Environment and Natural Resources Journal 2019; 17(3): 50-57

Seasonal Variation in Sexual Size Dimorphism in the Wrinkle-lipped Free-tailed Bat *(Chaerephon plicatus* Buchannan, 1800) Population in the Khao Chong Phran Non-hunting Area, Thailand

Nutthakarn Boonpha[1], Prateep Duengkae[1*], Supaporn Wacharapluesadee[2] and Chumphon Kaewket[3]

[1]*Department of Forest Biology, Faculty of Forestry, Kasetsart University, Chatuchak, Bangkok 10900, Thailand*
[2]*World Health Organization Collaborating Centre for Research and Training on Viral Zoonoses, Faculty of Medicine, Chulalongkorn University, Bangkok 10330, Thailand*
[3]*Tham Khang Khao-Khao Chong Phran Non-hunting Area, Photharam, Ratchaburi 70120, Thailand*

ARTICLE INFO

Received: 11 Oct 2018
Received in revised:
8 Feb 2019
Accepted: 11 Feb 2019
Published online:
4 Apr 2019
DOI: 10.32526/ennrj.17.3.2019.22

Keywords:
Body mass/ Cave/ Forearm length/ Insectivorous bat/ Larger male/ Rainfall

*** Corresponding author:**
E-mail:
prateepd@hotmail.com

ABSTRACT

The Khao Chong Phran Non-hunting Area has the largest population of wrinkle-lipped free-tailed bats (*Chaerephon plicatus*) in Thailand. We examined monthly variations in sexual size dimorphism through measurements of forearm length and body mass during 2016. Bats were captured in each month at dawn and dusk. Individuals were sexed, aged, measured and marked before release. During the year, we caught 1,715 individuals. Of these, we used only adult, non-pregnant individuals (405 males and 538 females) for our analysis. Males had significantly larger forearm lengths and body masses than females. The body masses of both sexes peaked at the beginning and end of the rainy season, and bats captured at dawn were heavier than those netted at dusk. Seasonal fluctuations in body mass were correlated with monthly variation in rainfall; the positive correlation is likely explained by the greater insect abundance during wet months. The climate in western Thailand is expected to become warmer and drier, with likely negative effects on populations of this species due to reductions in insect food resources. Maintenance of this large population of *C. plicatus* in the study area will depend on concerted conservation efforts and further research focused on population dynamics, prey availability and foraging habitats.

1. INTRODUCTION

Sexual size dimorphism occurs widely among animal taxa (Weckerly, 1998; Wu et al., 2014). Males are typically larger since size often attracts female attention and increases the chances of successful mating when males compete for breeding partners (McPherson and Chenoweth, 2012; Herron and Freeman, 2015). However, females may be larger than males in some species, likely because increased size improves reproductive success and can improve mobility in the later stages of pregnancy (Ralls, 1976; Stevens and Platt, 2015). Sex monomorphism also occurs among animal taxa (Hurtado et al., 2015). Several underlying mechanisms have been proposed recently to explain the occurrence of sexual size dimorphism: sexual selection, pairing success, reproductive success, population density differences, and Rensch's allometric rule (Lisón et al., 2014).

The order Chiroptera is the second largest order of mammals (Rex et al., 2008). Most species of bats in the families Emballonuridae, Mormoopidae, Noctilionidae, Phyllostomidae, and Pteropodidae have males that are larger than females. However, in the families Rhinolophidae and Vespertilionidae, the females tend to be larger (Ralls, 1976; Lisón et al., 2014; Dalhoumi et al., 2016). Sexual size dimorphism in bats has been identified by skull lengths and widths, canine tooth variation, body mass, and forearm length (Camargo and Oliveira, 2012; Wu et al., 2014; Dalhoumi et al., 2016; Goodman et al., 2017).

We studied the wrinkle-lipped free-tailed bat (*Chaerephon plicatus*), an insectivorous member of the globally distributed family Molossidae. All molossid bats have long, narrow wings that are adapted for rapid flight and foraging on wing (Voigt and Holderied, 2012). *C. plicatus* occurs in large populations across Southeast Asia. In Thailand, the species has been found in 17 cave roost locations that contain a total of approximately 8 million individuals (Boonkerd and Wanghongsa, 2002; Csorba et al., 2017). About 2.6 million bats roost in the Khao Chong Phran cave system, representing the largest population in Thailand. Moreover, this cave also houses another 14 species of bats, which are important food resources for raptors. For this reason, the system has been designated a no-hunting zone. Bat guano is harvested early every Saturday morning and sold as high nutrient fertilizer to interested agriculturists under the management of the Khao Chong Phran temple committee. Studies of population size, diet, and foraging habitat indicate that this bat species is a major contributor to ecosystem services and provides indirect benefits (economic value) to humans (Hillman, 1999; Leelapaibul et al., 2005; Hillman, 2006; Utthammachai et al., 2008; Kunz et al., 2011; Srilopan et al., 2018). However, the external morphology of the bat has not been well studied in terms of the similarity in appearance between sexes.

Therefore, we examined the patterns of seasonal variation in sexual size dimorphism through measurements of forearm length and body mass over one year. In addition, since the abundance of insects that are the main food resource for the bats is greatly influenced by rainfall (Cumming and Bernard, 1997; Srilopan et al., 2018), we examined correlations between monthly rainfall and fluctuations in bat body mass. This was the first year-round study in Thailand of sexual size dimorphism in *C. plicatu*s and this research can be used by policy makers to improve further sustainable bat-cave management in response to future climate change.

2. METHODOLOGY

2.1 Study site

The Khao Chong Phran Non-hunting Area (KCP) (13°43.2′N, 99°46.8′E) is located in Ratchaburi Province, central Thailand (Figure 1). The KCP covers 12 ha of limestone karst and has five caves. A large *C. plicatus* colony inhabits the largest cave, which is 40 m high, 50 m wide and 150 m long. Mixed deciduous and limestone forests grow in the KCP. The forest is surrounded by rice paddies, sugar cane plantations, and villages. The study area has a tropical monsoon climate with two seasons: the rainy season (May-October) and the dry season (November-April) (Hillman, 1999; Leelapaibul, 2003; Leelapaibul et al., 2005; Utthammachai et al., 2008; Utthammachai, 2009).

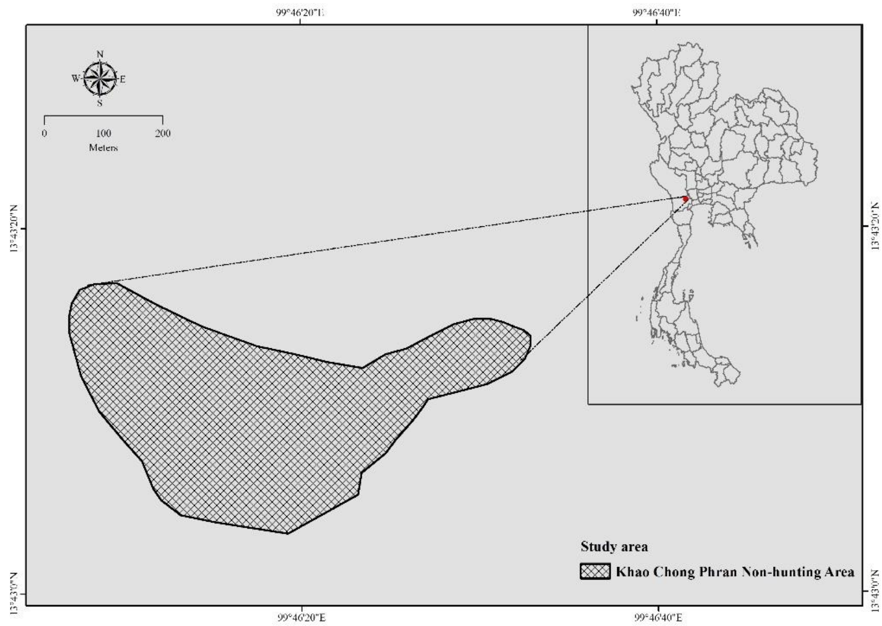

Figure 1. Map of Khao Chong Phran Non-hunting Area, Ratchaburi Province, Thailand

2.2 Methods

Our observations were made from January to December, 2016. In each month, we captured at least 100 bats per month by using hand nets with five m aluminum extension poles in two locations on consecutive days. Bats were first collected as they exited the main cave chamber at dusk (17:00-18:00). We captured ten individuals every 10 min. A second collection was made at dawn (07:00-08:00) after bats had returned to the cave to roost; we could only collect bats roosting in areas where the ceiling height was less than five m tall. Bats were held individually in porous cotton bags. Forearm length was measured with digital calipers (to the nearest 0.01 mm). Body mass (g) was determined with a digital scale. Animals were sexed by observing their reproductive organs and classified into one of two age groups, juvenile or adult, based on the extent of the cartilaginous and fused gaps of the metacarpal phalangeal epiphyses (Kunz et al., 1998; Encarnação et al., 2004). Individual adult females were classified into one of three reproductive categories (non-reproductive, pregnant, or lactating) by abdominal palpation and observations of milk on the nipples (Happold, 1989; Dalhoumi et al., 2016). All bats were marked with nail polish on a right foot claw to avoid repeated measurements on the same individuals. After handling, we released the bats.

2.3 Data analysis

We included only adult bats (excluding pregnant females) in the analyses. We first verified that the data were normally distributed. Student's t-tests were used to identify significant differences between the sexes. We used one-way analysis of variance (ANOVA) followed by the honestly significant difference (Tukey's HSD) multiple comparison test to examine seasonal variation in forearm length and body mass. Two-way ANOVA was used to examine the interaction between sex and season. Spearman's rank-order correlation coefficients (r_s) were used to examine the relationships between mass and (i) rainfall in each month of 2016 and (ii) the average monthly rainfall over a 25-year period. The analyses were performed with the R statistical package ver. 3.3.3 (The R Development Core Team, 2017).

3. RESULTS

We captured 1,715 individual bats. Of these, 657 were male (405 mature, 252 immature) and 1,058 female (657 mature, 401 immature). Among the adult females, 119 were pregnant, 121 were lactating, and 417 were non-reproductive. Therefore, we included 405 adult males and 538 adult females in the analysis. Male-biased sexual dimorphism was highly statistically significant for both forearm length ($t=8.93$, $df=941$, $p<0.001$) and body mass ($t=8.81$, $df=941$, $p<0.001$).

Forearm length and body mass were examined separately in the analyses of monthly variation. The forearm length of mature males exceeded that of females ($p<0.05$) in all months except March and July. The mean body mass of females significantly exceeded that of males only in September; in other months, males were heavier (Figure 2).

ANOVA and Tukey's pairwise comparisons showed that male forearm length did not differ significantly by month ($F_{11,393}=1.08$, $p=0.378$). Female forearm length was significantly different under the ANOVA ($F_{11,526}=1.88$, $p=0.039$), but Tukey's test indicated no significant differences between months. The body masses of both males and females varied significantly by month, and two significantly different groups were apparent. Male body mass peaked in June ($F_{11,393}=19.91$, $p<0.001$), and was lowest from January to April. Female body mass peaked in September ($F_{11,526}=41.52$, $p<0.001$) and was lowest in the dry season (January-May) (Figure 2).

Two-way ANOVA of the effects of sex and month on forearm length showed that both sex ($F_{1,919}=80.69$, $p<0.001$) and month ($F_{11,919}=1.93$, $p=0.03$) had significant effects, but the interaction term was not significant ($F_{11,919}=8.21$, $p=0.45$). Meanwhile, body mass exhibited significant differences in terms of sex ($F_{1,919}=130.48$, $p<0.001$) and by month ($F_{11,919}=51.968$, $p<0.001$), and the interaction between these variables was strong ($F_{11,919}=8.21$, $p<0.001$). Consequently, the body masses of both sexes exhibited seasonal variation.

Adult males trapped at dusk had an average body mass of 15.74±1.48 g (n=244); those trapped at dawn had an average body mass of 15.56±1.60 g (n=161). These differences were not significant ($t=-1.11$, $df=403$, $p=0.27$). In contrast, adult females collected at dawn were significantly heavier than those trapped at dusk ($t=4.65$, $df=401.12$, $p<0.001$). The average female body masses at dawn and dusk were 15.17±1.62 g (n=210) and 14.54±1.41 g (n=328), respectively.

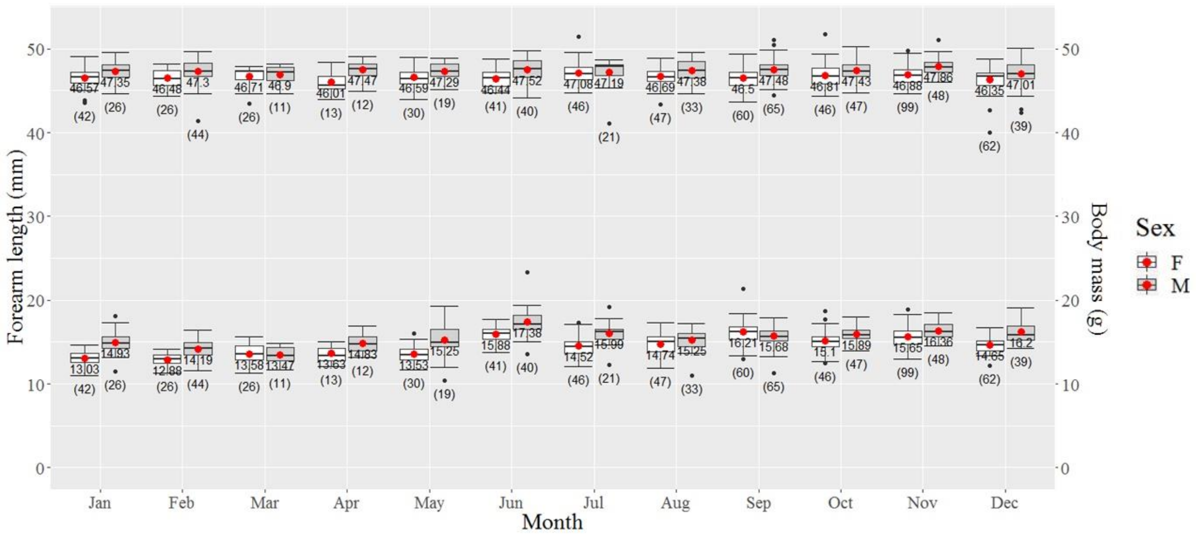

Figure 2. Monthly forearm length (upper) and body mass (below) of non-pregnant female (white bars) and male (gray bars) bats in January-December 2016 in the Khao Chong Phran Non-hunting Area, Thailand. Numbers in brackets indicate sample sizes. Boxes depict the 25th and 75th percentiles, lines within boxes mark the medians, red dots and adjacent numbers represent means, whiskers represent minimum and maximum values, and black dots indicates outliers.

Body mass was strongly correlated with (i) monthly rainfall in 2016 and (ii) average monthly rainfall over 25 years. The correlation was strongest for all pooled females (pregnant, lactating, and non-reproductive), followed in rank order by only non-pregnant females (Table 1).

The two seasonal peaks in body mass coincided with two seasonal peaks in rainfall, one at the beginning of the rainy season (May) and the second at the end (October) (Figure 3).

Table 1. Spearman's rank correlation coefficients for the relationship between monthly rainfall and body mass.

Adult category	Monthly rainfall 2016	p-value	Average monthly rainfall (1993-2016)	p-value
Adult males (n=405)	0.313	<0.01	0.267	<0.01
Adult females (n=657)	0.498	<0.01	0.469	<0.01
Adult females, non-pregnant (n=538)	0.449	<0.01	0.405	<0.01

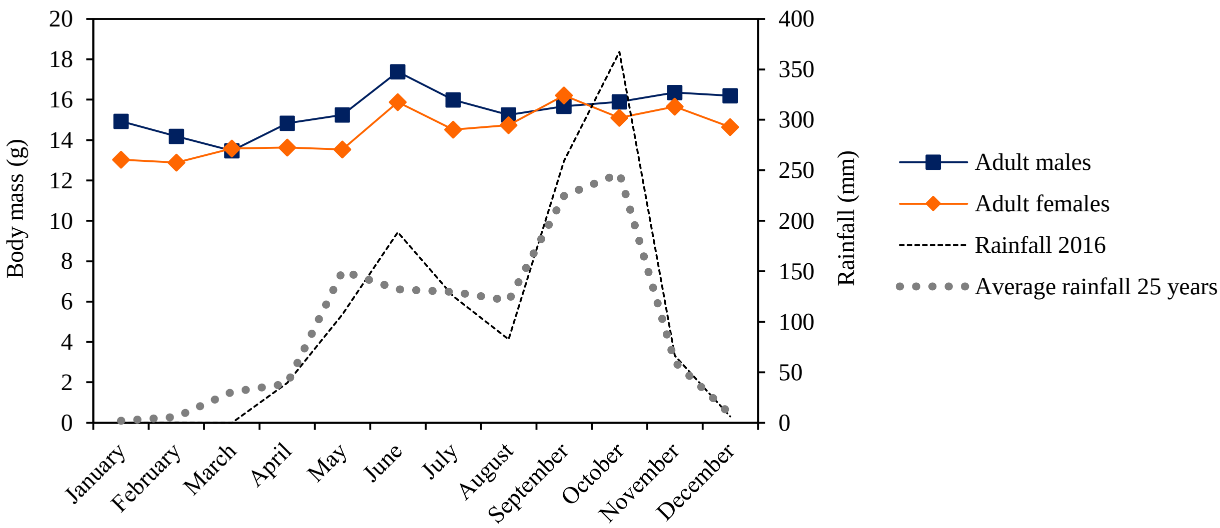

Figure 3. Seasonal fluctuations in the mean body mass of adult males and adult females (non-pregnant), monthly rainfall in 2016, and average monthly rainfall over 25 years (1992-2016).

4. DISCUSSION

We detected significant size differences between male and female *C. plicatus*, in agreement with an earlier study of Molossidae bats by Dalhoumi et al. (2016), who showed that males were larger. Morphological sex differences also occur in *Chaerephon leucogaster* populations found on Madagascar and the western Indian Ocean islands (Ratrimomanarivo et al., 2009). Sex differences have been reported for *Molossus bondae*, *M. coibensis*, and *M. molossus* in Panama (Gager et al., 2016). These size differences between sexes may be related to the mating systems of the species.

Adult males do not allocate energy resources to neonatal nurturing (Vivier and Merwe, 1997); therefore, males have a smaller food demand than lactating females (Barclay, 1991). When averaged over all months, male forearm length and body mass exceed those of females, presumably because males have more resources available for growth than reproductive females. Sex differences in size are also related to reproductive resource allocation in the Brazilian free-tailed bat (*Tadarida brasiliensis*), which has been found in a large population in central Texas. Male mating behaviors in bats were represented aggressive or passive. Aggressive males pull females from the group to mate. Mating is passive when males move quietly over groups of females to select individuals for copulation. Overt female and male-male competition is not seen in passive mating (Keeley and Keeley, 2004). The larger male body size in *C. plicatus* may be related to the occurrence of promiscuity in multi-male and multi-female polygynous groups (Weckerly, 1998; McCracken and Wilkinson, 2000; Racey, 2009). Detailed studies of reproductive behavior in *C. plicatus* will contribute to a better understanding of the relationship between sexual dimorphism and mating systems.

Adult males of *C. plicatus* were heavier than adult females, except during March and September when females were heavier. These discrepancies in March and September are likely due to incorrectly classifying females in the early stages of pregnancy as non-reproductive. *Chaerephon plicatus* is normally bimodally polyestrous. Parturition occurs in April and October in Cambodia (Furey et al., 2018) and in March and October in Thailand (Hillman, 1999). Gestation is reportedly 3.5 months in members of Molossidae (Krutzsch and Crichton, 1985). We detected pregnant females in April (n=52), and again in September (n=8) and October (n=55). Abdominal palpation likely failed to detect early pregnancies in March and September; therefore, missed pregnancies likely explained why the body mass of adult females in these two months exceeded that of males.

In this study, the overall body mass of female bats captured at dawn exceeded that of female bats collected at dusk (i.e., they gained weight after foraging), in agreement with measurements made (i) on a population of the same species inhabiting Chao Ram Cave, Sukhothai Province, Thailand (Wanghongsa and Boonkerd, 2000), and (ii) a population of *Rousettus madagascariensis* in northern Madagascar (Goodman et al., 2017). The reduced body weight in adult females at dusk (n=121) may also be explained by milk production and consumption by newborn bats in the months following parturition.

The body masses of both sexes fluctuated seasonally. This fluctuation was probably related to the reproductive cycle of the species and rainfall variability. Similar patterns occur in bats living in temperate zones, where populations hibernate during winter (Kunz et al., 1998). However, some of the temperate zone species are monoestrous (Oxberry, 1979). Body mass increased prior to the onset of winter food shortages in *Myotis lucifugus* in southern Vermont, United States (Kunz et al., 1998), Daubenton's bats (*Myotis daubentonii*) in Germany (Encarnação et al., 2004), both sexes of Kuhl's pipistrelle (*Pipistrellus kuhlii*), and Isabelline Serotine bats (*Eptesicus isabellinus*) in central Tunisia (Dalhoumi et al., 2016). A large body mass in males may promote successful reproduction (Kunz et al., 1998). Large fat reserves in females have been related to energetically costly pregnancies; therefore, females may gain mass for early reproduction (Kunz et al., 1998; Dalhoumi et al., 2016). For tropical bats like *C. plicatus*, food availability is closely related to rainfall patterns (Nurul-Ain et al., 2017) and food availability is important to explaining body mass variation between seasons, especially in polyestrous females (Cumming and Bernard, 1997). Monthly food availability (measured as insect abundance) is reportedly positively correlated with monthly rainfall, especially in tropical zones (Nurul-Ain et al., 2017). Insect abundances may also be highest one month after the rainfall peaks (Cumming and Bernard, 1997). In Thailand, insect abundances are highest during the rice growing period, which is in the rainy season (Srilopan et al., 2018). We found that bats of both sexes increased their body masses in a seasonally bimodal manner that was synchronized with rainfall variation in Ratchaburi province. The lowest adult male body mass (13.47 g) occurred in March during a dry period, and male body mass was low from January through April, i.e., in the dry season. Adult female body mass was low from January through May, falling to a minimum (12.88 g) in February.

A modeling exercise by the Climatological Center (2016) analyzed the annual weather data for the period 1970-2015 and predicted that the maximum-minimum temperature range would increase in western Thailand from 2016 through 2099. Annual precipitation was predicted to decrease slightly over this period, perhaps with negative effects on bat food resources. We suggest that to support this large population of *C. plicatus*, further research should focus on population dynamics, prey availability, and foraging habitat.

5. CONCLUSIONS

This study reveals that male *C. plicatus* had significantly larger forearm lengths and body masses than females. Both sexes had two seasonal peaks in body mass, one at the beginning of the rainy season and a second at the end. Body masses were positively correlated with monthly rainfall.

ACKNOWLEDGEMENTS

This research was supported by a Research Chair Grant and a grant for the establishment of the zoonotic viral networking system: developmental phase project of the National Science and Technology Development Agency (NSTDA). We also thank Aingorn Chaiyes, Yuwadee Ponpituk, Warong Suksavate, Supalak Siri, Pongsit Srikhunmuang, Apisada Rueangket, Ngamphrom Sukgosa, Suttikarn Srisodsuk, Thansuda Dowwiankan, Narongdet Detkong, and the other students at Department of Forest Biology, Faculty of Forestry, Kasetsart University, for their support in the field.

REFERENCES

Barclay RMR. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. Journal of Animal Ecology 1991;60(1):165-78.

Boonkerd K, Wanghongsa S. Management of bat caves. In: Pimmanrojakul W, editor. Annual Report of Wildlife Research Division. Bangkok: Royal Forest Department; 2002. p. 33-45 (in Thai).

Climatological Center. Changes in temperature and rainfall over Thailand under climate change [Internet]. 2016 [cited 2018 Aug 4]. Avialable from: http://climate.tmd.go.th/content/category/24 (in Thai).

Csorba G, Bumrungsri S, Francis C, Bates P, Ong P, Gumal M, Kingston T, Heaney L, Balete D, Molur S. *Chaerephon plicatus* [Internet]. 2017 [cited 2017 Mar 3]. Available from: http://www.iucnredlist.org/details /4316/0.

Cumming GS, Bernard RTF. Rainfall, food abundance and timing of parturition in African bats. Oecologia 1997;111(3):309-17.

Dalhoumi R, Aissa P, Aulagnier S. Seasonal variations of sexual size dimorphism in two Mediterranean bat species from Tunisia: the Kuhl's pipistrelle (*Pipistrellus kuhlii*) and the Isabelline serotine (*Eptesicus isabellinus*). Folia Zoologica 2016;65(2):157-63.

Camargo NFD, Oliveira HFD. Sexual dimorphism in Sturnira lilium (Chiroptera, Phyllostomidae): can pregnancy and pup carrying be responsible for differences in wing shape? PLoS One 2012; 7(11):e49734.

Encarnação JA, Dietz M, Kierdorf U, Wolters V. Body mass changes in male Daubenton's bats *Myotis daubentonii* (Chiroptera, Vespertilionidae) during the seasonal activity period. Mammalia 2004;68(4):291-7.

Fleming TH, Hooper ET, Wilson DE. Three Central American bat communitis: structure, reproductive cycles, and movement patterns. Ecology 1972;53(4): 555-69.

Furey N, Racey P, Ith S, Touch V, Cappelle J. Reproductive ecology of wrinkle-lipped free-tailed bats *Chaerephon plicatus* (Buchannan, 1800) in relation to guano production in Cambodia. Diversity 2018;10(3):91-100.

Gager Y, Tarland E, Lieckfeldt D, Ménage M, Botero-Castro F, Rossiter SJ, Kraus RH, Ludwig A, Dechmann DK. The value of molecular vs. morphometric and acoustic information for species identification using sympatric molossid bats. PLoS One 2016;11(3):e0150780.

Goodman SM, Rajemison FI, Olivà S. Morphometric patterns of secondary sexual dimorphism and seasonal differences in *Rousettus madagascariensis* from northern madagascar. Acta Chiropterologica 2017; 19(1):71-5.

Happold D, Happold M. Reproduction of Angola free-tailed bats (*Tadarida condylura*) and little free-tailed bats (*Tadarida pumila)* in Malawi (Central Africa) and elswhere in Africa. Journal of Rreproduction and Fertility 1989;85:133-49.

Herron JC, Freeman S. Evolutionary Analysis. 5th ed. England: Pearson Education Limited; 2015.

Hillman A. The study of Wrinkled-lipped bats (*Tadarida plicata*) at Khao Chong Phran, Ratchaburi. Journal of Thai Forestry Research 1999;1(1):72-83.

Hillman A. Monitoring of *Tadarida plicata* at Khao Chong Phran Non-hunting Area, Ratchaburi. Journal of Wildlife in Thailand 2006;13(1):31-42.

Hurtado N, Sepúlveda RD, Pacheco V. Sexual size dimorphism of a sensory structure in a monomorphic bat. Acta Chiropterologica 2015;17(1):75-83.

Keeley AT, Keeley BW. The mating system of *Tadarida brasiliensis* (Chiroptera: Molossidae) in a large highway bridge colony. Journal of Mammalogy 2004;85(1):113-9.

Krutzsch PH, Crichton EG. Observations on the reproductive cycle of female *Molossus fortis* (Chiroptera: Molossidae) in Puerto Rico. Journal of Zoology 1985;207(1):137-50.

Kunz TH, Wrazen JA, Burnett CD. Changes in body mass and fat reserves in prehibernating little brown bats (*Myotis lucifugus*). Ecoscience 1998;5(1):8-17.

Kunz TH, Torrez BE, Bauer D, Lobova T, Fleming TH. Ecosystem services provided by bats. Annals of the New York Academy of Sciences 2011;1223(1):1-38.

Leelapaibul W. The Diet and Feeding Factors of the Wrinkle-lipped Free-tailed Bat (*Tadarida plicata*) at Khao-Chong-Pran, Ratchaburi Province [dissertation]. Bangkok, Thailand: Kasetsart University; 2003 (in Thai).

Leelapaibul W, Bumrungsri S, Pattanawiboon A. Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. Acta Chiropterologica 2005;7(1):111-9.

Lisón F, Haz Á, Carlos GR, Calvo JF. Sexual size dimorphism in greater mouse-eared bat *Myotis myotis* (Chiroptera: Vespertilionidae) from a Mediterranean region. Acta Zoologica 2014;95(2):137-43.

McCracken GF, Wilkinson GS. Bat mating systems. In: Crichton EG, Krutzch PH, editors. Reproductive Biology of Bats. Cambridge: Great Britain at the University Press; 2000. p. 321-62.

McPherson FJ, Chenoweth PJ. Mammalian sexual dimorphism. Animal Reproduction Science 2012; 131(3-4):109-22.

Nolte MJ, Hockman D, Cretekos CJ, Behringer RR, Rasweiler JJ. Embryonic staging system for the Black Mastiff Bat, *Molossus rufus* (Molossidae), correlated with structure-function relationships in the adult. Anat Rec (Hoboken) 2009;292(2):155-68.

Nurul-Ain E, Rosli H, Kingston T. Resource availability and roosting ecology shape reproductive phenology of rain forest insectivorous bats. Biotropica 2017;49(3): 382-94.

Oxberry BA. Female reproductive patterns in hibernating bats. Journal of Reproduction and Fertility 1979; 56(1):359-67.

Racey P. Reproductive assessment of bats. In: Kunz TH, Parsons S, editors. Ecological and Behavioural Methods in the Study ofB. Maryland: Johns Hopkins University Press; 2009. p. 249-64.

Ralls k. Mammals in which females are larger than males. The Quarterly Review of Biology 1976;51(2):245-76.

Ratrimomanarivo FH, Goodman SM, Stanley WT, Naidoo T, Taylor PJ, Lamb J. Geographic and phylogeographic variation in *Chaerephon leucogaster* (Chiroptera: Molossidae) of Madagascar and the western Indian Ocean islands of Mayotte and Pemba. Acta Chiropterologica 2009;11(1):25-52.

Rex K, Kelm DH, Wiesner K, Kunz TH, Voigt CC. Species richness and structure of three Neotropical bat assemblages. Biological Journal of the Linnean Society 2008;94(3):617-29.

Srilopan S, Bumrungsri S, Jantarit S. The wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchannan, 1800) feeds mainly on brown planthoppers in rice fields of central Thailand. Acta Chiropterologica 2018;20(1):207-19.

Stevens RD, Platt RN. Patterns of secondary sexual size dimorphism in New World Myotis and a test of Rensch's rule. Journal of Mammalogy 2015;96(6): 1128-34.

The R Development Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing: Reference Index [Internet]. 2017 [cited 2017 Mar 6]. Available from: https://cran.r-project.org/bin/windows/base/old/3.3.3/.

Utthammachai K. Foraging Habitat Use by Acoustic Monitoring of *Tadarida plicata* (Buchannan, 1800) in an Agricultural Landscape, Ratchaburi Province [dissertation]. Bangkok, Thailand: Kasetsart University; 2009.

Utthammachai K, Bumrungsri S, Chimchome V, Russ J, Mackie I. Habitat use and feeding activity of *Tadarida plicata* in Thailand. Thai Journal of Forestry 2008;27(2):21-7.

Vivier L, Merwe MVD. Reproduction in the female Angolan free-tailed bat, *Tadarida (Mops) condylura* (Microchiroptera: Molossidae), in the eastern Transvaal, South Africa. Journal of Zoology 1997; 243(3):507-21.

Voigt CC, Holderied MW. High manoeuvring costs force narrow-winged molossid bats to forage in open space. Journal of Comparative Physiology B 2012;182(3): 415-24.

Wanghongsa S, Boonkerd K. Behaviour of bats (*Tadarida Plicata*) in Chao Ram cave, Sukhothai province, Thailand. Journal of Wildlife in Thailand 2000;8(1): 42-9 (in Thai).

Weckerly FW. Sexual-size dimorphism influence of mass and mating systems in the most dimorphic mammals. Journal of Mammalogy 1998;79(1):33-52.

Wu H, Jiang T, Huang X, Lin H, Wang H, Wang L, Niu H, Feng J. A test of Rensch's rule in greater horseshoe bat (*Rhinolophus ferrumequinum*) with female-biased sexual size dimorphism. PLoS One 2014;9(1):e86085.