). This was not true for opponents with longer forearms (Table 3; $N = 49$, binomial test: $P = 0.255$). The importance of body size in contest success relied on the level of escalation of contests (Table 3; $N = 81$, binomial test: $P < 0.0001$). Compared to non-physical interactions (Table 3; $N = 6$, binomial test: $P = 0.289$), heavier males were more likely to win only in the physical contests (Table 3; $N = 81$, binomial test: $P < 0.0001$). Males with longer forearms were not significantly more likely to win contests for any of the levels of escalation. Forearm length was significantly but not strongly correlated with body mass (Spearman rank correlation: $r = 0.177$, $P = 0.007$, $N = 230$ individuals). In many contests, individuals were larger for one body size measure but smaller for the other. Of the 111 interactions, 55 involved an opponent that was larger than its rival for body mass and forearm length. Out of these 55 contests, 37 were won by the larger males (Table 3; binomial test: $P = 0.014$). Individuals that were larger in the two measures of body size were significantly more successful within the physical contests (Table 3; binomial test: $P = 0.036$).

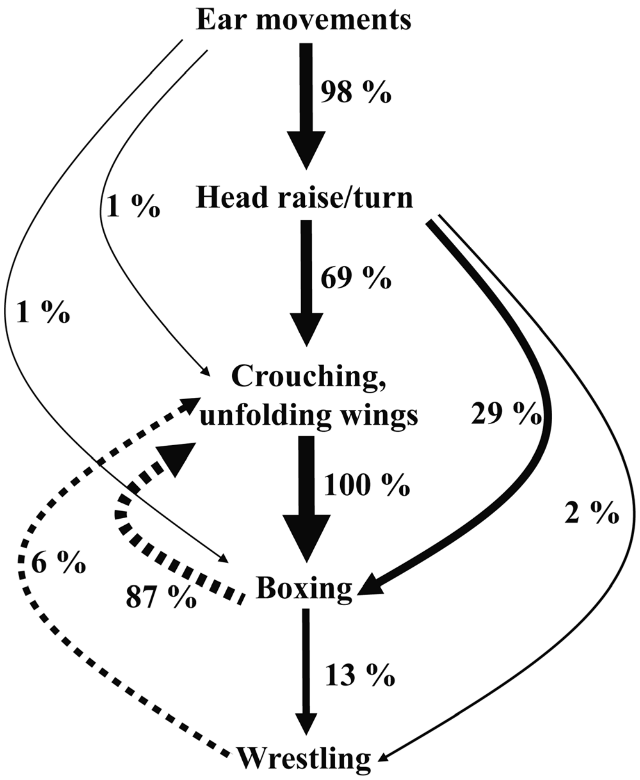

Fig. 2 Ethogram depicting sequence of behavioral phases of 222 male *Hipposideros armiger* during agonistic interactions. The numbers represent the transitions between behavioral phases as percentages. Arrow thickness broadens with transition frequencies

Determinants of the level of escalation

Binary logistic regressions showed that the level of escalation did not relate to the difference in mass between the heavier and lighter competitor ($\chi^2_1 = 0.683$, $P = 0.409$). However, there was a significant and positive relationship between the mass of the larger opponent and the level of escalation ($\chi^2_1 = 5.663$, $P = 0.017$; Fig. 3a) and between the smaller opponent and the level of escalation ($\chi^2_1 = 4.434$, $P = 0.035$; Fig. 3a). Additionally, there was no significant relationship between the forearm length of the shorter contestant ($\chi^2_1 = 0.626$, $P = 0.429$, Fig. 3b) or the difference in forearm length between the longer and shorter opponents and the level of escalation ($\chi^2_1 = 2.893$, $P = 0.089$). However, there was a significant positive relationship between the forearm length of the longer contestant and the level of escalation ($\chi^2_1 = 6.813$, $P = 0.009$, Fig. 3b). Contests that escalated to physical contests involved individuals with longer forearms than those that did not escalate to physical contests (independent sample t test: $t_{109} = -4.583$, $P < 0.001$).

Body size and contest duration

Among the 111 interactions, we only analyzed 69 fights that involved aggressive displays by both opponents.

Body mass

The differences in the body masses of the contestants were 0–47.4% of the mass of the lighter bat in the dyad (mean body mass difference = 6.50 ± SD 6.04 g; range 0.13–25.76 g). The heavier bats did not exhibit wing flapping more frequently than the lighter bats, but they performed significantly more boxing movements than the lighter bats (Wilcoxon signed-ranks test: wing flapping: $Z = -0.467$, $N = 69$, $P = 0.640$; boxing movements: $Z = -2.847$, $N = 69$, $P = 0.004$). In 63 physical contests, contest duration was significantly related to the body mass of the losing bat (Fig. 4; multiple linear regression: $t = 2.48$, $P = 0.016$), while contest duration was not significantly related to the body mass of the winner (Fig. 4; multiple linear regression: $t = -1.27$, $P = 0.208$).

Table 2 Descriptive statistics of contest duration and general agonistic behaviors of male *Hipposideros armiger*

Parameters	Mean ± standard deviation	Median	Range
Contest duration (s)	35.64 ± 39.00	18	3–217
Number of wing flaps[a]	54.30 ± 81.41	19	0–376
Number of boxing moves[a]	3.27 ± 3.31	2	0–16

[a] The total number combined across both opponents

Table 3 Proportion of contests won by the individual of larger body mass and with longer forearm at each level of escalation in interactions between *Hipposideros armiger*

Proportion won by individual larger in:	Level of escalation		
	Non-physical contests	Physical contests	Total
Body mass	6/8	75/103***	81/111***
Forearm length	5/8	44/103	49/111
Both categories	3/3	34/52*	37/55*

Proportions are shown as the number won by the larger individual over the total number of interactions at that level of escalation. In addition to the body mass and forearm length, we calculated the proportion of contests won by individuals that were larger for both mass and forearm length ("both categories"). Asterisks show statistically significant results for two-tailed exact binomial probability compared to the null expectation of 50% heavier bat wins. *$P < 0.05$; ***$P < 0.001$

In non-physical contests, no relationship was detected between contest duration and the body mass of the winner and the loser (Table S1).

Forearm length

Differences in forearm length ranged from 0 to 10.9% of the forearm length of the shorter bat in the dyad (mean forearm length difference 2.42 ± SD 2.34 mm; range 0.08–9.96 mm). Dyad opponents with longer forearms did not exhibit wing flapping or boxing more frequently than did dyad opponents with shorter forearms (Wilcoxon signed-ranks test: wing flapping: $Z = -0.075$, $N = 69$, $P = 0.940$; boxing: $Z = -346$, $N = 69$, $P = 0.729$). In both physical and non-physical contests, no relationship was detected between contest duration and forearm length (Fig. 5; multiple linear regression: winner's forearm, $t = -0.39$, $P = 0.696$; loser's forearm, $t = 1.28$, $P = 0.205$).

Discussion

In this study, we found that heavier males were more likely to win, supporting our initial hypothesis. In physical contests, contest duration was unrelated to the winner's mass but was positively correlated with the body mass of the loser. This supported the first prediction of our hypothesis: that males adopt a self-assessment strategy in contests. No relationship between body size and contest duration was detected for non-physical contests. This did not support any of the predictions of our hypothesis.

Body size and RHP

We found that heavier males were more likely to win. Males with larger body mass tended to be more involved in escalated contests. These results suggest that body mass in *H. armiger* is an appropriate proxy for RHP. Body mass is associated with fighting success in many taxa (reviewed in Archer 1998; Arnott and Elwood 2009) including bats (Williams 1986). For example, male tree lizards (*Urosaurus ornatus*) with larger body mass were more likely to win during agonistic

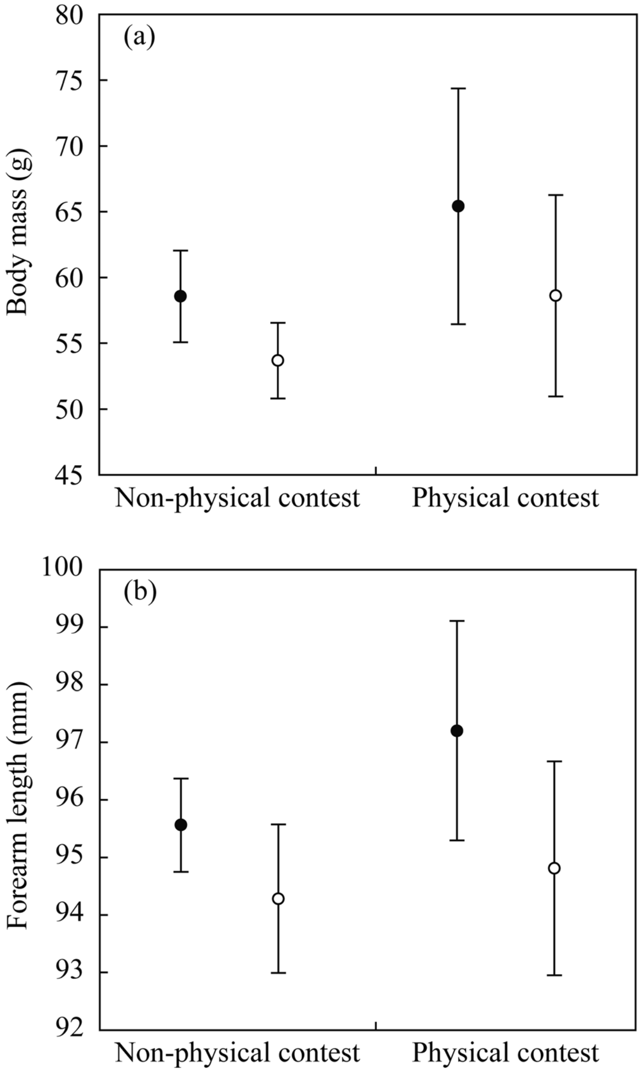

Fig. 3 Body size variables (**a** body mass; **b** forearm length) for the larger (closed circles) and smaller (open circles) opponent for each level of escalation in *Hipposideros armiger* contests. Plotted are means and standard deviations. $N = 8$ for non-physical contests and $N = 103$ for physical contests

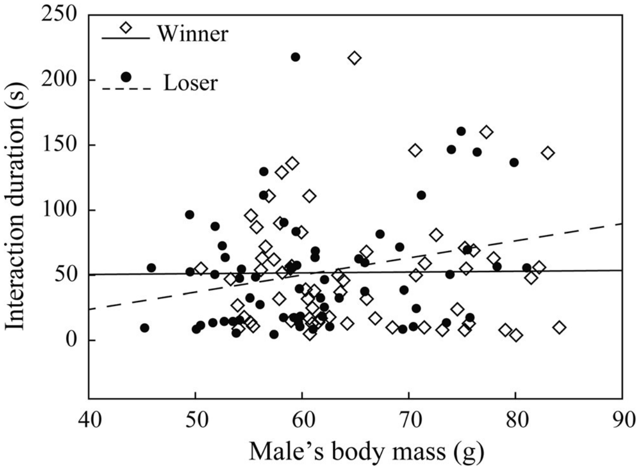

Fig. 4 Relationship between interaction duration and body mass of the winner (open diamonds; $P = 0.208$), and the loser (closed circles; $P = 0.016$) in *Hipposideros armiger*, respectively. The lines represent regression lines (solid line: winner; dashed line: loser). $N = 63$

interactions (Zucker and Murray 1996). Heavier male little free-tailed bats (*Tadarida pumila*) were more likely to win than lighter males during territorial contests (McWilliam 1988). However, we found that longer forearm length was unrelated to contest success. On the one hand, this may be because forearm length may not be tied to RHP in this species. On the other hand, this may be due to the fact that we had individuals with highly similar forearm lengths involved in agonistic interactions, even though the experimental bats were selected at random. Opponents with (a) similar body mass and (b) similar forearm length may have a potential influence on contests. For example, SAM suggests that decisions to retreat or to escalate in an agonistic interaction are based on the assessment of their opponent's RHP relative to their own RHP (Enquist and Leimar 1983; Enquist et al. 1990). If the RHP difference between the opponents is very small, the larger individuals in the dyad may make a wrong judgment and thus retreat first. In our study, differences in forearm length ranged from 0 to 10.9% of the forearm length of the shorter bat in the dyad. Thus, future studies could assess whether forearm lengths indicate success in agonistic interactions by comparing individuals with substantially different forearm lengths.

Assessment strategies

In physical contests, we found that contest duration was not correlated with the mass of the winner but was significantly and positively correlated with the body mass of the loser. Taylor and Elwood (2003) showed that by focusing on the relationship between contest duration and the winner's RHP, and between contest duration and the loser's RHP, it was possible to differentiate between self-assessment (E-WOA) and mutual assessment models (SAM), and between E-WOA and CAM. Mutual assessment and CAM state that the relationship between the loser's RHP and contest duration will be equal but opposite in sign to that of the winner's RHP (Taylor and Elwood 2003), which did not conform to our results. By contrast, our results showed a non-significant relationship between the body mass of the winner and fight duration. E-WOA predicts a weak or an insignificant positive correlation between the winner's RHP and contest duration (Taylor and Elwood 2003; Arnott and Elwood 2009), so our results are consistent with that model. Our result is in accord with the observation of self-assessment (E-WOA) from Prenter et al. (2006), who found a significant positive relationship between the loser's body mass and contest duration and a non-significant relationship between the winner's body mass and contest duration in *Gammarus pulex*. Together, these results are concordant with the predictions of self-assessment strategy, and the more appropriate model for *H. armiger* is E-WOA rather than SAM or CAM.

In non-physical contests, there was no relationship between body size and contest duration or intensity. These results showed a lack of support for the three assessment models. Together, our results show that *H. armiger* males use self-assessment in physical contests, while no assessment was used in the non-physical contests.

Our results add to the increasing evidence of self-assessment in animal combat (e.g., Bridge et al. 2000; Taylor et al. 2001; Jennings et al. 2004; Morrell et al. 2005; Prenter et al. 2006), providing the first behavioral observations of fighting strategy in bats. Self-assessment needs very limited cognitive complexity, i.e., opponents only know their own fighting abilities and are incapable of comparing them with information gathered about their contestants (Elwood and Arnott 2012, 2013). The reason why males in *H. armiger* depended on the assessment of their own RHP in combat, rather than the assessment of their opponent's RHP, remains

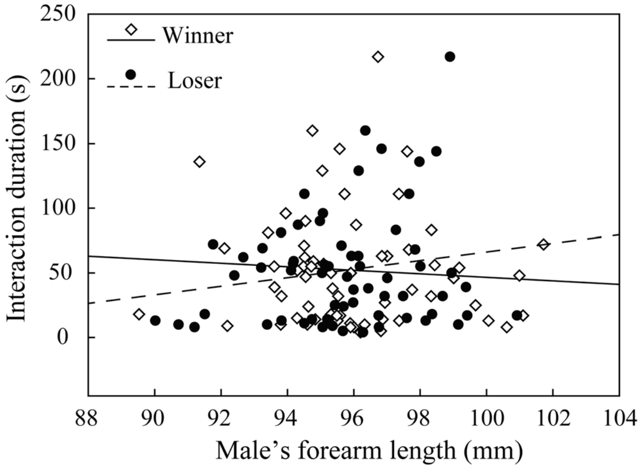

Fig. 5 Relationship between interaction duration and the forearm length of the winner (open diamonds; $P = 0.696$) and the loser (closed circles; $P = 0.205$) in *Hipposideros armiger*, respectively. The lines represent regression lines (solid line: winner; dashed line: loser). $N = 63$

unresolved. There are two possible causes for E-WOA. First, *H. armiger* males may have limited cognitive ability and thus only persist in relation to their own state. *H. armiger* may use one forearm with the wrist headmost for fast, repetitive boxing toward an opponent. It may be difficult for *H. armiger* to compare its own action of boxing with its perception of the force of boxing induced by the opponent while punching against the focal male. Thus, *H. armiger* will not have information about both displays and thus will be unable to judge relative magnitudes. Second, E-WOA might be a consequence of our artificial trial design. The agonistic interactions in our trial design are motivated to general agonistic behaviors evoked by the facts that individuals that normally maintain a distance of 10–15 cm apart are too close to one another.

Our data did not support mutual assessment in non-physical contests. This is not surprising given the small sample size for non-physical contests ($N = 6$ fights), so a larger sample size will be required in further studies. In the natural roost, *H. armiger* are most likely to be able to assess their opponent's RHP given daily agonistic interactions. Thus, agonistic interactions in this species are probably mediated by familiarity with neighbors, and thus may involve knowledge about the fighting ability of the opponent. Being involved in daily repeated interactions likely includes assessment of the opponent, gaining information from each encounter concerning the opponent's RHP. Additionally, in early non-physical contests, wing flapping displays (noncontact displays) of *H. armiger* males may provide information on body size because it is possible that wing flicking causes slight air movements that are detectable by the highly sensitive receptors on bat wings (Sterbing-D'Angelo et al. 2011). Thus, we speculate that *H. armiger* may use mutual assessment in non-physical contests when deciding whether to escalate.

Once the contest has escalated to a physical contest, the rival's abilities may no longer affect contest decisions, and the individuals may persist in a contest based on an estimate of their own energy budgets. Our results also confirmed that *H. armiger* may employ self-assessment in the laboratory physical contests. Similar assessment strategy can be found in killifish *Kryptolebias marmoratus* that adopt mutual assessment in non-physical contests and use self-assessment in physical contests (Hsu et al. 2008).

Several studies have demonstrated that mutual assessment (therefore, the RHP of the contestant) plays a role during physical contests (Enquist et al. 1990; Pratt et al. 2003; Kemp et al. 2006; Green and Patek 2018). However, our results showed that in a physical contest, the rival's RHP did not affect contest duration, which indicated that a winner's ability to inflict costs probably did not affect a loser's ability to stay in the contest. It is likely that in this species, winners do not impose substantial physical damage on losers during physical contests or that the ability of the winners to inflict physical costs is independent of their body size. However, we should be cautious of assuming that the results found during our study are also applicable in the wild since the experimental design was highly artificial. There are three reasons. First, there may be different valuable resources in the natural roost compared to the laboratory. In the natural roost, males are probably highly motivated to defend their territories, because territorial loss could result in a loss of mating opportunities. For example, in the presence of females at their territorial sites, male Seba's short-tailed fruit bats (*Carollia perspicillata*) defend vigorously against other males (Porter 1979; Williams 1986). In the laboratory, however, males were probably motivated to general agonistic behaviors induced by the fact that individuals that would normally maintain a separation distance of 10–15 cm (as described in the "Introduction" section) are too close to one another. Second, we could not observe previous fights or assess the effects of winning/losing experiences on fight outcomes due to dark environments and the high cluster densities in the roost cave. Experience from past interactions can influence the outcome of subsequent contests (Stuart-Fox and Johnston 2005). However, some studies have either not observed effects associated with winning previous interactions (*Agkistrodon contortrix*: Schuett 1997) or the effects were less pronounced and short-lived (*Gasterosteus aculeatus*: Bakker et al. 1989).

Future research could assess whether prior fighting experiences affect contest outcomes in the lab (see Hsu and Wolf 1999). Finally, the presence of other conspecifics may also affect the behavior of the communicating animals (Matos and Schlupp 2005). In this study, we could not rule out the "audience effect" but we ensured that there were eight bats within each trial and each bat would fight with a random and unfamiliar individual within each trial. Together, this procedure ensured the same situations within each trial. However, further experiments could determine whether the presence of a male audience affects the male-male *H. armiger* aggressive displays. Thus, our trial design allows us to draw conclusions about the assessment strategy during contests resulting from agonistic interactions provoked by close proximity between individuals (which normally are at least 10–15 cm apart). Whether the same or different assessment strategies occur in the wild needs to be investigated in further experiments under more natural conditions taking into account variables such as resource value potential, experience, audience effect, and male age.

Social vocalization and agonistic interactions

Costs of agonistic interactions can be mitigated when accompanied by acoustic communication (Silk et al. 2000; Logue et al. 2010). Territory holders may use acoustic signals to encode not only their own identity but also their competitive quality, aggression level, and motivation which can influence the decision whether to continue or cease the contest (Bradbury and

Vehrencamp 2011). For example, aggressive trills of male Seba's short-tailed fruit bats (*Carollia perspicillata*) encoded discriminable signatures, and males could discriminate among individuals based on these aggressive trills (Fernandez et al. 2014). Such discrimination is probably useful in facilitating neighbor recognition and thus allows for an economical response (Fernandez et al. 2014). The social vocalizations of female Asian particolored bats (*Vespertilio sinensis*) during agonistic interactions encoded reliable information about the body size and the quality of the sender, and acoustic variables strongly predicted the winning percentage (Zhao et al. 2018). The social vocalizations of Indian False Vampire bats (*Megaderma lyra*) encoded high aggression levels by increasing the syllable repetition rate and decreasing the intervals between call syllables (Bastian and Schmidt 2008). In the present study, among the 111 fights, 7 (6%) involved social calls by both opponents, 22 (20%) did not involve social calls by either opponent, 66 (59%) involved social calls only by the loser, and 16 (15%) involved social calls only by the winner. There was no significant difference in contest duration among above-mentioned four vocalization contexts. This result suggests that social vocal signals emitted by *H. armiger* may not indicate success in agonistic interactions. However, playback experiments are needed to unequivocally demonstrate that receivers can both perceive and utilize signal information to make decisions.

In summary, our results suggest that *H. armiger* make decisions by assessments of their own ability (self-assessment) rather than of their opponent's ability (mutual assessment) in physical contests. This is the first investigation concerning the assessment strategy of bats during contests. Further experiments focusing on the relationship between contest duration and energy expenditure or energy reserves of opponents are needed to assess whether each opponent sets its persistence time based on an estimate of its own current ability to continue in a costly interaction (E-WOA).

Funding This research was supported by the National Natural Science Foundation of China (grant nos. 31872680 and 31670390).

Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical approval Bats were captured by mist nets. Then, they were placed individually in cloth bags and transported to housing in temporary field experimental stations near the bat roosts. No bat suffered any obvious effects from the process of capture, transport, and experiment. No visible physical injuries were observed, although some contests involved physical contact. We removed the aluminum alloy bands before the bats were release. All of the captured bats were released in good health at their original site of capture after the completion of the experiment. Experimental procedures were in compliance with the National Natural Science Foundation of China for experiments involving vertebrate animals and were approved by Northeast Animal Research Authority in Northeast Normal University, China (approval number: NENU-W-2017-101).

Data availability The datasets analyzed during the current study are available from the corresponding author upon request.

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