
Preliminary Observations of Infant Ontogeny in the Philippine Tarsier (*Tarsius syrichta*) and the First Description of Play Behaviour and Its Ontogeny in Tarsiers

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Additional information is available at the end of the chapter

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Abstract

In this paper, I present the first observations on the ontogeny of tarsier infants during their first and second months and of the mother-offspring bond from birth until separation. Tarsier mother-infant pairs were observed to be solitary. Maternal care involved a cache and carry strategy with the infant spending around 66% parked alone whilst the mother was foraging. I observed the following behaviour: rest, grooming, suckling, play, being carried, jumping and climbing. Percentage of time spent in each activity was calculated. Furthermore, play was observed to include locomotor-, social- and object-directed behaviours. Acoustic communication between mother and infant was very frequent containing four different signals. During the first days after birth, the mother transported the infants about, but within a week, the infants started climbing branches on their own. For the first three weeks, the mothers carried infants orally after which they started to follow the mother over shorter distances, although for longer distances, up to 50 days of age, the mothers continued to carry them. The inter-birth interval was around 1 year, but the infants from the previous birth continued to sleep with the mother for up to 10 months.

Keywords: Philippine tarsier, *Tarsius syrichta*, ontogeny, behaviour, maternal care, play

1. Introduction

Tarsiers are small nocturnal primates from Southeast Asia, restricted to a few islands in the Sunda Strait (off Indonesia, Malaysia and Brunei) and on some islands of the Philippines. Only one of the extant species, Philippine tarsier (*Tarsius syrichta*), lives in the Philippines.

Despite a recent increase in studies of tarsiers, they remain the least studied primates. This is unfortunate given the pivotal phylogenetic position of tarsiers between strepsirrhines and other haplorrhines [1].

Sociality, mating system and group composition vary among tarsier species. Some species cluster together in small groups. For example, spectral tarsiers (*Tarsius spectrum*) exhibit substantial amount of gregariousness and sleep together in small family groups [2–4]. Similarly, Dian's tarsier (*Tarsius diana*) has been observed sleeping in small family groups involving either monogamously or polygynously bonded adults [5]. Finally, Lariang tarsiers (*Tarsius lariang*) live in small groups that include multiple individuals sleeping together [6, 7]. In contrast, western tarsier (*Tarsius bancanus*) [8] and Philippine tarsier [9–11] sleep and forage alone.

Apart from relatively well-studied spectral tarsier, little is known about the behaviour of tarsiers. The small size and cryptic nature of tarsiers make field observations, especially on the development of behaviour, difficult to obtain. In spectral tarsiers, birth is given to single offspring seasonally, mostly in April–May [12]. Although the data are more limited, a similar pattern appears to be present in the Philippine tarsier with births occurring between April and July [11]. At birth infants can weigh up to one-third of the body weight of mothers [13]. Being strictly insectivorous (or carnivorous) tarsier mother cannot transport the infant whilst hunting. Instead of being continually transported, infants are parked on a branch (or in a nest in the case of spectral tarsier) and left alone whilst the mother is foraging [2, 3]. The mothers return to the infants at regular intervals to feed them. In addition, on some visits the mothers may transfer them to another parking site. Variations on this kind of parking strategy also occur in several nocturnal strepsirrhines, such as *Galago*, *Microcebus*, *Cheirogaleus*, *Varecia*, *Lepilemur*, *Otolemur*, *Phaner* or *Arctocebus*, *Nycticebus* and *Perodicticus* (reviewed in [14]).

So far, study of infant and maternal behaviour in free-ranging tarsiers has been limited to the spectral tarsier [3, 4, 12]. In this species, the infant is parked and left alone for 43% of the time during the first 3 months. However, spectral tarsiers are a social species living in family groups, with alloparental care (i.e. *allocare*) provided by other group members, especially subadult females, for some of the time when the mother was absent. In contrast, for the solitary Philippine tarsier, preliminary data indicate that parental care is mainly provided by mother [11]. Little else is known about maternal behaviour and the development of behaviour in the young. For example, play behaviour is an important component of development in nearly all primate, and many non-primate, species [15, 16]. Yet, apart from a short note on play behaviour, present as a part of *allocare* in spectral tarsiers [2, 12] and in captive western tarsiers [17], play behaviour has not been described in detail in tarsiers.

In this paper, I present the preliminary observations on the ontogeny of Philippine tarsier infants during the first and second months of the age, as well as on the mother-offspring bond from birth until separation. Furthermore, I provide the first description of play behaviour in tarsiers.

2. Methods

2.1. Study site and animals

The observations on the Philippine tarsier (*T. syrichta fraterculus*) were conducted on Bohol Island, Philippines, as a part of a broader study. The landscape occupied by the tarsiers was composed of karst, narrow ravines and steep stony slopes with numerous cracked rocks covered by secondary forest. Two mother-infant pairs were observed during April and June 2009 at the Philippine Tarsier Sanctuary in Corella, Bohol, Philippines (9°41' N, 123°57' E) (elevation 100–200 m). The first infant (infant I) was born to mother I in a semi-captive enclosure [18] on 17 April 2009 and observed until 6 June 2009. The second infant (infant II) was born to a free-ranging radio-collared mother (mother II) on 30 April and was observed until 4 June 2009 when it was predated on by an unknown predator [19]. Additionally more limited observations were made on several other mother-infant pairs in Bilar, Bohol (9°44' N, 124°06' E) (elevation 220–380 m). One mother-infant pair (infant III and mother III) was observed on 22 May 2010, after they were rescued from poachers. During afternoon, they were kept in a cage, and in the evening, they were released in Forest Academic Research Area, limiting my observations to just the day when they were in the cage. Five additional infants (IV, V, VI, VII and VIII) were observed to be born to the same mother in a forested area at the Habitat Bohol Conservation Centre. Infant IV was first spotted on 22 May 2013. As it was being transported by the mother, I estimated its age to be around three weeks (based on behaviour; see below). They were irregularly checked until 5 March 2014. On 2 April 2014, the mother was found sleeping alone, suggesting that they had separated. Infant V was first spotted on 3 May 2014 and although very small was able to climb on its own a little on a branch; I estimated its age to be about 1 week. This infant was checked until 21 January 2015. Given that the mother was found alone on 20 March 2015 on the sleeping site, again it seems likely they had separated by this date. Infant VI was first spotted on 11 May 2015 and was still with the mother until 11 November 2015. The mother was spotted alone on 16 January 2016. Infant VII was first spotted on 26 April 2016 and was still with until 24 February 2017. Unfortunately, due to the lack of observers available in the field, period leading up to separation in those two infants was not sampled regularly. On the 11th of May the female was spotted with a newborn infant VIII and observed only for four days due to lack of observers and publication deadline. Observation periods are summarized in **Table 1**.

2.2. Data collection and analyses

We started observing infants I and II in the evening of the day when they were born. Both infants were observed irregularly during the study period by two observers. The mother-infant pairs were observed during evenings (starting between 16:45 and 18:00), from when they woke up and then followed until the infant was parked. Thereafter, the infant was observed on the parking spot until the mother returned, and then, if possible, the pair was followed again. Due to the difficult terrain and dense vegetation, it was not possible to locate the infant on every parking spot either when first deposited or during the night. Due to

Infant	Start of observation	End of observation/still sleeping with mother	Mother-infant separated
I	14th April 2009	6th June 2009	Unknown
II	30th April 2009	4th June 2009	Predated
III	22nd May 2010	22nd May 2010	Unknown
IV	22nd May 2013	5th March 2014	2nd April 2014
V	3rd May 2014	21st January 2015	20th March 2015
VI	11th May 2015	11th November 2015	16th January 2016
VII	26th April 2016	24th January 2017	Unknown
VIII	11th May 2017	14th May 2017	

Table 1. Observation periods of eight infants.

the difficulties in relocating infants later in the night, the results obtained during the study were biased towards the evening and, therefore, have to be considered as preliminary. The observed behaviour was recorded continuously using voice recorder. Infant carrying and play behaviour were photographed and video-recorded using a night vision video camera (SONY HDR-SR11). Vocalizations were recorded using digital recorders with built-in microphones (Olympus LS-10 and LS-11). In total we obtained 8.9 h of observation over 5 days for infant I and 65.1 h over 23 days for infant II. The length of focal follows was between 13 min and 12.3 h (the mean was 2 h 38 min). Infant III was observed during daytime from 10:30 and then for 1 h (18:30–19:30) in the evening after being released into the wild. The vocalizations from this infant were analysed. Mother-infant pairs IV, V, VI, VII and VIII were observed irregularly during the daytime and evening. In these pairs we focused mainly on recording the period when they were still sleeping, during which they were in contact or in close proximity, patterns of association not previously known for this species.

We recorded behaviour of the infants during individual focal follows [20] and developed a basic ethogram (see Section 3). We also recorded the distance between mother and infant: contact (physical contact), proximity (<3 m) and alone (>3 m). For further analyses the data were pooled together for infants I and II. The relative distances, time period and percentage time spent in each behaviour were calculated.

3. Results

The day before the mother I gave birth, she stayed very high (above 5 m) on the tree in the semi-captive enclosure. In contrast, the free-ranging mother II stayed no more than 1 m above the ground. Indeed, a week before giving birth, she was observed on occasion sleeping on the ground.

The mother-infant pairs were observed to be solitary. On two occasions (one each for each pair) another individual (most likely a male given its size) came within about 5 m of the mother-infant pair. The intruding individual was immediately chased away by the mother,

who was vigorously jumping towards the intruder and emitting several loud calls. Another similar encounter was observed for mother-offspring pair V. In this case, the intruding tarsier was observed at the top of the tree, more than 5 m from the mother-infant pair. It could not be ascertained whether the intruder was an unrelated adult male or the older offspring from the previous year who remained in the area.

3.1. Infant behaviour and time budgets

Tarsiers woke up shortly after our arrival or were already awake. After waking up the mother and infant spent some time on the sleeping site before they moved to another spot—where the infant was parked. During our observations the following behaviours were recorded. The activities and behaviours listed below are mutually exclusive:

Resting: an infant is awake but unmoving whilst sitting on a branch (**Figure 1**), a stance that was evident either shortly after waking up in the evening or during the night.

Grooming: an infant being groomed by the mother (only on two occasions was self-grooming by the infant recorded).

Suckling: an infant being nursed by the mother (**Figure 2**).

Play: an infant was considered playing when the movement or the body posture was awkward, exaggerated or incomplete; or the speed, aiming or accuracy of the movements was relaxed (criteria consistent with the definition of play developed by Burghardt [21]). See below for more details (Video 1).



Figure 1. A tarsier infant (infant II) resting on a branch in contact with its mother (photo by M. Řeháková).



Figure 2. A tarsier infant (infant VIII) suckling (photo by M. Řeháková).

Carried: an infant being carried by the mother and transported from one location to another (**Figure 3**).

Jumping: an infant jumping from one branch to another.

Climbing: an infant climbing up or down a branch.

Furthermore, we reported if the infant was:

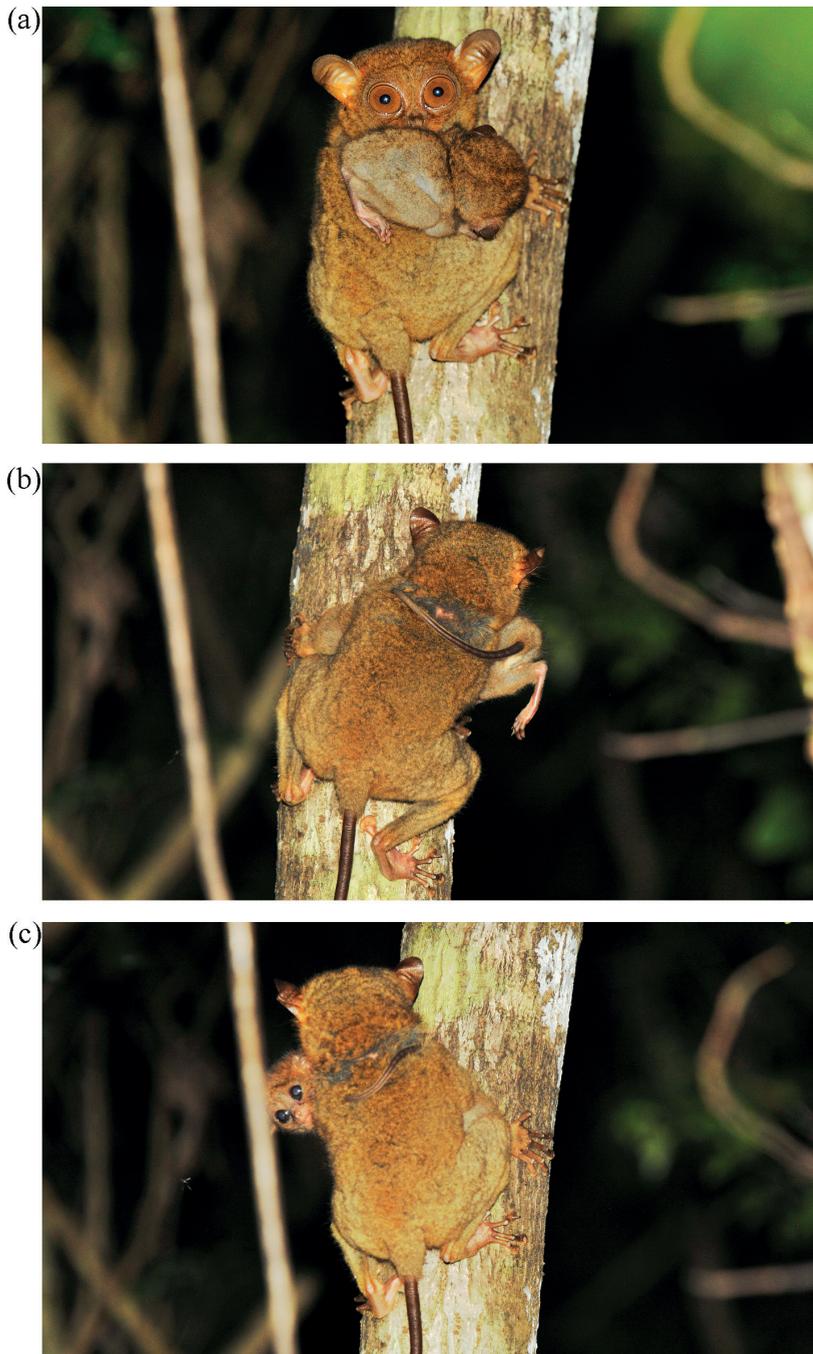


Figure 3. (a–c) A tarsier infant (infant I) being transported in its mother's mouth and holding slightly by its tail around the mother's neck (photo by P. Slavík).

With mother: mother is in contact or in proximity of the infant.

Parked: an infant is left on a parking spot whilst the mother goes for foraging. Also, when parked if the infant was visible, we recorded any of the above-listed behaviours that could occur.

And we recorded if the infant was:

In contact: in physical contact with the mother.

In proximity: within 3 m to the mother. Three metres was a maximal distance at which I could reliably identify an individual in the dense vegetation. Moreover, at this distance it is likely that the infant and mother were either in visual or acoustic contact.

Alone: more than 3 m from mother, only when the infant was parked.

Based on 74 h during which infants I and II were observed, infants spent 66% of time parked, and when parked, they were alone 99% of the time. When they were with the mother, infants spent 59% of the time in physical contact with her.

During the time spent with the mother, the infants spent 45% of time resting, 18% being groomed, 12% climbing, 7% jumping, 7% carried by the mother, 6% playing and 5% suckling. When parked the tarsier infants were mainly resting (93% of time), with jumping (5%), climbing (1%) and play (1%) occurring occasionally. The duration of behaviours varied: the mean duration for carries was 1.3 s (standard deviation (SD) = 1.7), 2.6 s (SD = 2.5) for climbing, 2.9 s (SD = 3.3) for play, 3.3 s (SD = 3.3) for grooming, 4.2 s (SD = 8.5) for jumping, 9.1 s (SD = 9.3) for suckling and 18.1 s (SD = 43) for resting.

3.2. Play behaviour

I observed locomotor, social and object play by both infants (I and II) during the study period. The infants started to perform play behaviour at the age of 2 weeks. Locomotor play involved climbing up and down on a branch and jumping for short distances back and forth, both when in proximity of the mother and whilst parked. Object play involved manipulating leaves or branches with hands or mouth. Social play could involve one-sided actions by the infant or in mutual play fighting. One-sided play occurred when the mother attempted to groom the infant, and it responded by touching and mouthing her head, back or tail. In addition, in situations when the mother was not engaged with the infant but was moving about in which case, the infant also touched and mouthed her tail and back whilst climbing on her. Mutual play fighting was observed later in the ontogeny. In infant I it was first observed at the age of 50 days. The mother was jumping around the canopy and apparently waited on landing at each new location for the infant, who was following her. Once the infant reached her, it grasped her back, and she responded leading to a mutual play fight that lasted for about 5 s. Mother turned back to the infant; both animals were grabbing each other by hands and mouthing/biting face to face. Then the mother turned away. Infant grabbed her back, but she did not respond anymore. Following termination of contact, the mother resumed her locomotion around the canopy. In infant II play fighting was first observed at the age of 34 days. Over a period of 6 min, I observed four events of play fight each several seconds long. As in the case with infant I, these play sessions occurred when the mother and infant were moving from the sleeping site to a new location and involved mutual grabbing and biting (Video 1).

3.3. Maternal transportation of infants and the mother-offspring bond

Tarsier locomotion involves climbing and vertical jumping, and during the first days after birth, the mothers transported the infants. The mothers used their teeth to pick up the infants by the skin on their backs when transporting them. The mother usually held infant by the skin on the back but also on the side or even belly in one occasion (which was not comfortable so the mother then changed the position). The infant did not hold on to the mother baby when being carried, but on several occasions, an infant was observed to wrap its tail around the mother's upper back and neck, which may have provided some additional support (**Figure 3**). On other occasions the infant's tail passively hanged downwards. On completion of the transportation, the infant was left on a parking spot, and the mother went foraging. Parking lasted from as little as 4 to as much as 235 min (mean = 112 min, SD = 97.6). On her return, the mother would feed the infant. She would stay with the infant between 6 and 138 min (mean = 57.6 min, SD = 49.7), then transported and parked it again on a different location. On average infants were parked 162 cm (range: 30–400 cm), and during the study, tarsier infants were parked throughout the female's home range.

The infants started climbing branches at the age of one week and began to follow the mother over shorter distances between the third and fourth weeks (infant I at 18, infant II at 23 days). The mothers appeared to encourage the infants to follow by emitting chirping vocalization [22]. For longer distances (several metres) infants were still transported by the mother. By the age of 50 days, when observations ceased on infant I, it was no longer being carried by the mother. Observations on infant II ended when it was 35 days old, and at this age, it was still being carried.

By the time observations ceased on infants I and II, they were both still sleeping with their mothers. Infant (juvenile) IV was observed sleeping with his mother up to 10 months, infant V up to almost 9 months, infant VI at least up to 7 months and infant VII at least for 10 months. The inter-birth interval for the mother of infants IV–VIII was around 1 year.

3.4. Acoustic communication

Acoustic communication between mother and infant was very frequent and included four different signals out of eight signals described in Philippine tarsier (see Ref. [22] for detailed descriptions and spectrograms):

Loud call: a single note vocalization, capable of being carried relatively far, able to be reliably heard and identified from distance of at least 50 m. The loud call note consists of two distinct parts: the *whistle* part with a limited frequency range and the final *smack* part with a substantial frequency range. In adults the loud call was recorded mainly around sunset in proximity to the sleeping site but also during the night. In mother-infant communication, it was apparently used to gain others' attention during the night or when the mother was returning to the parked infant.

Chirp: a soft call that was heard mainly in proximity to the sleeping site in the evening or in the morning. Chirp consists of several short, rapid, broadband notes in a descending series. It was the most frequent call used by both mother and infant, with the mother using it enticing the infant to follow her. Chirps were also emitted by a mother over several nights after she had lost her month-old infant [19].

Cheep: is a single note call, usually emitted repeatedly in a sequence. It was recorded from both a mother and her offspring (infant III) whilst being rescued from poachers. It was also recorded in a free-ranging female (mother II). In this case the cheep was interspersed in a sequence of other call types.

Twitter was recorded during communication between a mother and her offspring (infant III) during being rescued from poachers. The signal consists of two parts, an initial long cheeping sound followed by several short, frequency-modulated twittering notes.

4. Discussion

Given the limited time available to collect data on the two main focal infants and the limitations imposed by attempting to make observations in difficult terrain and dense vegetation for all subjects studied, there are obvious deficiencies in the present study. Nonetheless, given the paucity in our knowledge of tarsier ecology and behaviour, I believe that the findings from the present study provide some important clues that show both similarities across species of the family and differences that may reflect variation in socioecology.

Births in the current study of Philippine tarsiers occurred between mid-April and mid-May, a pattern consistent with previous observations on this species [11] and also in spectral tarsiers [12], although, another study of spectral tarsiers reported two birthing seasons – November/December and May [2]. Records of births and the available literature on gestation length, 191 for wild spectral tarsier, 178 days for captive western tarsier and Philippine tarsier [17, 23, 24], indicate that the mating season is between October and January. Changes in testicle volume suggest a mating season between September and November in Philippine tarsier and from August to January in western tarsier [25]. A pair of captive Philippine tarsiers was observed mating at the end of October 2015 and beginning of November 2016 at the Tarsius Project Conservation Centre in Bilar, Bohol. The female then gave birth at the beginning of May after 188 days, 172 days, respectively (in the latter case, the former mating might be overseen) [pers. observ.].

Philippine tarsiers neither built nests or seek and use tree holes for giving birth. The observations in the present study showed that prior to giving birth, females either stayed high in the trees or remained close to the ground. This difference was most likely an artefact as the semi-captive female moved up the tree to avoid visitors who entered the enclosure every day between 9:00 and 17:00.

At birth, the infant Philippine tarsiers were fully furred, and their eyes were open. For the first month, or so, the infants were transported orally by the mother. The infants did not cling to her fur, but as apparent from **Figure 3**, they could help support themselves with their tail when being carried. Gradually over the first 3 weeks, the infants followed the mother for short distances whilst still being carried over longer distances. The mothers actively encouraged following by chirping. Of the two main forms of locomotion in tarsiers [9], infants began climbing up and down branches in the first week and jumping short distances by the second week.

Comparison of the limited data on Philippine tarsiers with the better studied spectral tarsier is instructive. The main difference between these two species is in their pattern of sociality and consequences this has on the care provided to infants. In spectral tarsier, which lives in extended family units, care of infants is not limited to the mother, but can also be provided by other members of the family unit [2, 3]. A major contribution to infant care is that members of the family unit, other than the mother, can regularly visit infants whilst they are parked. This babysitting or guarding afforded by other members of the family may enable mothers to engage in longer periods of unfettered foraging. In contrast, Philippine tarsier mothers are strictly solitary, and so all infant care is provided solely by them. Indeed, in only three occasions was an adult, likely males, encroach within 5 m of a mother-infant pair, and on two occasions the intruding individual was immediately chased away by the mother, perhaps to prevent infanticide. In one case, in spectral tarsier, a neighbouring male was observed to kill an infant [26]. Although, in another solitary species, western tarsier, males were often captured in close proximity to infants suggesting that fathers may provide some allocare. Even so, whilst male western tarsiers often visit the area around the sleeping site of young infants, they have never been observed to provide any form of parental care [27], and in captivity, males of this species have been observed to be aggressive towards other individuals including infants [17]. Therefore, it remains an unresolved issue as to whether solitary species like Philippine and western tarsiers have opportunities for fathers to provide allocare or whether all adult males are a potential risk for infants and so provide a constraint on how long mothers can leave their young parked and unattended. Infants do seem to have the opportunity to stay with their mothers for a protracted period. For example, our observations of mother-offspring pairs IV–VIII indicate that Philippine tarsier offspring can remain with their mothers until shortly before the offspring from the next year is born. Also consistent with such prolonged mother-infant association is a study that found that for three females, the young from the previous year remained even after the young from the next year were born [28].

In the more gregarious species, spectral tarsier, infants spent between 39% (in the first month) and 50% (in the third month) of night time alone; otherwise they are in close proximity (less than 5 m) of the mother or another group member (i.e., an adult male or subadults of both sexes) [3]. On the contrary, the mainly solitary Philippine tarsier's infants spent 66% of observed time parked alone. Also there are differences in the bout lengths of parking, with spectral tarsier the mean length of a bout of parking being 27 min (SD = 18.12, range 1–124 min), whereas my findings on Philippine tarsier indicate that bouts of parking are longer, with a mean of 112 min (SD = 97.6, range 4–235 min). If unrelated adult males pose a threat to infants, then the greater amount of time Philippine tarsier infants are left alone would place them at greater risk. Differences in habitat usage between social and solitary species may mitigate these risks, but such possible socioecological differences remain unknown (**Table 2**).

Consistent with risks to infants when parked, not only from potentially infanticidal males but also from predators, when parked the infants mainly remained at rest (93% of time), with little time spent moving about. In contrast, during the period spent with mother, the infants spent only 45% of the time resting. When parked alone, infants only spent 7% of their time jumping,

	<i>Tarsius syrichta</i>	<i>Tarsius spectrum</i>	<i>Tarsius bancanus</i>
Births	April–May	May (or November/December)	
Gestation length	172–188	191	178
Nest	No	Tree hole	No
Sociality	Solitary	Family groups	Solitary
Care of infants	Mother	Mother and other family members	Mother
Time spent alone during the first 2–3 months	66%	39–50% of time	
Mean length of a bout of parking	112 min	27 min	

Table 2. Comparison of data about reproductive behavior of three tarsier species.

climbing and playing, whereas when with the mother, 25% of their time was engaged these activities. Obviously, when with the mother, there was also the opportunity to engage in social behaviour (e.g., grooming, being carried and suckling), and these made up the remaining time spent being active.

Other than some preliminary reports on play of spectral and captive western tarsiers [2, 12, 17], there is little detail available on the play in tarsiers. The present study contributes to filling this void, by providing repeated observations of play in Philippine tarsiers. All three, commonly noted types of play—locomotor (solitary), object and social play [21]—were present in the Philippine tarsiers. The locomotor and the object play began earlier in ontogeny than social play. Locomotor play involved infants jumping and climbing around surrounding branches, and object play involved grasping, pulling and chewing leaves and small twigs. Social play, given that all other tarsiers were excluded from their vicinity, necessarily was restricted to infants engaging the mother, and this could take one of two forms. There was one-sided play, in which the infant grasped and mouthed the mother, who did not respond and remained passive or continued with ongoing behaviour, such as climbing. In play fighting the interactions were two sided, with both partners grasping, mouthing and grappling with one another. Similarly, in captive western tarsiers, these grappling bouts were characterized by the infant hopping at the mothers head and face with hands outstretched and mouth agape, followed by a short tussle in which mother and infant mutually mouthed and pawed at one another [17]. This pattern contrasts in many ways to the more gregarious spectral tarsier. In this species social play appears to be more frequent and easily observed [pers. observ.], and this may in part be because the infant has several other group members, not just the mother, as potential play partners. Indeed, mothers do not seem to play with infants, and although adult males do, it is less frequent compared to that involves the subadults, especially the females [12]. The differences in opportunity for social play may also account for the apparent species differences in the age of onset of social play: starting around the third week in spectral tarsiers and between 4 and 6 weeks in Philippine tarsiers. Similarly, social play reported in spectral tarsiers includes chasing and play fighting ([2], pers. observ.), whereas in the Philippine tarsiers and western tarsiers [17], it is mostly limited to short bouts of grappling. More detailed comparisons of the developmental onset, as well as the frequency and content of social play across a wider range of solitary and gregarious species of

tarsiers, are needed to fully evaluate the causes of these species differences. Moreover, given that the social play in some primate species with more complex social systems can vary in marked ways with small differences in social systems (e.g., [29–32]), the possibility that even the small differences in degree of gregariousness can lead to significant differences in social play seen in tarsiers could provide novel insights into the evolution of such play [21].

The present study provides new information on the role of acoustic communication in mother-infant pairs. Mothers periodically transport infants to new locations, park them and the move around the neighbouring vicinity to forage. During these periods when the infants are parked alone, both the mother and infant emit vocalizations. The frequency of such calling appears to be much higher than in comparable situations when adults are foraging on their own with having an infant nearby. The most frequently emitted calls were chirps and less often loud calls. These two calls are also emitted outside the context of a mother-infant pair, suggesting that these signals may be used in a variety of contexts. Two signals, cheep and twitter, were only recorded during mother-infant pairs, suggesting that these have a unique role among such pairs. Cheep was recorded in rescued animals that were kept in a small cage before being released and may be a kind of distress call. However, it was also recorded in a free-ranging mother, who emitted this call in sequence along with other call types. The contextual relevance of all these calls needs further study to understand when they are emitted and why.

This present study also provides valuable information on the life history of Philippine tarsiers. Of the six infants observed, one was predated, representing a mortality rate of 17% during the first months of age. It is interesting that the predation occurred during the daytime when the infant was with its mother [19] rather than during night, when parked alone, when it would be expected that infants would be more vulnerable (see above). Although it may also be the case that during the daytime the tarsiers are sleeping and so likely less attentive to the presence of potential predators, unfortunately, data on mortality rates during day versus night are not available. A female Philippine tarsier can have (and raise) an offspring every year, as indicated by the five infants produced consecutively in one female during the present study. The inter-birth interval was around 1 year. The minimum inter-birth interval reported was 187 days in a captive female [24]; however, this infant did not survive, perhaps indicating that this may be shorter than the optimum.

In conclusion, the present study provides some preliminary, but important, data about Philippine tarsier life history and behaviour. These tarsiers can have one offspring per year, with an 83% chance of survival. Maternal care was documented to follow the cache and carry strategy with the infant spending around 66% parked alone whilst the mother was foraging. In this solitary species, infant care was provided solely by the mother. During the first days and weeks after birth, the mother transported their infants when moving to new locations. Whereas the infants were observed to start climbing on branches at the age of 1 week, they were transported orally until 3 weeks of age. Even though they started to follow the mother over shorter distances from three weeks, for longer distances, they were still transported by the mother until 50 days of age. Time budget data showed that when with the mother, infants spent 45% of their time resting, 18% grooming, 12% climbing, 7% jumping, 7% being carried by the mother, 6% playing and 5% of time suckling. Both infants engaged in locomotor, social

and object play. Acoustic communication was very frequent between mothers and infants and included four different signals. Infants were observed sleeping next to mother up to 10 months, which is consistent with an inter-birth interval of 1 year that seems to be the case from study.

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