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ORIGINAL PAPER

# Seasonal reproductive synchrony in colonies of the Jamaican fruit–eating bat (*Artibeus jamaicensis*) in southeast Mexico

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## Abstract

In tropical ecosystems, environmental conditions are often less constraining, leading to an increase in the reproductive potential of several species of mammals. One of the strategies to enhance this reproductive potential is to exhibit postpartum oestrus, which is common among different bat families. In the Yucatan Peninsula, we observed for over 2 years two colonies of marked individuals of the Jamaican fruit–eating bat, *Artibeus jamaicensis* to determine their reproductive activity. Females presented postpartum oestrus that allows them to have a second annual parturition. During the peak period of parturition, a marked increase in attempts and successful mating events were observed among the bats roosting within the caves. Births were recorded but in lower proportion in the remaining months of the year; however, no copulation attempts or matings were recorded from October to January in both caves and in both years. A delayed embryonic development after the second birth might explain the continuous parturition events recorded for *A. jamaicensis* in Yucatan.

**Keywords** *Artibeus jamaicensis* · Bat colonies · Breeding season · Postpartum oestrus · Reproductive synchrony · Yucatan

## Introduction

Reproductive synchrony is when the mating events in a population are seasonally matched, and both sexes of that population are available for copulation. For this pattern to occur, it is necessary for individuals to evaluate the environmental conditions such as availability of resources, cost of reproduction, life expectancy, and severity of harsh situations (e.g. extended drought), among many ecological and social factors that can influence the decision of an individual to reproduce (Happold and Happold 1991; Heideman et al. 1992; Heideman and Utzurrum 2003; Saldaña-Vazquez et al. 2020). Pregnancy and lactation lead to increased energy demand for individual females, so reproductive success should be improved when these stressful periods coincide with periods of higher resource availability (Fleming et al. 1972; Bradbury and Vehrencamp 1977). In several bat species, a synchronous reproductive pattern with seasonality and food resource availability as central factors has been documented (Bernard 1994; Heideman 1995; Racey and Entwistle 2000; Porter and Wilkinson 2001). In Neotropical frugivorous bats, reproduction cycles are often concentrated at the end of the dry season and the beginning of the rainy season, when favourable climatic conditions occur. Frugivorous bats tend to accumulate fat and protein reserves by consuming high-energy fruit as well as other available resources, such as pollen, leaves, and insects (MacSwiney et al. 2012; Molinari and Soriano 2014).

The Jamaican fruit–eating bat (*Artibeus jamaicensis*) is primarily frugivorous, but its feeding habits can change in response to food availability throughout the year, thus favoring its wide distribution and abundance in the Neotropics (Ortega and Castro-Arellano 2001). The Jamaican fruit–eating bat is predominantly a cave dweller (Arita 1996) and actively uses dissolution cavities throughout the year, forming compact clusters of individuals, the membership of which varies throughout the year (Ortega and Arita 1999).

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For much of the year, the group comprises sexually inactive females, allowing males to enter the groups continuously, with a high frequency of visits presented by adult males, and the constant presence of one dominant male per group that does not show a particularly active agonistic behaviour (Ortega and Arita 2000). However, during the offspring birth period, the groups form harems: clusters of females very stable in their composition, with the presence of dominant males that monopolize these clusters of lactating females, preventing access by other males to the females with agonistic interactions (Ortega and Arita 2000, 2002).

In Trinidad, *A. jamaicensis* breeds throughout the year (Goodwin and Greenhall 1961) but, in northwestern Costa Rica, Stoner (2001) found reproductive females only from February to June. In Barro Colorado Panamá, *A. jamaicensis* females present two reproductive events per year, producing one pup in each cycle (Wilson et al. 1991). Females give birth in February–March, followed by a mating event where fertilization and implantation are carried out normally with a usual gestation period between 3.5 and 4 months (Wilson et al. 1991). A second birth peak occurs in June–August with a second mating event, but implantation is followed by an embryonic delay (Fleming 1971; Fleming et al. 1972; Wilson 1979), in which the implanted blastocyst enters a resting phase and development is delayed for approximately 2.5 months until resources are more abundant (Neuweiler 2000). Females of *A. jamaicensis* are able to display postpartum oestrus, in which they can simultaneously be pregnant and lactating (Keast and Handley 1991). The oestrus cycle is controlled by the time of parturition, except in those females that, for reasons unknown, do not give birth during a particular reproductive period. The highest frequency of attempted and successful copulation (when an adult male mounts one of the females and mates for several seconds, not longer than 2 min) occurs during the third and fourth days after parturition (Keast and Handley 1991). The testes of the males are enlarged while females are in postpartum oestrus, and the degree of synchrony in the system indicates that males may be able to inseminate females during the periods that overlap with the highest frequency of births (Wilson et al. 1991).

The Yucatan Peninsula, located in the southeast of Mexico, presents few variations in topography, with low habitat heterogeneity and vegetation that consists of tropical dry forest that is highly disturbed due to substitution by farmland. The rainy period is well defined in this area, beginning at the end of May and finishing around mid-September. This is also the hurricane season, a season during which there is a greater supply of water for the plants, with high fruit production as a consequence. The marked seasonality of rains in the Yucatan Peninsula allows animals to be reproductively predictable during the time of greatest abundance of resources. *Artibeus jamaicensis* in Yucatan has been reported to feed on the approximately 5 to 10 species of fruit trees that are produced throughout the year, but its diet becomes more varied in the rainy season, when an increase of up to 21 different varieties of fruit has been recorded (Flores Martínez et al. 1999–2000). *Artibeus jamaicensis* preferably consumes the fruits of *Ficus*, from which it extracts more than 50% of the dry mass and converts it into metabolizable calories that provide great amounts of energy by consuming almost twice its body mass daily (approx. 50 g) in fruits (Morrison 1978, 1980; August 1981; Teixeira et al. 2009). The highest abundance of fruits is from July to September, while the months of December and January present lower values of fruit consumption (Flores-Martínez et al. 1999–2000). In this region, *A. jamaicensis* has been observed to include a wide variety of cultivated species that are abundant in the orchards in its diet, as well as complementing it with other elements, such as pollen, insects, nectar, and leaves (Kunz and Diaz 1995; MacSwiney et al. 2012; Fabianek 2014).

*Artibeus jamaicensis* is an abundant resident species of caves in the south of Yucatan (Arita 1996) showing two reproductive peaks: February–March and June–July (Ortega and Arita 1999). Fleming (1971) discovered a postpartum oestrus in *A. jamaicensis* that explained this pattern of two reproductive events. We, therefore, wish to establish whether the maximum peak of births of offspring coincided with the sexual activity displayed by the males. We hypothesized that, following the parturition of females, there will be differences in the male mating behaviour, measured as the number of copulation attempts and copulation success events, compared to that of the non-parturition period. Given the proximity and similar environmental conditions, we expect that our data collected over two breeding seasons and individuals from colonies within two different caves will be similar.

## Materials and methods

Limestone predominates the Yucatan Peninsula region, allowing dissolution of the soil and the development of caves, within which there are cavities with particular microenvironmental characteristics that provide suitable perch sites for bats (Arita and Vargas 1995). We studied bat colonies of *A. jamaicensis* in two major caves of the Yucatan Peninsula; research was conducted for 24 months, from January 1996 to February 1998. The Akil (20° 14′ N, 89° 22′ W) and Murciélagos (20° 09′ N, 89 13′ W) caves are located in the elevated area known as Sierrita de Ticul (90 m asl) and were selected due to their continuous presence of large populations of *A. jamaicensis*. The Murciélagos cave has a corridor of 80 m in length, with a main chamber of 20 by 30 m and an average height of 5 m. We estimate that a population of *ca.* 250 Jamaican fruit–eating adult bats roost in the dissolution cavities and walls of this particular section of the cave. The Akil cave has a main chamber of 10 by 10 m with an average height of 2.5 m, and an estimated population of 200 adult individuals (Ortega and Arita 1999). The sex ratio of *A. jamaicensis* populations in both caves was 1:1 (Ortega and Arita 1999).

Individuals from the groups perched in the dissolution cavities were captured using bucket traps (Kunz et al. 1983, 1996; McCracken and Bradbury 1981). Lone bats perched on the walls and roof were captured directly by hand-held net or mist net after being disturbed. Individuals were marked on the forearms with coloured plastic rings (AVINET, Inc., XB size / 4 mm diameter). The ring on one forearm was used to distinguish the specific group, while two rings were used on the other forearm as a binary code for individual identification; group's mark was on the right forearm for males and left for females (Ortega and Arita 1999). The captures from the first year were carried out a month (beginning of January 1996) before observations started to allow bats to recover from the disturbance related to the marking process. At the beginning of the second year of the study, bats with no rings were captured and marked with color rings assigned to the specific group where they belong. We followed the guidelines for the use of wild mammal species in research as recommended by the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016). This project used collection permits issued by the Mexican Ministry of the Environment to H. T. Arita.

Ossified epiphyses were used to classify individual adults, while bats with cartilaginous joints were considered juveniles (Brunet-Rossinni and Wilkinson 2009). This categorization was corroborated by measuring body mass using a 0.1-g precision spring scale balance and measuring the length of the forearm with a mechanical caliper of accuracy ± 0.1 mm, considering that the adults are always heavier and with longer forearms than the juveniles (Ortega and Arita 1999). The reproductive condition in males was evaluated using the position of the testicles (abdominal or scrotal), while in females, we considered three categories: pregnant, lactating, or no reproductive signs. Bats were released after capture and undisturbed until the following month, when behavioural observations began. The breeding season was defined from February to August, when $>80\%$ of the adult females were lactating. However, in the period from September to January, most of the adult females presented no signs of reproductive activity (Ortega and Arita 2000).

We marked a total of 97 females and 84 males from 20 different harems from both caves: 8 harem groups in Akil cave and 12 harem groups in Murciélagos cave. Harem size varied from four to 18 females per group (mean $=9.72$, SE $=0.08$, $n=20$, Ortega and Arita 2000). Individuals were identified using the unique colour of the plastic ring on each bat, and were categorized as adult males, adult females, and juveniles. Newborn pups were considered within the juvenile category until they learned to fly and left the perch site. Each observation day, we began with a scan surveillance of all marked groups to record the membership of the adult individuals associated in each harem, in addition to reporting the presence of newborn pups. Later, we observed one focal harem group per day, for 6 h daily starting at 7:00 and finishing at 15:00. Observation sessions began early in the morning with 2-h-long periods of constant observation followed by an hour of rest, until completing the accumulated total of 6 h observations per day. We observed each of the 20 harem groups for a total of 6 h every month, for a total of 120 h of observation each month and 2880 h of observations for the 2-year study. A diffused light lamp was used to illuminate the cave chamber without causing direct disturbance to the groups. The field team used binoculars, stopwatch, and behavioural activity record sheets to register the observations.

We determined sexual behaviour when a male approached the potential sexual partner and prowled around her until she finally allowed him to smell her genital area. An attempted copulation response was recorded when the male approached a female and tried to mount her, but for some reason, they separated from each other immediately. Successful copulation behaviour was recorded when the adult male mounted one of the females that belonged to the studied harem group and mated for several seconds. The presence of a newborn attached to one female was counted as one new member of the group when the initial scan surveillance was carried out every day in a certain cave. However, it is possible that when observations were carried out in one cave, we missed parturitions events in the other cave. Because females of *A. jamaicensis* have been reported to be highly receptive during the days following childbirth (Fleming 1971), we consider the presence of a new pup as indicative of imminent oestrus. We used these observations to quantify the reproductive activity of adult individuals within groups (Ortega and Arita 2000).

We compared the mating attempts, successful copulations, and number of parturitions observed, between the sampled caves (Akil and Murciélagos) over time (Shapiro-Wilks normality test, Mann–Whitney U test). The relationship between the number of successful copulations and the number of births was analyzed by means of Spearman's correlation (r), which gives us the relationship between two variables using a monotonic function. We compared the mating behaviour within the previously defined breeding (February–August) and non-breeding seasons (September–January) by analyzing the data with a Mann–Whitney test. We used Spearman's correlation to determine a relation between the forearm length of dominant male bats and the number of recorded successful copulations. For all analyses, we used the statistical software JMP®, Version 10 (SAS Institute Inc., Cary, NC, 1989–2019).

## Results

We captured and marked 181 bats, approximately two-thirds of the estimated population for each cave. Most of the individuals that were marked (approximately 68%) roosted solitary in the walls and ceiling of the cave; the sexual proportion of these bats were 4 adult males: 1 adult females. The remaining 32% of all captured individuals clustered in discrete groups inside of solution cavities. The composition of those clusters was typical of harem groups (*ca.* 9 females + one or two adult males).

Parturition period was similar between caves and years, with the highest number of pups recorded from March to August. The number of parturitions between cave Akil ($n = 193$) and Murciélagos ($n = 168$) did not differ significantly (Mann–Whitney U = 277, $p = 0.5$). Our observations of attempted and successful copulation events showed an indication of postpartum oestrus in both caves since, following the first births (February–April) and the second parturition period recorded during the months of June and July (Figs. 1 and 2).

We observed a total of 28 copulation attempts in both sampled caves (Akil = 15, Murciélagos = 13). The resident males were only observed to attempt to copulate during the parturition season (Fig. 2). The highest number of observed successful copulations by resident males within the harem groups coincided with the months of the greatest availability of resources (February–August, breeding season) in both Murciélagos cave (1st season: n = 15, ± SE = 0.39; 2nd season: n = 11, ± SE = 0.52) and Akil cave (1st season:

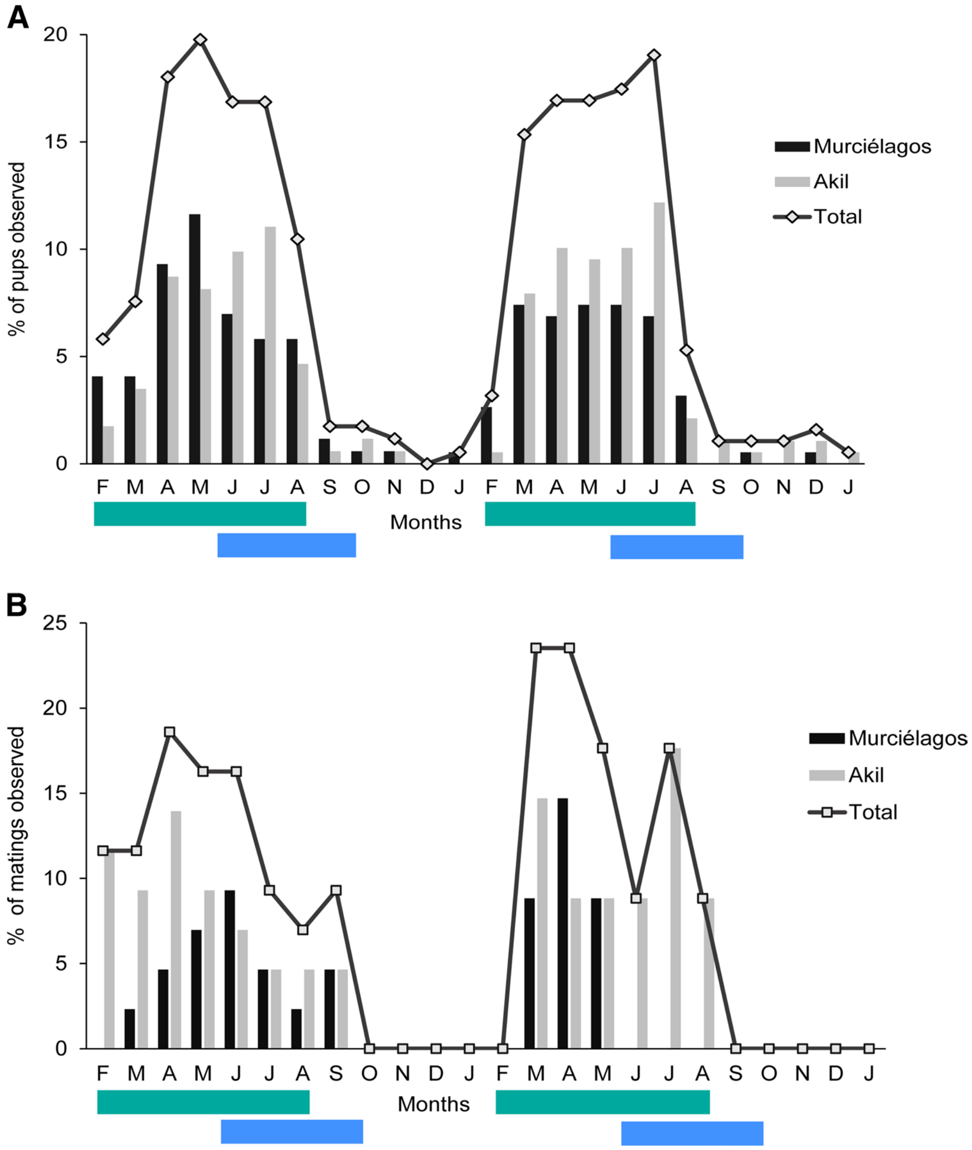

**Fig. 1** Observed seasonal synchrony between **A** percentage of newborn pups born per month and in total and **B** percentage of mating's recorded per month and in total for *Artibeus jamaicensis* in two caves in the Yucatan Peninsula, Mexico. The percentages were calculated considering the total number of newborn pups and the number of successful copulations observed in the entire study, respectively. Green bars indicate the correspondent breeding season, and the blue bars correspond to the rainy season

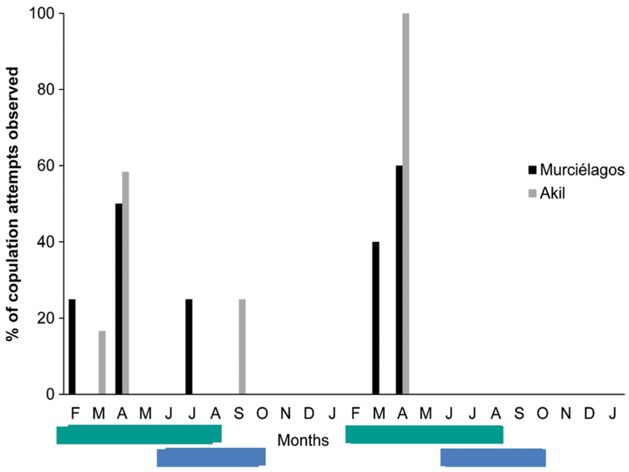

**Fig. 2** Percentage of copulation attempts recorded per month for *Artibeus jamaicensis* in two caves in the Yucatan Peninsula, Mexico

n = 28, ± SE = 0.61; 2nd season: n = 23, ± SE = 0.63), but the number of observed copulations were low outside of this period (Fig. 1). These data also presented a non-normal distribution (Shapiro-Wilks, W = 0.83, $p < 0.01$) and no significant difference was found between the number of successful copulations in the two caves (Mann–Whitney, U = 211, $p = 0.11$). In the months prior to the highest number of parturition events (February–March), the majority of the resident males presented scrotal testes (90%).

In Akil cave, an increase in copulations of resident males within harem groups was observed, consistent with the parturition timing of the females (Fig. 3a) with a significant correlation coefficient ($r_s = 0.75$, $p < 0.01$). A similar pattern was observed in the Murciélagos cave, where copulations of resident males in the harem groups (one for each group) increased in the parturition season (Fig. 3b). This relationship presented a statistically significant correlation coefficient ($r_s = 0.69$, $p < 0.01$). The number of copulation attempts was not statistically significantly different between the caves (Mann–Whitney U = 39.5, $p = 0.54$).

## Discussion

Reproduction studies on *A. jamaicensis* have been carried out in many sites throughout its distribution. Most reproductive information comes from individuals captured during flight whereas detailed studies at a specific roosting sites over long periods, which are necessary for elucidating details of a reproductive cycle, are still missing (Wilson et al. 1991). In the present study, we followed 20 groups of *A. jamaicensis* for a 2-year period in two caves in order to describe if postpartum oestrus in *A. jamaicensis* explained the pattern of two reproductive events previously reported for this species (Ortega and Arita 1999). Our observations showed that the males mainly had two types of frequent behavioural interactions with the females shortly after parturition. These were attempts to mount, in which the males first approached to evaluate the receptivity of the females, but females moved away from the male, and successful copulations, in which the male sustained copulation with the female for few seconds to minutes. These observations were significantly higher during the greater number of parturition events, but decreased in frequency in the subsequent months when newborn pups were not observed, thus suggesting postpartum oestrus.

In the monogamous prairie voles (*Microtus ochrogaster*), postpartum oestrus occurs regularly, but can be reduced because pup stimulation or lactation inhibits female receptivity (Witt et al. 1990). Postpartum oestrus has not been commonly documented in bats but has been recorded in at least 33 species of six families of bats (Badwaik and Rasweiler 2000). Among some bats,

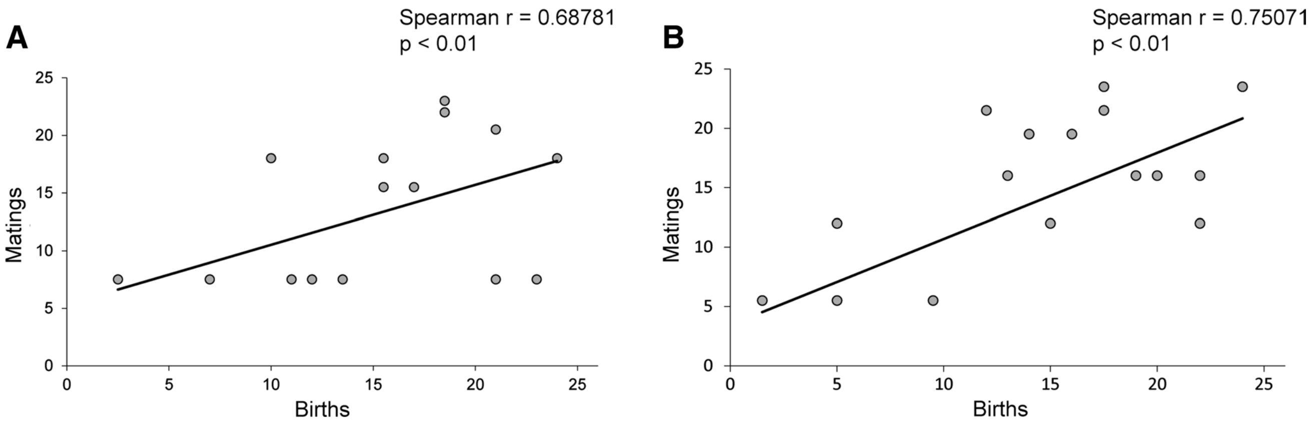

**Fig. 3** Correlation between matings of dominant male bats and number of parturitions observed among the different females within the harem groups. **A** Murciélagos cave. **B** Akil cave

however, females exhibit postpartum oestrus when the pup is recently born, and in fact, newborn infants are usually attached to the mothers during the copulations (Keast and Handley 1991; J Ortega pers. obs.). The few detailed behavioral observations of postpartum oestrus on *Artibeus jamaicensis* are from a captive colony where males successfully copulate with females on day 2 after parturition with a peak of copulations between days 3 and 4 (Keast and Handley 1991). Detailed studies are needed to fully understand the reproductive cycle of bats and also the hormones, sociality, and environmental variables involved in the process.

The timing of bat parturition is well documented in several species and it has been postulated that environmental factors and the abundance of food can affect this synchronization; however, in the same way, the transmission of chemical signals between individuals of the colony can promote the synchronization of births in a particular group of females (Porter and Wilkinson 2001; Heideman and Utzurrum 2003; Durant et al. 2013; Ruiz-Ramoni et al. 2017). Our results indicate that the reproductive cycle (i.e. copulation, pregnancy, lactation) of the individuals in both sites was similar, probably influenced by postpartum oestrus and the season of the year**.** The Jamaican fruit-eating bat in the Yucatan Peninsula presents a prolonged reproductive period from mainly from February to August, but with a higher proportion of births in two periods (February–March and June and July), a pattern also reported for the species in Colombia (Castillo-Navarro et al. 2017). It is important to note that births were also recorded but in lower proportion in the remaining months of the year; however, no copulation attempts or matings were recorded from October to January in both caves and in both years. A delayed embryonic development after the second birth might explain the continuous parturition events recorded for *A. jamaicensis* in Yucatan as observed for the same species in Panama (Fleming 1971).

The first period with the highest parturition event is recorded in the months of February and March, but the frequency is almost 30% lower than that recorded in the peak (June–July) of the rainy season (Ortega and Arita 1999). A similar pattern has been observed for *A. jamaicensis* in Costa Rican forests, where pregnancy diminished by 15% during the dry season in comparison to the wet season (Heithaus et al. 1975). Both in the Yucatan and Costa Rican forests, *A. jamaicensis* includes mainly pollen from various flower species in its diet during the dry season (Heithaus et al. 1975; MacSwiney et al. 2017). During the time of the present study, Flores-Martínez et al. (1999–2000) found in the same sites a lower richness and abundance of food items below the roosting sites of *A. jamaicensis*. It is possible that although these resources might be better quality food, they are not so abundant as the variety of fruits that these species consume during the wet season (Flores-Martínez et al. 1999–2000), compromising the number of females that engage in reproduction.

The mating systems of bats have been documented in several studies, showing a high diversity of behaviours. However, the general condition is that both sexes have roles of particular influence on each other, especially during the reproductive season (Rossiter et al. 2000; Kerth and Morf 2004; Dechmann et al. 2005; Toth and Parsons 2013; Günther et al. 2016). For example, males of *A. jamaicensis* present very specific behavioural patterns during the mating season, being very active in their defence of groups of females and being willing to visit them when they are lactating (Ortega and Arita 2000). On the other hand, during the breeding season, the females form stable and compact groups, and become more sociable with each other, presenting constant physical contact, in addition to permitting the approach of the males (Ortega and Maldonado 2006; Wilde et al. 2018). Removal experiments on these resident males have shown that satellite bats, or non-resident males, are willing to fill vacant spots and will perform the same type of female defensive/assessment behavioural activity. The results also show that such replacement takes place more rapidly when the females are receptive to copulation in the breeding season (Ortega and Arita 2002). Resident males of the groups of *A. jamaicensis* present agonistic behaviours towards possible competitors for the receptive females. These combative behaviours are much more frequent and intense during the breeding seasons (Ortega and Arita 2000).

The approaching behaviour presented by the resident males to receptive females for attempts at copulation was recorded in low frequency (28 times), but these attempts were observed mainly in the days following parturition in comparison with the rest of the year. The latest attempts observed occurred in September at Akil cave. The frequency of successful copulations in resident males is the highest during the parturition season when it is documented that females are more receptive due to postpartum oestrus. However, we cannot rule out that copulation might continue sporadically as in a captive colony in Costa Rica the latest copulations recorded occurred 25 days postpartum (Keast and Handley 1991).

As other studies have pointed out, mating events in observational samplings with free-ranging bats are difficult to register (Rodríguez-Herrera et al. 2020), even in studies with considerable hours of video recording (Voigt and Schwarzenberger 2008). In the present study, after 2 years of observation, we recorded 77 events of successful mating paired with the highest abundance of pups in the population. In the following years, the use of technological advances in the form of proximity sensors, small ultrasonic microphones, and biosensors attached to the bodies of bats will undoubtedly reveal the complex social relationships of bats in the wild in finer detail.

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**Author contribution** JOR performed the experimental design, fieldwork, analyzed the data, and wrote the manuscript. EGG collaborated in analyses and writing the manuscript. DDMS and MCMG wrote the manuscript.

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**Data availability** Not applicable.

**Code availability** Not applicable.

## Declarations

**Ethics approval** We followed the guidelines for the use of wild mammal species in research as recommended by the American Society of Mammalogists (Sikes and The Animal Care and Use Committee of the American Society of Mammalogists 2016). This project used collection permits issued by the Mexican Ministry of the Environment to H. T. Arita.

**Consent to participate** All participants consent to their participation in this publication.

**Consent for publication** All participants have read the manuscript and consent to the publication of this research.

**Conflict of interest** The authors declare no competing interests.

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