The Philippine Tarsier (*Tarsius* [*Carlito*] *syrichta*): Activity Patterns, Social Behaviour and Population Endangerment Risk in Bilar, Bohol

by

Filip Jaromir Wojciechowski

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Supervisor: Professor Katarzyna A. Kaszycka, PhD, DSc

Assistant Supervisor: RNDr. Milada Řeháková, PhD

Institute of Human Biology and Evolution
Faculty of Biology
Adam Mickiewicz University

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II. LIST OF PUBLICATIONS

1. **Wojciechowski, F.J.**, Kaszycka, K.A., Wielbas, A.M., Řeháková, M. (2019). Activity patterns of captive Philippine tarsiers (*Tarsius syrichta*): Differences related to sex and social context. *Folia Primatologica* 90: 109–123. DOI: 10.1159/000495612.

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2. **Wojciechowski, F.J.**, Kaszycka, K.A., Řeháková, M. (2020). Social behavior of a reproducing pair of the Philippine tarsier (*Tarsius syrichta*) in captivity. *Journal of Applied Animal Welfare Science* 23: 493–507. DOI: 10.1080/10888705.2019.1689505.

   IF: 1.122 **MNiSW:** 70 points

3. **Wojciechowski, F.J.**, Kaszycka, K.A., Otadoy, J.B. (2021) Utilizing local community knowledge of the Philippine tarsier in assessing the Bilar population endangerment risk, and implications for conservation. *Journal for Nature Conservation* 62: 126028. DOI: 10.1016/j.jnc.2021.126028.

   IF: 2.482 **MNiSW:** 100 points

III. SUMMARY

The Philippine tarsier (*Tarsius* [= *Carlito*] *syrichta*) is one of the least studied tarsiers – obligatory animal protein diet eating nocturnal primates inhabiting islands of South-East Asia. It is an endemic species found on several Philippine islands of Visayan and Mindanao regions. The Philippine tarsier has not been a subject of extensive studies because it is extremely difficult to observe due to its cryptic activity, small body size and the difficult habitat that it occupies. There is also no established captive population of the species anywhere in the world - making it impossible to study *ex-situ*. At the same time, the species is threatened with extinction due to habitat loss and hunting.

To fill the gaps in our knowledge, my doctoral dissertation focuses on two aspects related to the Philippine tarsier: behavioural and conservation. The detailed observations of the species' behaviour, which are the subject of the first two articles of the dissertation, were conducted at the "Subayon Conservation Centre for the Philippine tarsier" in Bilar, Bohol in the Philippines. The data on activity patterns was collected in 2015 on wild-caught male and female individuals, over 384 hours (in two social contexts: solitary and paired), also regarding social interactions between them for a consecutive two mating seasons (in 2015 and 2016 – including 468 observation hours). The focus of the third article is the Philippine tarsier conservation, specifically understanding its successful use as a "flagship species" among the local community by interviewing 325 residents from five villages in Bilar.

The data shown in the dissertation is of an applied nature. Firstly, the dissertation presented the first quantitative data on the behaviour of the Philippine tarsiers, which may assist in practical considerations for keeping this highly sensitive, difficult-to-breed species in captivity. Secondly, the results of the ethnoprimatological study revealed the state of knowledge and attitudes of Filipinos towards this primate, as well as the threats to the Philippine tarsiers population in Bilar. It was shown that the species has the potential to be an effective "flagship species", which, together with other information obtained from local people, may help to guide education and conservation strategies in this area of Bohol Island.

Key words: *tarsiers behaviour*, *captive breeding*, *primate conservation*

IV. STRESZCZENIE

Wyrak filipiński (*Tarsius* [=*Carlito*] *syrichta*) jest jednym z najsłabiej zbadanych wyraków – odżywiających się dietą pochodzenia białkowego nocnych naczelnych, zamieszkujących wyspy Azji Południowo-Wschodniej. Jest to gatunek endemiczny występujący na kilku filipińskich wyspach w regionach Wisajów i Mindanao. Wyrak filipiński nie był przedmiotem szeroko zakrojonych badań, ponieważ jest niezwykle trudny do obserwacji ze względu na swoją nocną aktywność, niewielkie rozmiary ciała i trudne siedliska, które zasiedla. Nigdzie na świecie nie istnieje również populacja tego gatunku w niewoli, co uniemożliwia prowadzenie badań *ex-situ*. Jednocześnie gatunek ten jest zagrożony wyginięciem z powodu utraty siedlisk i kłusownictwa.

Aby wypełnić luki w dotychczasowej wiedzy, moja praca doktorska koncentruje się na dwóch aspektach związanych z wyrakiem filipińskim: behawioralnym i ochroniarskim. Szczegółowe obserwacje zachowań gatunku, które są tematem pierwszego i drugiego artykułu pracy, były przeprowadzone w „Subayon Conservation Centre for the Philippine tarsier" w Bilar na wyspie Bohol na Filipinach. Dane na temat wzorców aktywności zostały zebrane w 2015 r. podczas 384 godzin obserwacji (w dwóch kontekstach społecznych: samotnie i w parze) na samcu i samicy pozyskanych na wolności, natomiast dane na temat interakcji społecznych między nimi zostały zebrane w ciągu dwóch kolejnych sezonów godowych w 2015 i 2016 r. (468 godzin obserwacji). Trzeci artykuł skupia się na ochronie wyraka filipińskiego, a konkretnie na zrozumieniu jego skutecznego wykorzystania jako „gatunku flagowego" wśród lokalnej społeczności na podstawie wywiadów z 325 mieszkańcami z pięciu wiosek w Bilar.

Dane ukazane w rozprawie doktorskiej mają charakter aplikacyjny. Po pierwsze, w pracy przedstawiono pierwsze dane ilościowe dotyczące zachowań wyraka filipińskiego, które mogą przysłużyć się do wytyczenia strategii hodowlanych dla gatunku. Po drugie, wyniki badania etnoprymatologicznego ukazały stan wiedzy i stosunek Filipińczyków wobec tego naczelnego oraz zagrożenia populacji wyraków filipińskich w Bilar. Wykazano, że gatunek ten ma potencjał, aby być skutecznym „gatunkiem flagowym", co wraz z pozostałymi informacjami uzyskanymi od miejscowej ludności, pomoże w wytyczeniu strategii edukacyjnej oraz konserwatorskiej w tym rejonie wyspy Bohol.

Słowa kluczowe: *zachowania wyraków*, *rozmnażanie w niewoli*, *ochrona naczelnych*

V. DISSERTATION OUTLINE / SELF-PRESENTATION

The Philippine tarsier (*Tarsius* [*Carlito*] *syrichta*) is one of 14 species of the Tarsiidae family inhabiting islands of South-East Asia. They are small, nocturnal, and they are the only primates known to have an obligatory animal protein diet. The Philippine tarsier is endemic to secondary lowland rainforests of few Philippine islands of Visyayan and Mindanao regions. Based on the morphological and genetic evidence, the taxonomy review splits tarsiers into three distinct groups (Groves & Shekelle 2010)(Fig. 1): an eastern group inhabiting Sulawesi and neighbouring islands (12 species), a western group with one species – Horsfield's tarsier – found on Borneo, Sumatra and smaller islands in the vicinity, and the Philippine group, having solely the Philippine tarsier (Fig. 2).

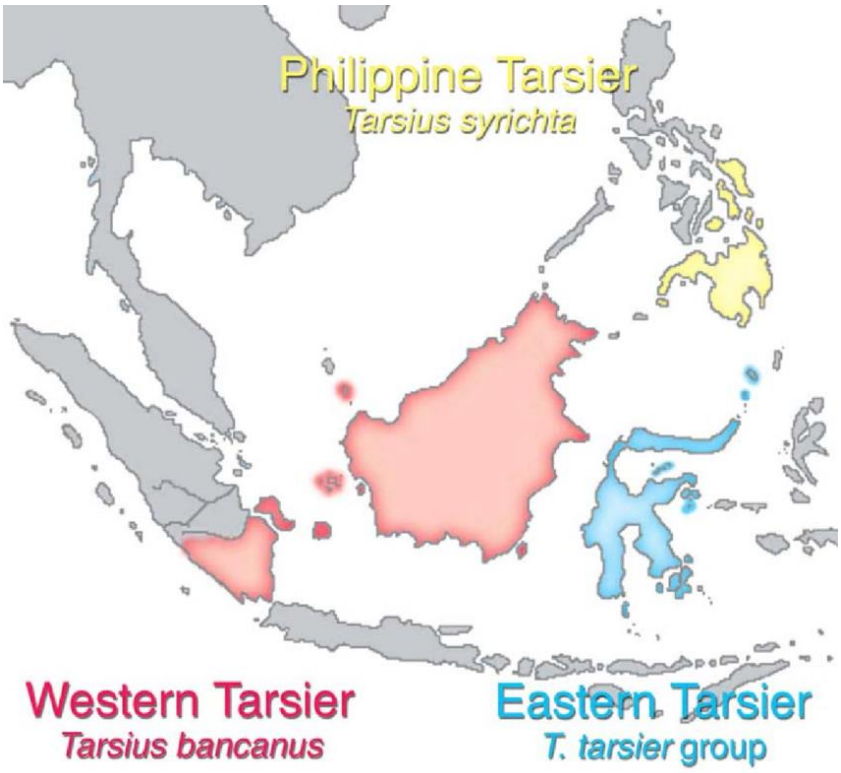

Fig. 1. Distribution of Extant Tarsiers (Shekelle 2008).

Fig. 2. The Philippine tarsier in the Subayon Conservation Centre for the Philippine tarsier in Bilar, Bohol (Photo: F.J. Wojciechowski).

The Philippine tarsier is not adequately understood in terms of ecology and behaviour. There have been only few studies conducted on the species, investigating home ranges, locomotor patterns and habitat use (Dagosto & Gebo 1997; Dagosto, Gebo & Dolino 2001; Neri-Arboleda, Stott & Arboleda 2002), predation (Řeháková-Petrů, Peške & Daněk 2012a), vocalization (Řeháková-Petrů, Policht & Peške 2012b; Gursky-Doyen 2013), and infant ontogeny and play behaviour (Řeháková 2018). Based on radio-telemetry studies on small sample, the Philippine tarsier is considered non-gregarious and non-monogamous, having a noyau/dispersed polygyny social system (e.g., Dagosto et al. 2001) and solitary foraging and sleeping patterns (Neri-Arboleda et al. 2002).

The lack of data derives from the fact that the species is extremely difficult to observe due to its nocturnality, small body size and the difficult habitat it occupies. It is also difficult to maintain in captivity and all attempts to establish a viable captive

population have failed with no recorded cases of successful second-generation reproduction for Philippine tarsiers (Fitch-Snyder 2003). The difficulties in breeding tarsiers have been attributed to their sensitivity to stress, diet consisting exclusively of live prey, nutritional requirements, as well as specific climatic conditions.

The Philippine tarsier without proper conservation is also vulnerable to extinction (Neri-Arboleda 2010, Gursky, Salibay, Grow & Fields 2017). Its IUCN Red List of Threatened Species categorization has changed a number of times: from Endangered (EN), through Lower Risk/Conservation Dependent (LR/CD), Data Deficient (DD), to its current Near Threatened (NT) status, last assessed in 2015 (Shekelle 2020), but a suggestion has later been made to upgrade its status to Vulnerable (VU)(Gursky et al. 2017). Nationally, it is listed as Other Threatened Species (OTS) (DENR 2019), and its acquiring and possession without a permit is punishable under Republic Act no. 9147 (2001). The main threats to the Philippine tarsier include deforestation (habitat loss), hunting for the illegal pet trade, as well as natural disasters (Shekelle 2020; Shekelle, Gursky, Merker & Ong 2015; Wright, Simons, & Gursky 2003).

To address the gaps in the scientific knowledge on the Philippine tarsier behaviour and to improve the species captive welfare and reproduction, the "Subayon Conservation Centre for the Philippine tarsier" (hereafter referred to as Subayon Conservation Centre) was established in Bilar, Bohol, which also engaged with community environmental outreach and *in-situ* field research. The presented doctoral dissertation compiles the research I conducted while I was working there.

The dissertation is a compilation of three original research papers published in scientific peer-reviewed journals. The focuses of the dissertation are behavioural (first and second articles) and conservation (third article) aspects of the Philippine tarsier.

The first article (Wojciechowski, Kaszycka, Wielbass & Řeháková 2019) provides the results on Philippine tarsier activity patterns, modification of its behaviour according to sex and social context, fluctuations of behaviours during 12-h night cycles, and compares the data gathered with other tarsiers species.

The second article (Wojciechowski, Kaszycka & Řeháková 2020) presents the data collected on social interactions of the Philippine tarsiers, including copulatory behaviour as well as an assessment of spatial proximity between sexes, their sleeping patterns, vocalization, temporal fluctuations in social interactions, special proximity, and vocalizations.

The third article (Wojciechowski, Kaszycka & Otadoy 2021) demonstrates the knowledge of the Philippine tarsier in the local community, attitudes towards its conservation, the variables responsible for shaping them, as well as the most suitable channels for knowledge transmission regarding the species. The article ends with a formulation of recommendations for the planning of a species conservation strategy in the area.

The first paper provides a description of the species' behaviour via a study of the activity patterns of an opposite-sex pair. The specific aims of the study were to: (1) reveal the activity patterns of male and female Philippine tarsiers during their waking hours; (2) establish whether the Philippine tarsier modifies its activity budget according to social context (mating vs. non-mating season); (3) determine the changes in tarsier activity patterns over 12-h nightly cycles; (4) compare the activity budgets of the Philippine tarsier with available data on the western and eastern species of tarsiers.

To reach the aforementioned aims, a wild-caught pair of tarsiers was observed for a total of 384 h (23,040 data points) via instantaneous sampling (Altmann 1974) at 1-min intervals for eight 12-h periods of time per each animal sex-social context.

Except the main objective of the second study to provide the first accounts of social behaviour of the species, the specific aims were to: (1) describe and quantify social interactions between individuals; (2) provide information on tarsier copulatory behaviour; (3) assess spatial proximity between the male and the female, and determine their sleeping patterns; (4) assess vocalizations of the sexes and their contexts; (5) determine the temporal (nightly and hourly) fluctuations in social interactions, the distances spent by the sexes from each other, and their vocalizations.

To investigate these aims, the same pair of individuals was observed over two consecutive mating seasons in 2015 and 2016 for total of 468 hours (28,080 data points). The animals were observed for 12 hours and, again, "instantaneous sampling" at 1-minute intervals was employed to collect data on the proportion of activity budget spent on social behaviour as well as distance between the individuals. Occurrence of social interactions and vocalizations was recorded *ad libitum*.

The observed pair of tarsiers was captured in August 2014 (male) and in June 2015 (female; Fig. 2), ca. 7 kms from the Subayon Conservation Centre, at localities distanced from each other by about 4 km. The tarsiers were housed in naturalistic outdoor enclosures planted with natural vegetation (Fig. 3), built specifically for the scientific purpose of captive breeding. The enclosure used for observations of the solitary animals comprised an approx. 8.5-m^2 cage. When paired for the mating season, the tarsiers were housed in conjoined cages (approx. 17 m^2)(Fig. 4). The primates were provided with live food once per day, which consisted of combination of wild-caught and captive-bred arthropods (Wojciechowski et al. 2019).

Fig. 3. The Philippine tarsier's enclosure (view from the outside) in the Subayon Conservation Centre in Bilar, Bohol (Photo: F.J. Wojciechowski).

Fig. 4. The Philippine tarsier's enclosure (view from the inside) in the Subayon Conservation Centre in Bilar, Bohol (Photo: F.J. Wojciechowski).

As for the conservation aspect of the dissertation, the main objective was to increase the knowledge of the Philippine tarsier conservation in Bohol by better understanding its use as an effective 'flagship species' among the local community. To explore this topic, 325 persons among the local community of five villages of Bilar (forested and non-forested areas) were interviewed during October 2016 to November 2017 using interviewer-administered questionnaires (with a mixture of fixed-response and open-ended questions). The questions were designed to answer the specific goals, namely to: (1) investigate the knowledge of the Philippine tarsier in the local community; (2) assess attitudes towards its conservation and the variables responsible for shaping them, as well as the most suitable channels for knowledge transmission regarding the species and; (3) formulate recommendations for the planning of a species conservation strategy in the area.

The results with regards to activity patterns revealed an array of interesting insights in line with the aforementioned objectives. The Philippine tarsier exhibited no significant differences in their activity budgets when solitary, both spending most of their time scanning, resting, foraging and travelling. This result appears to corroborate the suggestion of Defler (1995) that despite differences in body size males and females need not necessarily differ significantly in their activity budgets, at least during non-mating season. During the mating season the male allocated significantly more time to travelling and foraging, while less to other activities than while solitary. This pattern of change to more active behaviour during the mating season may reflect the natural activity patterns of the males as predicated by their socially dispersed social system, where males are required to roam in search of receptive females, leading to higher activity levels. Analysis of the combined activity budgets for the sexes in two social

contexts revealed changes in time spent on a number of activities during the mating season – the time spent travelling and foraging increased markedly at the expense of that spent resting. In addition, scanning decreased for the paired individuals placed in a larger enclosure. I suggest it might be linked to environmental factors, such as limited opportunities for locomotion and may explain the high frequency of scanning for the tarsier individuals when solitary.

The tarsiers exhibited nightly fluctuations in time spent on various activities. The individuals kept solitary exhibited a bimodal pattern for travelling time, with rises occurring at the beginning and at the end of the night, whereas tarsiers kept paired spent significantly more time travelling at the end of the night; patterns which are rather consistent with the data available for other Tarsiidae species (Crompton & Andau 1987, Merker 2006). The paired Philippine tarsiers foraged at a high level during the first half of the night while feeding always peaked in the first, or the first and the second hours after waking, which might be influenced by their captivity, where prey is immediately available to tarsiers. During the data collection, tarsiers also performed regurgitation and reingestion, the first evidence of this act in other primates than Catarhhini (old world monkeys and apes) – this might be a compensatory behaviour owing to a scarcity of food during downpour weather conditions.

The observations of social behaviour yielded first accounts with regards to this species. The reproducing pair of Philippine tarsiers allocated a scant proportion of their activity budget to social behaviour. The social interactions between individuals were mostly affiliative and sexual, with more time allocated to sexual activity during the 2015 than the 2016 season, and somewhat more time allocated to affiliative than sexual interactions during the second season. This difference between the mating seasons

might be due to the fact that the male tarsier exhibited increased sexual interest towards a new, unfamiliar female.

Allogrooming was found to be the most common affiliative interaction, initiated with almost equal frequency by both sexes, and it is suspected that it fulfils a hygienic function. The agonistic interactions were the least frequent in both seasons and it was the female which initiated the majority of them, winning all conflicts by forcing the male to retreat, which is associated with female dominance in the Strepsirhini species (e.g., Kappeler, 1989; Dammhahn & Kappeler, 2005; Ramanankirahina, Joly & Zimmermann 2011). The affiliative interactions were performed equally by the opposite sexes, yet agonistic interactions mainly by the female; thus, it could not be concluded that there was any clear-cut evidence of female dominance. During the study, two copulation events were witnessed – both during the 2015 season. The female was sexually receptive for three days, during which the individuals mated once per day, on the first and third day during her estrus. The tarsiers mated immediately after their activity began and the copulation lasted ca. 5 min. After the last copulation, sexual interactions between individuals conspicuously declined and never raised again. The average number of agonistic behaviours for female towards the male (rejecting him) happened only at a slightly lower rate before than after copulation. The agonistic interactions were only increased for three consecutive days after the last copulation. In 2015, the animals spent more time at furthest distances from each other after mating events, rather than before them. The female gave birth after both mating seasons. The first offspring was born after 187–185 days of gestation (from copulations to birth), following the 2015 season, yet it did not survive. The second offspring, born after the 2016 season, has survived over a year.

The pair was observed to share sleeping sites for about half of the study period. The male emitted the majority of vocalizations, and more often during the 2015 season. The female emitted vocalizations mainly in an aggressive context, which might have reflected a mate choice strategy. She also vocalized at an increased rate during the time of her receptivity, which might be interpreted as a form of signalling of her reproductive status. Both tarsiers vocalized the most during the first and the last hour/hours of the night, similar to patterns observed in the wild.

The research results for the conservation aspect of this dissertation provided important information to improve the strategy for the protection of the Philippine tarsier. The species is widely recognized in the area, however, its vocalizations were only recognised occasionally. The tarsiers were observed more often in villages located in forested areas, and more often encountered by men (especially local resource suppliers), and people engaged in income-generating activities, than women and other respondents. Local people also possessed high level of general knowledge about the species, although details pertaining to tarsiers' diet and species' occurrence were less known. It is suggested that limited knowledge on diet and the islands inhabited by these primates is driven by the popularity of tarsiers as a main tourist attraction on the Bohol Island, portrayed as insects eaters. It turned out that less than half of the local residents (especially men) had seen or heard about tarsiers in Bilar, yet a minority of people encountered the animals themselves in the area. Here, the connection between the frequency of visits to wild areas, and accumulation of greater knowledge about tarsiers was identified. The most important channels of knowledge about the Philippine tarsier were word-of-mouth and personal experiences of the local people, followed by media.

Local people not perceiving tarsiers as an endangered species, although, in their opinion, they should be protected. Interestingly, over half of the respondents believed in the increase in the number of tarsiers in the area. The very high popularity of the species, which is shown to tourists, could possibly give the impression to the local populace that tarsiers' numbers are not in jeopardy. Moreover, most of the respondents of this study, especially men, found the Philippine tarsier useful, largely for economic reasons, which also was the second major justification for its protection. Finally, it was ascertained that hunting is widespread in the area, with many interviewees having seen or heard about the hunting of tarsiers in Bilar, although only a minority admitted to capturing tarsiers themselves. The respondents reported that tarsiers are being caught for sale and as pets. Simultaneously, tourist facilities and foreigners were identified as destinations where the animals are being trafficked, which provides a grim outlook for the Philippine tarsiers (which do not thrive in captivity well).

In summary, the studies included in this dissertation provide the first detailed description of both the Philippine tarsier's social and non-social behaviours. The results might help in the evaluation of activity budgets in a wild-to-captivity spectrum, providing practical considerations for the housing of the species. The pair separation resulted in successful breeding, and it can be hypothesized this to be a suitable housing method for the Philippine tarsier. The female gave birth after both mating seasons with the second offspring surviving, indicating that despite some observed agonism, welfare was not compromised and that agonism may be a natural element of courtship. The observed increased rate of female vocalization and increased distances between the individuals, along with fewer sexual interactions after copulations might be indicators used to determine the time of receptivity, as well as the time at which copulation occurs.

It is also recommended to pay special attention to tree species, quantity, and arrangement when designing and maintaining the tarsier's enclosure.

Finally, the high environmental knowledge of local forest resource suppliers was demonstrated, and they should be the main stakeholders in the conservation strategy through inclusion in any research activities and by involvement in sustainable tourism. The species is seen by local people as worth protecting, but complementary conservation education is recommended (especially for local teachers), to reinforce the perception of tarsiers as an integral part of the ecosystem – as having aesthetic value, not only economic. Furthermore, collaborative work between researchers, tourism stakeholders and netizens is suggested to promote tarsiers in their natural settings, and to delete images in which they are shown in contact with humans. The comprehensive use of social media to strengthen public conservation education and engagement with the Filipino netizens will prove necessary. Last, but not least, it is proposed that the results and recommendations of this dissertation should be passed to legal tourist destinations in order to improve the tarsiers' husbandry and survival rate, while simultaneously driving a decrease in the demand for these wild individuals.

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VI. MANUSCRIPT 1:

Activity patterns of captive Philippine tarsiers (*Tarsius syrichta*): Differences related to sex and social context.

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Name of author	WOJCIECHOWSKI FILIP J. https://orcid.org/0000-0002-3598-9109
Affiliation	• Department of Human Evolutionary Ecology, Institute of Anthropology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland • Wings of Serenity Inc., Tagbilaran City, 6300 Bohol, Philippines • University of San Carlos Biology Department, Arnoldus Science Complex, Talamban Campus, Nasipit, Cebu City 6000, Philippines
Contribution	• Designed the experiments; • Collected the data; • Analysed the data; • Wrote the paper, • Revised the text.
Contribution %	**60%**
Date and signature	19.06.2021 ..... Wgarel

Name of author	KASZYCKA KATARZYNA A. https://orcid.org/0000-0003-1348-1037
Affiliation	• Department of Human Evolutionary Ecology, Institute of Anthropology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland
Contribution	• Analysed the data; • Wrote the paper, • Revised the text.
Date and signature	1.06.2021 ..... KA Kaszycka

Name of author	WIELBASS ALEXANDER M.
Affiliation	Linköping, Sweden
Contribution	• Designed the experiments; • Collected the data.
Date and signature	22-06-2021

Name of author	ŘEHÁKOVÁ MILADA https://orcid.org/0000-0002-6087-1612
Affiliation	Tarsius, z.s., Děčín, Czech Republic
Contribution	• Designed the experiments; • Submitted comments.
Date and signature	27.6.2021

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Activity Patterns of Captive Philippine Tarsiers (*Tarsius syrichta*): Differences Related to Sex and Social Context

Filip J. Wojciechowski[a–c] Katarzyna A. Kaszycka[a]
Alexander M. Wielbass[d] Milada Řeháková[e]

[a]Department of Human Evolutionary Ecology, Adam Mickiewicz University, Poznań, Poland; [b]Wings of Serenity Inc., Tagbilaran City, Philippines; [c]Department of Biology, University of San Carlos, Cebu City, Philippines; [d]Linköping, Sweden; [e]Tarsius, z.s., Děčín, Czech Republic

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Tarsiers · Activity budget · Time budget · Activity rhythm · Mating season · Non-mating season · Primate behaviour

Abstract

Among tarsiers, nocturnal, obligatory faunivorous primates inhabiting islands of South-East Asia, the Philippine tarsier (*Tarsius* [= *Carlito*] *syrichta*) is one of the least studied. To date, activity patterns of this threatened species have not been the subject of any investigation. In the present study, we provide the first quantitative data on how captive male and female *T. syrichta* apportion their time for various activities in two social contexts: solitary and paired. We found that the sexes do not differ in activity budgets during the non-mating season, both spending most of their time scanning, resting, foraging and travelling. Comparison of activity budgets of the sexes between the mating and non-mating seasons revealed that although both tarsiers noticeably increased travelling time at the expense of time spent resting, the male changed his behaviour to a much greater extent than the female. We also report on fluctuations in the tarsiers' activities throughout a night and compare time budgets of *T. syrichta* with available data on the western and eastern species of tarsiers. The results extend the current knowledge of tarsier behaviour and may also assist in practical considerations for keeping this highly sensitive, difficult-to-breed species in captivity.

KARGER

E-Mail karger@karger.com
www.karger.com/fpr

Filip J. Wojciechowski
Department of Human Evolutionary Ecology
Faculty of Biology, Adam Mickiewicz University
PL–61-614 Poznań (Poland)
E-Mail philip.wojciechowski@gmail.com

Introduction

Primates exhibit considerable variation in activity budgets, which are influenced by multiple factors, including environmental conditions, social variables, age, sex, rank, body size and human disturbances [Isbell and Young, 1993; Defler, 1995; Menon and Poirier, 1996; Gursky, 2000; Phiapalath and Suwanwaree, 2010; Habali et al., 2012]. Changes in time allocated to various activities have also been recorded in captivity. These might be attributed to differences in enclosure size and complexity, husbandry routines and social composition [Melfi and Feistner, 2002; Hosey, 2005; Jaman and Huffman, 2008]. Studies on activity patterns may assist in improving the welfare and monitoring of primates in captivity [Hosey, 1989; Little and Sommer, 2002; Mallapur, 2005; Milozzi et al., 2012]. They are equally important in evaluating the behaviour of captive animals under different conditions within the "wild-captive continuum" [Melfi and Feistner, 2002; Todd et al., 2008]. Below we present a detailed description of the activity patterns of captive Philippine tarsiers.

The Philippine tarsier, *Tarsius* (= *Carlito*) *syrichta*, belongs to a group of species of the family Tarsiidae – nocturnal obligatory faunivores inhabiting islands of South-East Asia. It is endemic to the Philippine islands and is found particularly on Bohol, Samar, Leyte and Mindanao [Neri-Arboleda et al., 2002; Shekelle and Arboleda, 2008]. Within *T. syrichta*, 3 subspecies – *T. s. syrichta*/*carbonarius*/*fraterculus* – have previously been described [Hill, 1955]. Recently, however, Brown et al. [2014] revised the Philippine tarsier taxonomy recognizing 3 evolutionary lineages that do not correspond to the above-mentioned subspecies. Groves and Shekelle [2010] proposed to classify extant Tarsiidae in 3 genera: *Tarsius* (eastern group of species), *Cephalopachus* (western monotypic genus) and *Carlito* (Philippine monotypic genus). In this paper we have used the generic name *Tarsius* for all Tarsiidae following the rationale: "The generic name emphasizes not a greater degree of difference but rather the belonging-together of the species included in the genus" [Mayr, 1963, p. 341]. "Monotypic genera are justified when, and only when, a single, isolated known species is so distinctive that the probability is that it belongs to a generic group of otherwise unknown ancestral, collateral, or descendent species" [Simpson, 1963, p. 9]. Morphological and genetic evidence [Musser and Dagosto, 1987; Dutrillaux and Rumpler, 1988; Groves, 1998] seems to support the split of the tarsiers into two distinct groups: an eastern group and a western-Philippine group.

As with its taxonomy, *T. syrichta* has been relatively sparsely studied in terms of its ecology and behaviour. Although some of these aspects, e.g. home ranges, locomotor patterns and habitat use [Dagosto and Gebo, 1997; Dagosto et al., 2001; Neri-Arboleda et al., 2002], predation on tarsiers [Řeháková-Petrů et al., 2012a], vocalization [Řeháková-Petrů et al., 2012b; Gursky-Doyen, 2013], infant ontogeny and play behaviour [Řeháková, 2018] have been investigated, the detailed behavioural repertoire and activity patterns of this species have not yet been the subject of any study. We also lack behavioural data on *T. syrichta* in captivity, except for some anecdotal observations of tarsiers captured on Mindanao [Wharton, 1950], or on habitat use and grouping of *T. syrichta* within a semi-captive environment in Corella, Bohol [Jachowski and Pizzaras, 2005]. In contrast, eastern and western tarsiers have been studied to a much greater extent in both the wild and captivity. Extensive data are available especially for *Tarsius spectrum* (= *tarsier*) [MacKinnon and MacKinnon, 1980; Gursky, 1997, 2000, 2002a, 2005; Gursky-Doyen, 2010, 2011], and also for *T. bancanus* [Niemitz,

1984b, c; Roberts and Cunningham, 1986; Crompton and Andau, 1987; Roberts and Kohn, 1993; Yustian, 2007; Crompton et al., 2010]. There are two possible reasons for the lack of behavioural data on *T. syrichta*. First, it is extremely difficult to observe this "cryptic" and small nocturnal primate in the very dense forest-covered slopes it inhabits. Second, it is equally difficult to maintain in captivity [Neri-Arboleda, 2001]; all attempts to establish a viable captive population have failed [Fitch-Snyder, 2003].

The IUCN, in 2008, classified *T. syrichta* as Near Threatened [Shekelle and Arboleda, 2008]. In 2015, the species was listed as one of the World's 25 Most Endangered Primates [Schwitzer et al., 2015]. The factors contributing to this classification are mainly deforestation and the illegal pet trade. Until recently, tarsiers were abused in tourist displays, being shown to visitors during the day time, causing stress [Petrů, 2010]. Without proper conservation, the species is vulnerable to extinction [Neri-Arboleda, 2010]. In consequence, in 2014, the Subayon Conservation Centre for the Philippine tarsier was established in Bilar, Bohol, to study this species in captivity and to develop guidelines for its long-term husbandry.

In this study we aimed to: (1) reveal the activity patterns of male and female *T. syrichta* during their waking hours; (2) establish whether *T. syrichta*, a seasonally breeding primate, modifies its activity budget according to social context (mating vs. non-mating season); (3) determine the changes in tarsier activity patterns over 12-h nightly cycles; and (4) compare the activity budgets of *T. syrichta* with available data on the western and eastern species of tarsiers. This paper provides a detailed description of the Philippine tarsier behaviour via study of the activity patterns of an opposite-sex pair during the non-mating versus mating season.

Materials and Methods

Study Site and Subjects

The study was conducted at the Subayon Conservation Centre for the Philippine tarsier in Bilar, Bohol, on a wild-caught *Tarsius syrichta fraterculus* endemic to the island [Hill, 1955]. The site, not open to visitors, is located on the edge of old secondary forest, 307 m above sea level (9°40.176' N, 124°06.096' E). The mean annual temperature at the site was 24.3 °C, mean humidity 95.2%, with the rainy season lasting from June to January. The tarsiers were caught by local project staff at the end of August 2014 (male) and in mid June 2015 (female), approximately 7 km from the Conservation Centre, from two areas about 4 km apart. Based on weight and teeth, both were was assessed to be adult specimens.

The animals were housed in naturalistic outdoor enclosures, furnished with a variety of vegetation (among others: *Leea manilensis*, *Swetenia macrophylla*, *Ficus pseudopalma*, *Tabernamontana* sp., *Pandan* sp.). The enclosures were built of wire mesh covered by a soft nylon net, supported by horizontal and vertical steel bars, with a cement layer at the base of the side walls. The roof was constructed in the same manner as the walls, allowing rain to come through the ceiling. The ground substrate consisted of natural soil with some stepping stones. The enclosure used for observations of the solitary animals comprised an approximately 8.5 m^2 cage (measuring 3.1 m length × 2.7 m breadth × 2.4 m mean height). When paired for the mating season (*T. syrichta* was described to be a once-a-year seasonal breeder [Neri-Arboleda et al., 2002; Wright et al., 2003]), the tarsiers were housed in conjoined cages (total area approx. 17 m^2), connected through rolled-up netting. Before being paired for the mating season, the animals were familiarized with each other in adjacent enclosures for more than a week. The primates were provided with live food once per day (prey was randomly shaken out of containers onto the vegetation) at around 4 PM, before their natural activity began. The food consisted of wild-caught crickets (*Gryllus assimilis*, *Gryllus bimaculatus*), katydids (*Mecopoda elongata*, *Phaneroptera falcata*, *Morsimus* sp.),

Table 1. Catalogue of activities recorded for the Philippine tarsiers and their descriptions

Behaviour	Code	Description
Resting	RE	Animal motionless with both hands and feet grasping a branch/stem with eyes open or closed and ears not moving
Scanning	SC	Animal stationary surveying the environment with eyes open; head moving slowly from side to side or up and down and/or ears in motion
Travelling	TR	Animal in motion (e.g. leaping, climbing, quadrupedalism) resulting in a change of the animal's location, excluding movements associated with foraging
Foraging	FO	Animal searching for food, either stationary with head moving rapidly around, with eyes and ears in motion and/or in movement towards prey item and grasping it
Feeding	FE	Animal eating, i.e. transferring food item to mouth and/or processing it
Scent-marking	SCM	Animal rubbing cheeks or genital area against vertical support as well as animal rubbing forearms against its head
Self-grooming	SGR	Animal manipulating a part of its body with tongue, hands or feet
Other	OTH	Rare activities: defaecation, regurgitation and reingestion, licking branches
Social	SOC	Animal interacting with another animal of the opposite sex

grasshoppers, cicadas, moths, dragonflies, praying mantids, beetles and huntsman spiders, as well as captive-bred mealworms (*Tenebrio molitor*) and crickets (*Acheta domesticus*).

Data Collection

We constructed the ethogram for this study after the initial 104 h of observation of the male tarsier, 2 months subsequent to capture, when he had already become habituated. We recorded the following activities: resting, scanning, travelling, foraging, feeding, scent-marking, self-grooming, social and other (for definitions see Table 1).

We observed the activities of the male and female tarsiers in two social contexts: solitary – housed separately – and paired – housed together for the mating season (October to November; see Wright et al. [2003]). The periods of observation were: (1) December 23, 2014, to January 28, 2015, for the male when solitary, (2) October 16 to November 10, 2015, for the two individuals when paired, and (3) December 15, 2015, to January 5, 2016, for the female when solitary. Data were collected for a total of 384 h (23,040 data points) via instantaneous sampling [Altmann, 1974] at 1-min intervals for eight 12-h periods of time (5,760 min) per each animal sex-social context. The tarsiers were not tagged or marked in any way, but reliably recognized by individual characteristics, such as size and facial differences. Three people carried out the observations using headlamps covered with green cellophane filters (objects were easier to see in green). The degree of agreement among the observers (interobserver reliability), determined prior to the study by simultaneous data recording, was at least 95%.

Observations were converted into fractions of 1-h intervals. The animals sometimes disappeared from the view of the observer, and there are different ways of dealing with the out-of-sight problem [Lehner, 1996; Paterson, 2001]. In this study, the time at which a particular activity was observed was divided by the time in which a given individual was visible to the observer during a particular 1-h interval. The total time in which the individuals were out of sight was: 1% (57

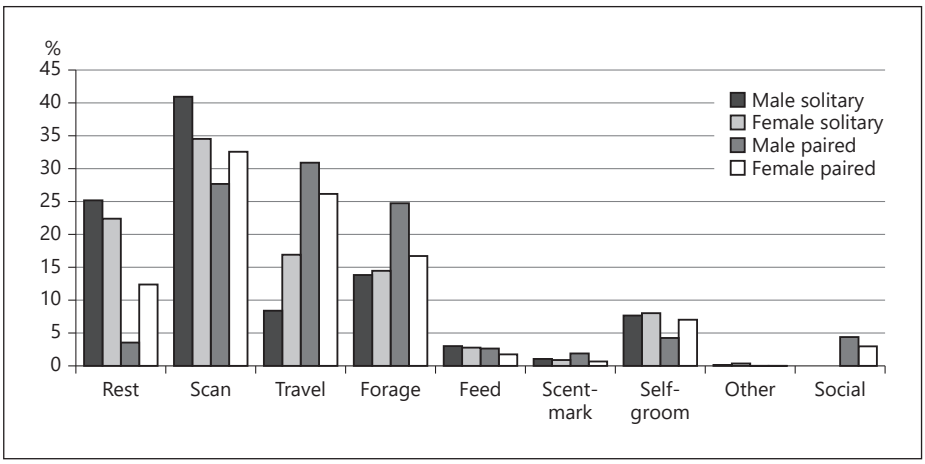

Fig. 1. The apportionment of time for various activities of *T. syrichta* for both sexes and social contexts.

min) for the solitary male; 4% (247 min) for the solitary female, 4.5% (261 min) for the paired male, and 6% (346 min) for the paired female.

Statistical Analyses

We tested the significance of differences between various activities and between individuals using parametric and non-parametric tests depending on whether the data were distributed normally with homogeneous variances or not. To compare the time budgets, we employed analysis of variance (ANOVA) and the Kruskal-Wallis test. In cases of heterogeneity of variance, Welch's correction was used. We ran the appropriate post hoc comparisons (Tukey's test or the pairwise multiple comparison of mean ranks) to determine the differences between particular activities for the chosen pairs. Comparison of the time spent on social behaviour was performed using Student's *t* test. The *t* test or the Mann-Whitney U test was used to compare the mean duration of different activities between the mating and non-mating seasons. To determine changes in activity patterns over the 12-h nightly cycles, we divided the observation time into several time intervals: twelve 1-h, four 3-h, three 4-h and two 6-h. For each type of activity and each sex-social situation, the appropriate tests were used (ANOVA or the Kruskal-Wallis test for comparing multiple groups, and the *t* test or the Mann-Whitney U test for comparing two groups). We then chose the quarterly interval, for which the highest number of statistically significant differences existed. Data were analysed using *Statistica 11* (Statsoft Inc.) and Microsoft Excel. All tests for two samples were two-tailed; the significance level α was set at 0.05.

Results

Comparison of Individual Activity Budgets by Sex and Social Context

We analysed the mean percentage of time allocated to various activities for the male and female tarsiers in both social arrangements (individual activity budgets). The comparisons are shown in Figure 1 and Table 2.

Table 2. Mean percentage of time (and standard deviation) spent on various *T. syrichta* activities for both sexes and social contexts (solitary and paired)

Behaviour	Male solitary		Female solitary		Male paired		Female paired	
	mean	SD	mean	SD	mean	SD	mean	SD
Resting	25.1	5.6	22.4	10.7	3.5	3.6	12.3	4.6
Scanning	40.9	3.9	34.5	5.1	27.7	9.7	32.5	5.6
Travelling	8.4	3.0	16.9	3.3	30.9	13.7	26.1	8.8
Foraging	13.8	2.9	14.4	5.1	24.7	4.5	16.7	3.4
Feeding	3.0	1.3	2.8	0.7	2.6	0.9	1.7	0.5
Scent-marking	1.0	0.4	0.9	0.3	1.9	1.0	0.6	0.3
Self-grooming	7.6	1.7	8.0	1.7	4.2	0.8	7.0	2.0
Other	0.2	0.2	0.3	0.5	0.1	0.1	0.1	0.1
Social					4.4	1.4	3.0	1.3

Table 3. Summary of post hoc comparisons (*p* values) for differences in activity budgets for each sex-social context pair

Behaviour	MS-FS	MS-MP	FS-FP	MP-FP
Resting	1	*0.0003*	0.5285	0.4716
Scanning	0.2146	*0.0018*	0.9324	0.4444
Travelling	0.1618	*0.0005*	1	1
Foraging	0.9918	*0.0002*	0.6789	*0.0025*
Feeding	0.9589	0.8537	0.1304	0.2254
Scent-marking	1	0.9007	0.9948	*0.0052*
Self-grooming	0.9594	*0.0014*	0.6026	*0.0090*
Social				*0.0490*

MS, male solitary; FS, female solitary; MP, male paired; FP, female paired; the italicized values are statistically significantly different.

Post hoc pairwise comparisons (Table 3) revealed that the sexes exhibited no significant differences in their time budgets when solitary (MS-FS), although the female – on average – spent twice as much time travelling than the male (Table 2). Conversely, we found some differences between the activity budgets of the male and female when paired (MP-FP) – the male spent significantly more time foraging, scent-marking and engaging in social behaviour, while less time was spent on self-grooming. He also – on average – spent less time resting than the female. During the mating season, the male changed his time budget significantly in 5 out of 7 activities compared with the non-mating season (MS-MP) – resting, scanning and self-grooming less frequently, while travelling and foraging more often. Conversely, there was no significant difference in the female's time budget between the non-mating versus mating season (FS-FP). Although the paired female devoted – on average – more time to travelling, while less to resting, than when solitary, this difference was insignificant (Fig. 1 and Tables 2, 3).

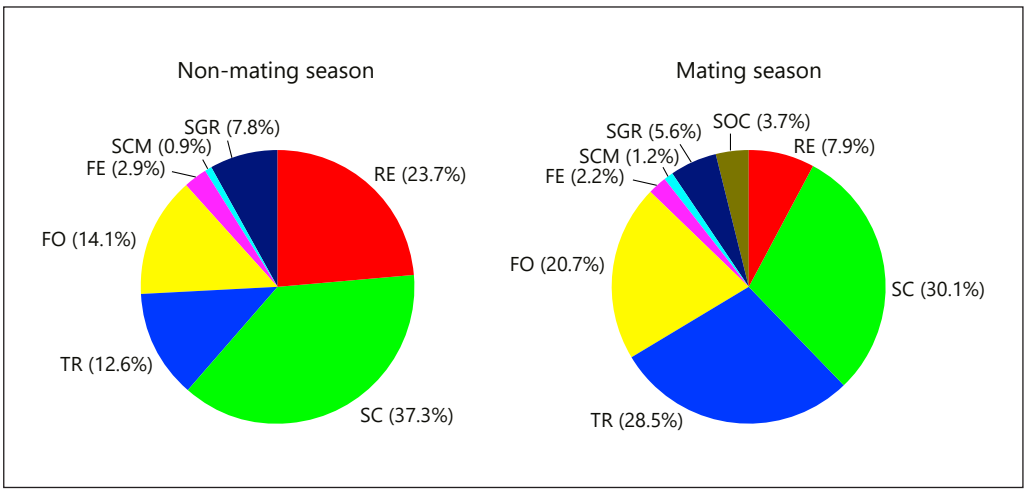

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Fig. 2. Comparison of activity budgets for *T. syrichta* during the non-mating (solitary) and mating (paired) season (for activity codes, see Table 1).

Comparison of Activity Budgets for Non-Mating versus Mating Season

We analysed the time budgets of both sexes for both social contexts to ascertain the extent to which the overall activity budgets for the tarsiers kept solitary and paired for the mating season differed (Fig. 2).

During the non-mating season, the solitary tarsiers spent the largest portion of their waking hours scanning, followed by resting, foraging and travelling. The remaining 4 activities constituted a smaller part of the animals' time budget (in sum approx. 12%). During the mating season, although the most common activity for the paired sexes was still scanning, the time spent resting markedly decreased, while there was an increase in that spent travelling and foraging. The remaining 5 activities constituted about 13% of their time budget, of which 3.7% were social interactions. Significant differences between the mean duration of these activities in both social contexts were found for resting ($p = 0.000$), scanning ($p = 0.004$), travelling ($p = 0.000$), foraging ($p = 0.001$) and self-grooming ($p = 0.002$).

Comparison of Activity Patterns within Quarterly Time Intervals

We used quarterly time intervals to determine changes in the *T. syrichta* activities over the 12-h cycles and found fluctuations (peaks and dips) in some activities. The percentages of time allocated to the major activities within particular intervals for all sex-social contexts are shown in Figure 3, while the results of statistical tests for the differences are given in Table 4.

In the non-mating season, the solitary male exhibited the greatest fluctuation in the time spent resting. He was most active over the first and the last quarters of a night; during the second and the third quarters, this pattern was reversed. In the case of the solitary female, the most noticeable difference was that the time spent scanning significantly increased over the third and the fourth quarter of a night compared to

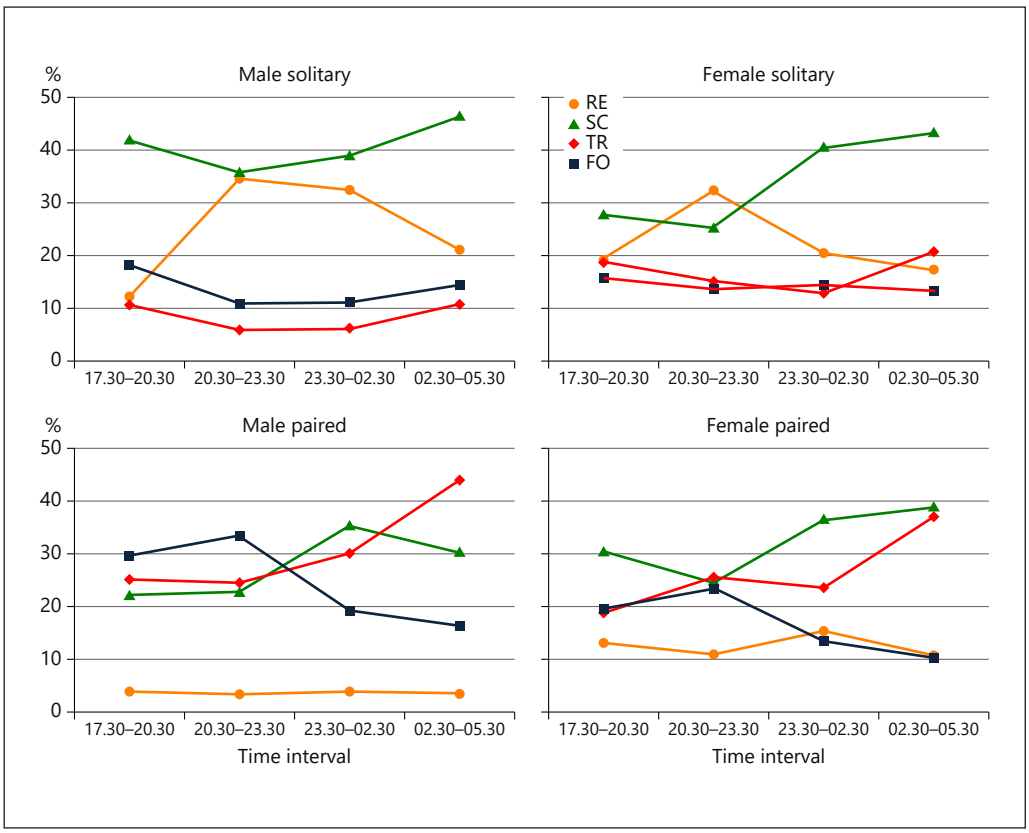

Fig. 3. Activity patterns of major behaviours of *T. syrichta* for both sexes and social contexts within quarterly time intervals. RE, resting; SC, scanning; TR, travelling; FO, foraging.

the first and the second. For resting and travelling, only weak fluctuations were observed (Fig. 3; Table 4).

In the mating season, the paired male showed the greatest fluctuations in the time spent travelling and foraging. The male was very active throughout the entire night. In the first half of a night he foraged most, while at the end, he foraged least and travelled most. Resting remained very stable and at a low level (below 5%) for all time intervals. The paired female showed significant fluctuations for the time spent on all activities except resting. During the second quarter of a night, the female spent the same amount of time on travelling, scanning and foraging, whereas by the end of a night, scanning and travelling were at peak levels, while foraging had dipped (Fig. 3; Table 4).

Both sexes displayed greater fluctuation in nightly activities during the mating season than when solitary. Irrespective of sex-social context, feeding, self-grooming and scent-marking were more frequent at the beginning of a night and less frequent at the end of a night.

Table 4. Results of statistical tests (*p* values) for differences in quarterly activity patterns for both sexes and social contexts, and post hoc comparisons showing pairs of quarters between which significant differences existed

Behaviour	Male solitary		Female solitary		Male paired		Female paired	
	p	quarters' difference	*p*	quarters' difference	*p*	quarters' difference	*p*	quarters' difference
Resting	*0.001*	1–2, 1–3	0.217		0.966		0.550	
Scanning	0.050		*0.000*	1–3, 1–4 2–3, 2–4	0.066		*0.005*	2–3, 2–4
Travelling	0.047	–	0.299		*0.036*	2–4	*0.007*	1–4
Foraging	0.068		0.675		*0.000*	1–3, 1–4 2–3, 2–4	*0.000*	1–4 2–3, 2–4

Discussion

Activity Patterns of Tarsius syrichta

We found that both sexes of *T. syrichta* exhibited no significant differences in their activity budgets when solitary. Various other studies have revealed evidence both for [Watts, 1988; Mitani, 1989; Shanee and Shanee, 2011; Li et al., 2014] and against [Strier, 1987; Defler, 1995; Hemingway, 1999] differences in primate time budgets according to sex. This variability may result from differences in body size, where sexually dimorphic species experience different daily energy expenditures for male and female, while in monomorphic species the energy requirements are similar [Key and Ross, 1999]. Defler [1995] found that *Lagothrix lagotricha* do not differ in activity budgets between the sexes even though the adult males weigh more than adult females and speculated that it is possible that size sexual dimorphism might have not been sufficient to affect the animal's behaviour. The results of our study appear to corroborate the above suggestion that despite differences in body size, males and females need not necessarily differ significantly in their activity budgets, at least during the non-mating season.

For the male *T. syrichta*, a significant difference in activity budgets occurred between the solitary and paired arrangements. During the mating season the male allocated significantly more time to travelling and foraging, while less to resting, scanning and self-grooming than while solitary. An increase in male activity level during the breeding season has been documented for a few cheirogaleid species: *Cheirogaleus medius* [Foerg and Hoffmann, 1982], *Microcebus berthae* [Dammhahn and Kappeler, 2005] and *M. murinus* [Kraus et al., 2008], where high male mobility was observed in the presence of females in oestrus, and this has been suggested to increase the chance of encountering receptive females. Observations of wild *T. syrichta* suggest a solitary dispersed social system in which the male's territory overlaps the smaller territories of more than one female [Dagosto et al., 2001; Neri-Arboleda et al., 2002]. Within this social structure males are required to roam in search of receptive females, leading to higher activity levels. Thus, the pattern of change to more active behaviour during the mating season evidenced in our study may reflect the natural activity patterns of the males as predicated by their social system.

Analysis of the combined activity budgets for the sexes of *T. syrichta* in two social contexts revealed changes in time spent on a number of activities during the mating season. It is interesting to note that although scanning was the most frequent activity in both social contexts, it decreased from approximately 38 to 30% for the paired individuals placed in a larger enclosure. Wood et al. [2000] revealed that sifaka *Propithecus verreauxi coquereli* spent significantly more time scanning in small outdoor and indoor enclosures than in a large natural habitat enclosure and linked these to environmental factors, such as limited opportunities for locomotion. Their findings may explain the high frequency of scanning for the tarsier individuals when solitary. Considering that *T. syrichta* were held in an outdoor enclosure surrounded by nature, scanning would still, however, be an important sign of vigilance serving for early detection of predators.

While scanning was maintained at the highest level in both social contexts, the time spent travelling and foraging increased markedly in the mating season, at the expense of that spent resting. The increase in travelling time might be explained by the doubling of size of the enclosure space for the paired tarsiers in comparison to that when solitary. However, although both sexes showed an increase in time allocated to travelling, the difference was significant only for the male. With regard to the foraging time, Gursky [2002b] found that *T. spectrum* changed its activity budget depending on distance to another adult group member. When the distance was ≤10 m to another individual, *T. spectrum* foraged more than when they were further apart, which Gursky [2005] explained as a result of a decrease in foraging efficiency.

T. syrichta exhibited fluctuations in time spent on various activities throughout the night. The solitary individuals exhibited a bimodal pattern for travelling time with rises occurring at the beginning and at the end of the night. During the mating season, the tarsiers spent significantly more time travelling at the end of the night. Studies conducted on the wild *T. bancanus* [Crompton and Andau, 1987] and *T. dianae* (= *dentatus*) [Merker, 2006] revealed two peaks for locomotor activity and distance travelled: the first shortly after dusk, and the second before going to sleep at dawn. A two-peak activity rhythm was also described by Nietsch [cited in Merker, 2006] for the wild *T. spectrum*. Activity patterns of the wild *T. syrichta* revealed by Neri-Arboleda et al. [2002] showed that both sexes were most active in hourly distance travelled in the first hour after dusk. The early activity peak for the wild tarsiers is explainable by their being quickly able to reach beneficial hunting grounds [Merker, 2006]. With regard to the peak at the end of the night, Crompton and Andau [1987] and Merker [2006] suggested that since the foraging areas were far away from the sleeping sites, travelling back increased the frequency of this activity.

For the paired *T. syrichta* in this study, foraging was at a high level during the first half of the night, while feeding (irrespective of the sex-social context) always peaked in the first, or the first and the second, hour after waking. Foraging by captive *T. bancanus* peaked during the first hour of its activity, when it caught the highest number of prey [Roberts, 1988]. The highest peaks of feeding after waking in the two above studies are probably influenced by the captive settings, in which the animal prey is supplied at a constant rate each day, being immediately available to the tarsiers without them having to travel long distances. In observations under semi-wild conditions, where the tarsiers were not provided with food but where animal prey was able to enter the enclosure freely, *T. bancanus* exhibited a bimodal feeding cycle [Niemitz, 1984b].

Table 5. Mean percentage of time spent by 4 tarsier species on chosen activities (or joint categories)

	T. syrichta		*T. bancanus*		*T. dianae*	*T. spectrum*	
Study type:	captive, outdoor		captive, indoor	free-ranging	free-ranging	free-ranging	
Social system:	noyau		noyau	noyau	pair bonds	pair bonds	
Place:	Bohol		US zoo	Borneo	Sulawesi	Sulawesi	
Number:	♂♀S	♂♀P	2 pairs	2 pairs	1♀ + 3♂	5♀	3 pairs
Reference:	1	1	2	3	4	5	6
SC + FO	51.8	50.8	78	60.1	44	46.4	–
FE	2.9	2.2	2	2.1	4 events witnessed	7.0	–
SC + FO + FE	54.7	53.0	80	62.2	44	53.4	55
RE	23.7	7.9	13	10.8	21	14.7	16
TR	12.6	28.5	1	26.5	28	25.7	23

S, solitary; P, paired; SC, scanning; FO, foraging; FE, feeding; RE, resting; TR, travelling.
1, present study; 2, Roberts and Kohn, 1993; 3, Crompton and Andau, 1986 ; 4, Tremble et al., 1993 ; 5, Gursky, 1997; 6, Gursky, 2005.

Possibly associated with feeding is the act of regurgitation and reingestion (R/R) which we observed in this study. R/R has been recorded among captive primates (macaques, baboons and the apes) [Baker and Easley, 1996], but ours is the first evidence of this phenomenon in prosimians. R/R behaviour has been linked to boredom in captivity, space restriction, stress, low levels of stimulation, suboptimal diet [Capitanio, 1986; Lukas, 1999; Cassella et al., 2012] or the absence of feeding opportunities after the daily food portion had been served and eaten [Baker and Easley, 1996]. The number of R/R events in our study was low (20 occurrences), they were noticed more frequently for the female, and most events were observed when it rained – usually between the 3rd and 4th h of the animals' activity. Heavy rain forces tarsiers to hide, thus preventing them from foraging – as observed for *T. spectrum* and *T. bancanus* [MacKinnon and MacKinnon, 1980; Niemitz, 1984a]. R/R in *T. syrichta* may, therefore, be a compensatory behaviour owing to a scarcity of food during downpour weather conditions.

Activity Budgets of T. syrichta *versus* T. bancanus, T. dianae *and* T. spectrum

We compared activity budgets of *T. syrichta* with previously published time budgets for 3 other tarsier species: *T. bancanus* [Crompton and Andau, 1986; Roberts and Kohn, 1993], *T. dianae* [Tremble et al., 1993] and *T. spectrum* [Gursky, 1997, 2005]. Some difficulties arose owing to the diverse types of these studies – 3 species were observed in the wild, while *T. syrichta* and some *T. bancanus* were studied in captivity (with the latter in indoor housing). Despite these limitations, basic comparisons can still be made.

Table 5 reveals that the time spent on scanning and foraging combined locates *T. syrichta* between the Bornean *T. bancanus* and both the Sulawesi *T. dianae* and *T. spectrum*. Two percentage values for the captive *T. bancanus*, however, seemed anomalous: scanning and foraging appeared much too high, while travelling much too low (probably due to the markedly different housing conditions; see Roberts and Kohn [1993]), and therefore we omitted these from the comparisons. *T. syrichta*

spent, on average, a similar amount of time to both *T. bancanus* samples on feeding, while for the *T. spectrum* females this value was much higher. However, when scanning, foraging and feeding were combined, *T. syrichta* was very much like *T. spectrum*. For resting time, the solitary *T. syrichta* resembled *T. dianae*, while, interestingly, the paired *T. syrichta* resembled the solitary wild *T. bancanus*. Finally, the mean time spent travelling for the paired *T. syrichta* was similar to that for the 3 other free-ranging tarsier species, while the solitary *T. syrichta* had no equivalent. On comparing the activity budgets of the Philippine tarsier with the data for the western and eastern species of tarsiers, our data do not point to *T. syrichta* having a substantially greater similarity in activity budget to *T. bancanus* than to *T. spectrum* and *T. dianae*.

In summary, we have presented a description of *T. syrichta* behaviour via study of the activity patterns for a pair of opposite sex individuals in the mating and non-mating season. While we are aware of the obvious limitations of this study owing to the small sample size, our results provide the first quantified account of the time allocated to various activities of the Philippine tarsier, data which would be difficult to collect in the wild. It is crucial to ascertain the extent to which results obtained in this study may differ from those in the wild and under different captive conditions. Evaluation of activity budgets in such a spectrum may help in practical considerations for housing *T. syrichta* in captivity.

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Disclosure Statement

The authors have no conflicts of interest to declare.

Author Contributions

M.Ř., A.M.W. and F.J.W. designed the experiments; F.J.W. and A.M.W. collected the data; F.J.W. and K.A.K. analysed the data, wrote the paper and revised the text; M.Ř. submitted comments.

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VII. MANUSCRIPT 2:

Social behavior of a reproducing pair of the Philippine tarsier (*Tarsius syrichta*) in captivity.

AUTHORSHIP CONTRIBUTION STATEMENT

FILIP J. WOJCIECHOWSKI, KATARZYNA A. KASZYCKA, MILADA ŘEHÁKOVÁ (2020). *Social behavior of a reproducing pair of the Philippine tarsier (Tarsius syrichta) in captivity.* Journal of Applied Animal Welfare Science, 23:4, 493-507.

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Name of author	WOJCIECHOWSKI FILIP J. https://orcid.org/0000-0002-3598-9109
Affiliation	• Department of Human Evolutionary Ecology, Institute of Anthropology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland • Wings of Serenity Inc., Tagbilaran City, 6300 Bohol, Philippines
Contribution	• Designed the experiments; • Collected the data; • Analysed the data; • Wrote the paper, • Revised the text.
Contribution %	**65%**
Date and signature	19.06.2021 .....

Name of author	KASZYCKA KATARZYNA A. https://orcid.org/0000-0003-1348-1037
Affiliation	• Department of Human Evolutionary Ecology, Institute of Anthropology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland
Contribution	• Analysed the data; • Wrote the paper, • Revised the text.
Date and signature	1.06.2021 ..... KA Kaszycka

Name of author	ŘEHÁKOVÁ MILADA https://orcid.org/0000-0002-6087-1612
Affiliation	Tarsius, z.s., Děčín, Czech Republic
Contribution	• Designed the experiments; • Submitted comments.
Date and signature	27.6.2021 ..... Řeháková .....

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ARTICLE

Social Behavior of a Reproducing Pair of the Philippine Tarsier (*Tarsius syrichta*) in Captivity

Filip J. Wojciechowski[a,b], Katarzyna A. Kaszycka[a], and Milada Řeháková[c]

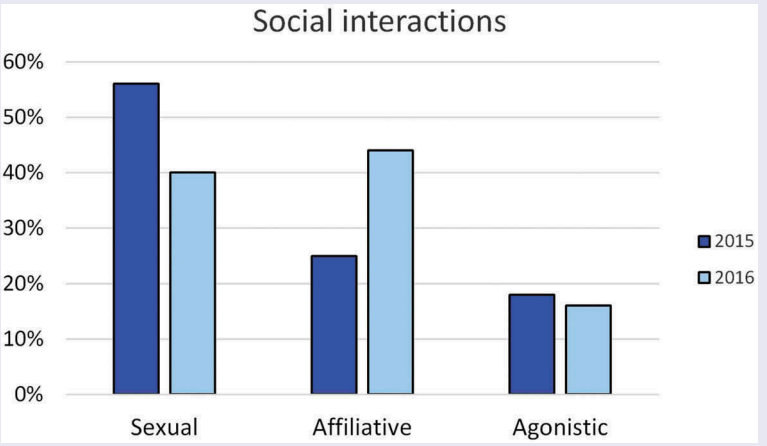
[a]Department of Human Evolutionary Ecology, Institute of Anthropology, Adam Mickiewicz University, Poznań, Poland; [b]Wings of Serenity Inc., Tagbilaran City, Bohol, Philippines; [c]Tarsius, z.s., Děčín, Czech Republic

KEYWORDS
Nocturnal primates; affiliation; aggression; mating; captive breeding

ABSTRACT

Social interactions of the nocturnal primates are not well studied. One of the species for which social behavior is scarcely known is the Philippine tarsier (*Tarsius* [= *Carlito*] *syrichta*). We observed a reproducing pair of captive individuals over two mating seasons for two consecutive years. The tarsiers spent approximately 4% of their activity budget on social interactions; ca. 20% of time in 0–1 m proximity to each other; and shared sleeping sites for half of the study time. The majority of the animals' social interactions were peaceful: affiliative and sexual (83%), and the smallest component of the behavior was agonistic (17%). We witnessed two copulation events (one per estrus day), each lasting ca. 5 min, and both occurring just after waking. We revealed temporal – nightly and hourly – fluctuations in the frequency of social interactions, in the distances the individuals spent from each other and in the number of vocalizations. The results present the first assessment of the social behavior of the Philippine tarsier, much needed to improve the captive breeding management for this highly sensitive species threatened with extinction.

Frequency of social interactions (sexual, affiliative, agonistic) of the Philippine tarsiers during two consecutive mating seasons, when the animals were unfamiliar (2015) and familiar (2016) with each other.



CONTACT Filip J. Wojciechowski philip.wojciechowski@gmail.com Department of Human Evolutionary Ecology, Institute of Anthropology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, Poznań 61-614, Poland

Introduction

Over the past decades, the knowledge of social systems of nocturnal primates has expanded and its perception has been shifted from "solitary" (having no social interactions except for the mating season [Crook & Gartlan, 1966]) to "solitary foragers" (foraging alone, yet gregarious at their sleeping trees [Bearder, 1987; Müller & Thalmann, 2000]). Although still acknowledged as predominantly non-gregarious, it is now accepted that they sometimes do form social networks, recognize other individuals whose home ranges overlap with their own (Richard, 1985) and interact with one another, while do not spend a considerable amount of time in close proximity (Sterling & McCreless, 2006). To understand primate social complexity, one has to consider all components of their social systems, such as: social organization ("the size, sexual composition and spatio-temporal cohesion of a society"), mating system (reproductive interactions between individuals, or the way in which a group is structured in relation to sexual behavior), and social structure, which refers to "the pattern of social interactions and the resulting relationships among the members of a society" (Kappeler & van Schaik, 2002, pp. 709–710).

Despite the evidence that most nocturnal primates are more gregarious than previously thought, the components of their social systems are not equally understood, as most of the studies rely on trapping and/or radio-tracking, which provide information on social organization and mating system, but with marginal emphasis on the patterns of social interactions (e.g., Dammhahn & Kappeler, 2005; Fietz, 1999; Müller, 1998; Radespiel, 2000; Schwab, 2000). Nevertheless, a few studies have attempted to quantify social interactions for several nocturnal primates, such as lorisoids (Nekaris, 2006; Pimley, Bearder, & Dixson, 2005; Radhakrishna & Singh, 2002; Wiens & Zitzmann, 2003), golden-brown mouse lemur (*Microcebus ravelobensis*) (Weidt, Hagenah, Randrianambinina, Radespiel, & Zimmermann, 2004) and spectral tarsier *(Tarsius spectrum* = *T. tarsier*) (Gursky, 2000, 2007).

The tarsiers, a group of species of the family Tarsiidae, inhabiting islands of South-East Asia, are the most unusual of all living primates. They show a mixture of prosimian (lower primates) and anthropoid (higher primates) features, and have features of their own (Fleagle, 2013). They are amongst the smallest primates, have the biggest night-adapted eyes of all mammals (relative to their body weight), a rounded head, a unique form of arboreal locomotion known as vertical clinging and leaping, and are the only obligatory faunivorous primates. Evidence, both morphological and genetic, seems to support the split of the tarsiers into two groups: an eastern group, and a western-Philippine group (Dutrillaux & Rumpler, 1988; Groves, 1998). The majority of tarsier species are now threatened, vulnerable or endangered (IUCN, 2019).

Of all nocturnal primates, the tarsiers are relatively sparsely described in terms of their social system, although, the data on social organization and mating system for at least some species are available. Spectral tarsiers (belonging to the eastern group and the species most extensively studied in the field) are considered gregarious animals living with their partners in mostly monogamous (some in polygynous) small family groups (Gursky, 1995, 2007; Gursky-Doyen, 2010; MacKinnon & MacKinnon, 1980). This species exhibits a considerable amount of social behavior between individuals at the sleeping trees and during nightly activity (Gursky, 2000), and time spent in proximity to other group members has been shown to be longer than would be expected from chance (Gursky, 2005). Of the other Sulawesi species, Dian's tarsiers (*Tarsius dianae* = *T. dentatus*) display facultative polygyny (Merker, 2003), while the Lariang tarsier (*Tarsius lariang*) was identified as monogamous (Driller, Perwitasari-Farajallah, Zischler, & Merker, 2009). The western tarsiers (*Tarsius* [= *Cephalopachus*] *bancanus*), on the other hand, are non-gregarious, with most data from the wild indicating a noyau/dispersed polygyny system (Crompton & Andau, 1987; Yustian, 2007), while data from semi-wild and captivity suggest that pair-living seems to be the rule (Niemitz, 1984; Wright, Toyama, & Simons, 1986b). Physical contact between these animals in the semi-wild setting was described as very rare and restricted only to sexual partners during copulations, fights, and mother-infant interactions (Niemitz, 1984).

Records of behavioral observations on the Philippine tarsier (*Tarsius* [= *Carlito*] *syrichta*) are scarce. The species is considered non-gregarious and non-monogamous, having a noyau/dispersed polygyny social system (e.g., Dagosto, Gebo, & Dolino, 2001) and solitary foraging and sleeping patterns (Neri-Arboleda, Stott, & Arboleda, 2002). Quantitative data on how captive male and female *T. syrichta* apportion time for their various activities during non-mating and mating seasons were provided by Wojciechowski, Kaszycka, Wielbas, and Řeháková (2019). Greater frequency of social behaviors of the wild-caught Philippine tarsiers over the western tarsiers kept in pairs in similar housing conditions was noted by Haring, Wright, and Simons (1985). On the other hand, the vocal repertoire of the Philippine tarsier (Řeháková-Petrů, Policht, & Peške, 2012) resembles that of the non-gregarious western tarsiers (Niemitz, 1979), and not the richness of vocal communication of the gregarious spectral tarsier (Nietsch, 1999). McComb and Semple (2005) suggested that vocal repertoire facilitates social bonding in primates.

To understand the Philippine tarsier social behavior is not only of scientific value. The tarsiers are also known to be one of the most difficult primates to breed successfully in captivity. First attempts at keeping these primates in western facilities began in 1850, but regular imports have occurred since 1940 (Fitch-Snyder, 2003). Philippine tarsiers were the most common, with 130 specimens being obtained from the Philippines over the years. However, only 22% of them survived captivity for more than 5 years with most not surviving long after transport (Fitch-Snyder, 2003). There have been 37 known births registered for the species in North America and Europe, but 20 of these were stillbirths or died the same day. The fate of those that survived birth was also dire, because 89% of captive-born tarsiers lived less than a year and there were no recorded cases of successful second-generation reproduction for Philippine tarsiers (Fitch-Snyder, 2003). Only one hand-raised offspring from (Haring & Wright, 1989) Duke University Primate Center survived for nearly 5 years. The difficulties in breeding tarsiers have been attributed to their sensitivity to stress, diet consisting exclusively of live prey, nutritional requirements as well as specific climatic conditions.

To ensure the long-term reproductive success of these primates in captivity, knowledge of species' social interactions is crucial. It has been proved that behavioral monitoring can provide an important tool to evaluate reproductive problems in captive animals (Lindburg & Fitch-Snyder, 1994). The studies on social behavior have helped to recommend adequate social housing and pairing in some Strepsirhini species, such as lemurs (Kappeler, 1989), galagos and lorises (Fitch-Snyder & Jurke, 2003; Welker & Welker, 1989). Vocal signals may also provide clues to understanding the reproductive biology of primates in captivity and may be used to determine a female's estrus or success of the introduction of mates (Swaisgood & Schulte, 2010).

The principal aim of this study was to describe the social behavior of a reproducing pair of captive Philippine tarsier during its mating seasons. The specific goals were to: (1) describe and quantify social interactions, (2) provide information on tarsier copulatory behavior, (3) assess spatial proximity between the male and the female, and determine their sleeping patterns, (4) assess vocalizations of the sexes and their contexts, and (5) determine the temporal (nightly and hourly) fluctuations in social interactions, the distances spent by the sexes from each other, and their vocalizations.

Materials and methods

Subjects and housing

The study was conducted at the Subayon Conservation Center for the Philippine tarsier in Bilar, on the island of Bohol (9°40.176′N, 124°06.096′E) on a pair of adult *T. syrichta fraterculus* individuals over two mating seasons. The tarsiers were caught in the wild approximately 7 km from the Conservation Center in August 2014 (male) and June 2015 (female) and in localities distanced about 4 km from each other, which is beyond the average home range for the sexes, thus assumed to not be closely related or familiar to each other prior to the research. They were housed in an outdoor enclosure imitating their natural habitat and exposed to local climate conditions, with a mean annual temperature of 24.4°C and mean humidity of 95.2%. The dimensions of the enclosure were 17 m^2 (6.2 m length x 2.7 m breadth x 2.4 m height) and comprised two

conjoined compartments with an opening of 2.2 m x 1.3 m between them. The enclosure was constructed of horizontal and vertical steel bars, connected by wire mesh covered by a soft nylon net, and supported by a cement layer at the base of the side-walls. The substrate was a natural soil with several locally occurring species of vegetation (trees and bushes). The tarsiers were provided with live food – a combination of wild-caught and captive-bred prey (Wojciechowski et al., 2019) once per day, approximately an hour before their activity began.

Data collection

The observations were carried out over two consecutive mating seasons in 2015 and 2016. During the first mating season, observations were carried out over the period 16/10 – 9/11/2015 (19 nights of data collection), during the second – over the period 14/10 – 11/11/2016 (20 nights of data collection), yielding 468 h of observations in total (= 28,080 data points). The animals, individually recognized by size and facial differences, were observed for 12 h per night, from 5.30 PM to 5.30 AM. We paired the tarsiers for mating in mid-October based on field observations of seasonality of birth occurrences (Neri-Arboleda et al., 2002; Řeháková, pers obs) and the available information on gestation length (Gursky, 2007; Izard, Wright, & Simons, 1985). Three observers collected the data using headlamps covered with green cellophane filters. The degree of agreement among the observers determined prior to the study by simultaneous data recording, was at least 95%.

A partial ethogram for this study (excluding sexual behaviors observed later) was created for the first four nights after pairing (12/10 – 15/10/2015), prior to actual data collection. The catalog of all behaviors includes affiliative (allogrooming, mutual display), agonistic (swipe, defensive face, wrestling, attack) and sexual interactions (sniffing, following scent, mounting, copulation) (Table 1). Data on the proportion of activity budget spent on social behavior were obtained by "instantaneous sampling" at 1-min intervals (Altmann, 1974). Occurrence of social interactions and vocalizations was recorded *ad libitum*. During each social interaction, the initiator of the behavior was identified. At the same time, the distance between individuals (at each 1-min interval) was recorded in the following categories: (1) 0 m – physical contact, (2) >0–1 m – close proximity, (3) >1–2 m, (4) >2–7 m (the maximum distance the tarsiers could be apart from each other in the enclosure).

Statistical analyses

Data were analyzed using parametric and non-parametric tests depending on whether the data were distributed normally with homogeneous variances, or not. The assumption of normality was checked using Shapiro–Wilk test, while the assumption of equal variances, by Bartlett's test. To determine if

Table 1. Ethogram of social behaviors recorded for the pair of captive Philippine tarsier.

Social category	Behavior	Description
Affiliative	Allogrooming	Animal touching fur or body of another individual with fingers or tongue
	Mutual display	Animals opposite to each other with continuous eyes contact, and an array of motor patterns, such as jumping or climbing
Agonistic	Swipe	Animal raising forelimbs and swinging/throwing them rapidly toward another individual
	Defensive pose	Animal motionless with open mouth and teeth visible, sometimes accompanied by raised forelimbs
	Wrestling	Animals mutually grabbing and grappling each other
	Attack	Animal jumping at another individual from close distance, sometimes accompanied by biting
Sexual	Sniffing	Male places nose to inspect anogenital area of a female
	Following scent	Animal following and sniffing urine trail left by another animal
	Mounting	Male covering female's body dorsally with both hands and placing his pubic area against her anogenital region, but pelvic thrusting does not occur
	Copulation	Male mounting female with pelvic thrusting and presumed intromission

there were statistically significant differences between types of social interactions and distances between the individuals within each mating season, we then used the Kruskal–Wallis test. We applied the pairwise Wilcoxon rank-sum *post-hoc* comparisons with the Holm's correction to determine the differences between each of the chosen pairs. The assumption of the equality of variances across groups was verified with the *F*-test. We then used the *t*-test or the Mann–Whitney *U*-test to determine whether there were statistically significant differences between the types of social interactions, distances, and vocalizations between both mating seasons and (except for distances) between the sexes. In cases of homogeneity of variance, Student's *t*-test was used, while in cases of heterogeneity of variance, Welch's *t*-test. Statistical tests were performed using the R Statistical Software (R version 3.5.0; R Core Team, 2018). Two-tailed probabilities are reported and statistical significance at $\alpha = 0.05$ accepted.

Results

Social interactions

We analyzed how much time of the tarsiers' activity budget was allocated to social activities and counted the number of social interactions during both mating seasons, i.e., when the animals were unfamiliar (2015) and when they were familiar (2016) to each other. In 2015 – the tarsiers spent 3.6% of their time budget on social activities (1,393 interactions recorded *ad libitum*), while in 2016 – 4.2% (1,115 interactions). No significant differences between both studied years either in the mean percentage of time devoted to social activities or in the total number of social interactions were found ($p = 0.42$ and $p = 0.07$, respectively).

During the first mating season, the predominant interaction was sexual then affiliative (56% vs. 25%), while during the second season – sexual and affiliative interactions were almost equal (40% vs. 44%). Agonistic interactions were the least performed behaviors in both studied years (18% and 16%, respectively). A statistically significant difference between the two studied seasons was found for sexual interactions (see Table 2).

Of all the social interactions that occurred in the first mating season, 65% were initiated by the male and only 35% by the female (the difference was found significant; $p = 0.000$); in the second season, this proportion was 70% vs. 30%, respectively ($p = 0.001$). Affiliative interactions were initiated slightly more often by the male than the female in both seasons (53% vs. 47%), of which allogrooming comprised ca. 96% of all affiliative interactions, while mutual display – ca. 4%. Sexual behaviors were initiated solely by the male (100%), while agonistic behaviors mostly by the female (97%): these occurred in a spatial context – when the male was approaching the female or in a sexual context – when the male performed sniffing or mounting, all of these forcing the male to retreat.

Table 2. The total proportion of time and the daily mean spent by the tarsiers on each type of social interactions in both mating seasons, standard deviation (SD), results of statistical tests (*p*-values) for the differences in occurrence of the types of behaviors in a given season, and *post-hoc* comparisons showing pairs of behaviors between which significant differences existed.

Interactions	Proportion %	Daily mean *N*	SD	*p-value*	difference
2015 ($N = 19$)				0.0005	1–2, 1–3
1. sexual	56.3	41.3*	29.2		
2. affiliative	25.3	18.6	13.5		
3. agonistic	18.4	13.5	10.6		
2016 ($N = 20$)				0.0000	1–3, 2–3
1. sexual	40.1	22.4	16.3		
2. affiliative	43.6	24.3	10.8		
3. agonistic	16.3	9.1	5.9		

* significant difference in the occurrence of tarsiers' sexual interactions on the days before and during copulations (days 1–9; $N = 65$), and after copulations (days 10–19; $N = 20$).

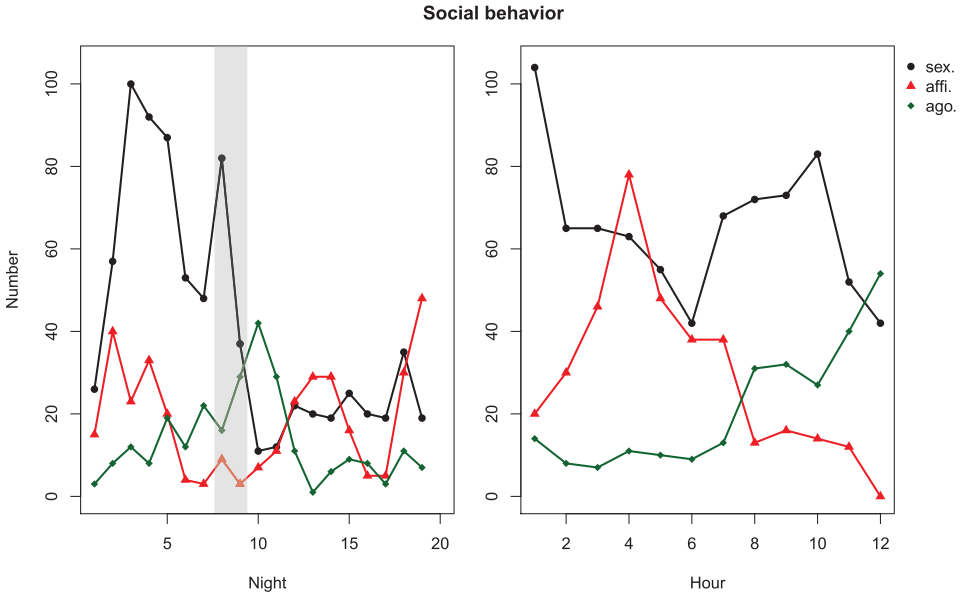


Figure 1. Nightly (N = 19) and mean hourly (N = 12) fluctuations in the number of social interactions for the reproducing pair of Philippine tarsiers (sex. – sexual, affi. – affiliative and ago. – agonistic) during the 2015 mating season. The gray bar indicates days of copulation occurrence.

We used the nightly (N = 19) and mean hourly (N = 12) time intervals to investigate possible changes/fluctuations in the tarsiers' types of social behavior. As the unmistakable copulation events were observed only during the first (2015) mating season, we have chosen here to show the results of this season only. The number of incidences of three types of social interactions during the above–mentioned time intervals are shown in Figure 1.

The number of sexual interactions fluctuated the most and were at peak levels over the first half of observations – until the ninth night. There was a significant difference in the occurrence of the tarsiers' sexual interactions between the days before and during 2015 copulations, and the days after copulations (mean: 65 vs. 20 interactions; p = 0.0004). Affiliative and agonistic interactions did not vary to as much an extent as sexual interactions, though peaks and dips were also observed. It is worth pointing out that the agonistic interactions reached the highest value on the 10th night when a concomitant drop for sexual interactions was observed (Figure 1). In terms of hourly fluctuations, sexual interactions were most frequently performed during the first and 10th hour of the night and were at the lowest levels in the sixth and the 12th hour. Affiliative interactions peaked in the fourth hour, while were at lowest levels at the end of the night when the agonistic interactions were at peak (Figure 1).

Copulatory behaviors

We witnessed two copulation events – both during the 2015 mating season. The first occurred on October 24 (eighth day of observation) at 5.30 PM just after the male had awoken and while the female was still resting, and lasted for 4:47 min. The second copulation event was observed on October 26 (ninth day of observations) at 5.49 PM, after the female had awoken, and lasted ca. 5.5 min. The two observed mating events happened on the same sleeping tree (one of the three preferred), which had oblique to steep branches. The animals slept separately on both days before copulation. In both cases, the male approached the female from the back, grasped her with his hands, positioning his legs on her, while thrusting dorsally. The number of thrusts could not be counted

owing to the limited visibility. When thrusting stopped, the male still clung to the female until she vocalized twice to reject him several seconds after.

The tarsiers exhibited many more sexual interactions prior to days of copulation than afterward – the number of these clearly decreased (and did not rise again) after the last copulation event. Then, for the following two nights, the female did not allow the male to approach her closely, and, as previously noted, her aggressive behavior was at its most intense (compare Figure 1). These nights she tolerated the proximity of the male less than during other nights, which she manifested by initiating more frequent attacks and wrestling (77% of all incidences of these interactions were observed during the 2015 season). These behaviors were more severe than the swipe and defensive pose, resulting, on the most serious occasions, in biting which would cause injury to the male. This reached a point where the observers considered separating the animals but the severity of aggressive behavior abated during the following days and the sexes continued being kept together until the end of observation period.

The date of the copulation events during the 2016 mating season is uncertain. Considering the time when the tarsiers exhibited the highest number of sexual interactions, copulation could have occurred on the sixth/seventh observation days – October 20/22 – before actual observations had begun (i.e., before 5.30 PM). Two offspring were born – one after the first mating season (on April 29 2016; on the following day the infant was found dead), and the other after the second season (between April 30 and May 1 2017, surviving). The cause of the first offspring death is not known. It was seen carried by the female after birth, and the camera traps installed at the enclosure did not register the new-born falling to the ground. It therefore cannot be ruled out that it died during birth.

Distance between individuals and sleeping patterns

In both mating seasons the tarsiers spent the greatest proportion of time (ca. 60%) at >2–7 m distance from each other (the maximum distance allowed for in the enclosure), and the smallest proportion of time (7%) in direct physical contact (0 m). The pair spent an additional 13% of the

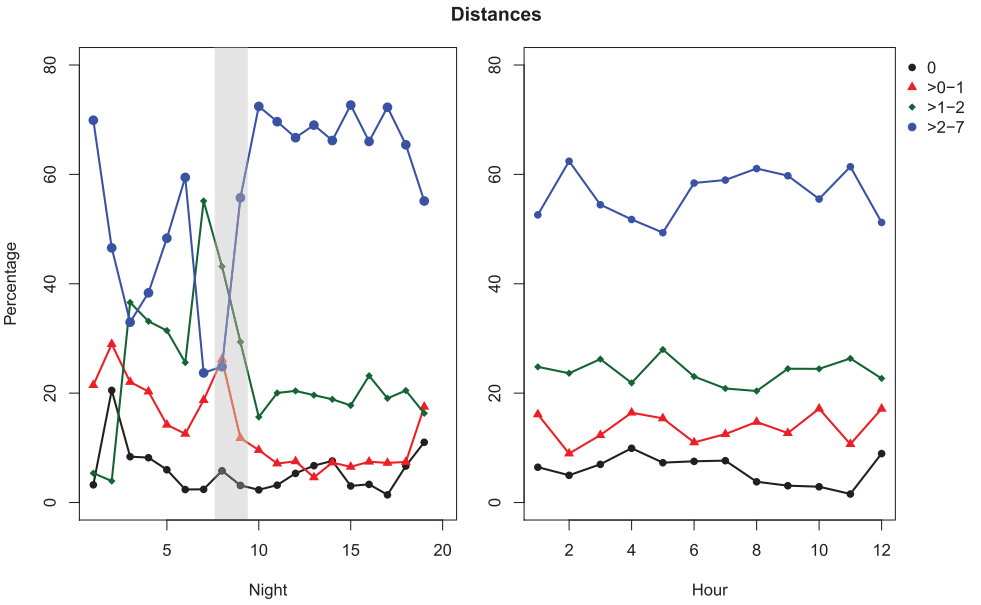


Figure 2. Nightly (N = 19) and mean hourly (N = 12) patterns of the distances [in %] (0 m, >0–1 m, >1–2 m, >2–7 m) spent apart from each other by the captive male and female Philippine tarsier pair during the 2015 mating season. The gray bar indicates days of copulation occurrence.

time in close proximity to each other (>0–1 m). There were no significant differences in particular proximities between the two seasons, except for one – spent at >1–2 m distance (2015: 24% vs. 2016: 16%; p= 0.01). The nightly and hourly fluctuations in the distance the tarsiers spent from each other during the 2015 observation period are presented in Figure 2.

Before and during the days of copulations (days 1–9), fluctuations in the distances were frequent and there were many peaks and dips in the amount of time spent closer together or farther apart. Starting from the next day after the last copulation until the end of the observation period (days 10–19), fluctuations became negligible and the time spent at particular distances remained at a stable level with most of the time spent at the maximal distance category. Interestingly, there were no hourly fluctuations in the distances the tarsiers spent from each other (Figure 2).

During the first mating season, the tarsiers slept together for 9 days (for 3 days at the beginning and for 6 days at the end of the observation period), and separately for 10 days (in-between those periods). During the second season, the tarsiers slept together for 7 days, while separately for 13 days; however, on three out of those 13 times, they slept nevertheless in a close (ca. 30 cm) distance to each other.

Vocalization

The tarsiers vocalized more often when paired than when kept alone – the male 33 times more often and the female twice more often. In both mating seasons the male emitted significantly more vocalizations than the female (2015: N = 1597 vs. N = 482; p = 0.000 and 2016: N = 1153 vs. N = 263; p = 0.02). The male vocalized significantly more often during the 2015 than the 2016 season (p = 0.01), while no significant difference in vocalizations between the seasons was observed for the female. No specific context for male vocalizations was recognized. The female vocalizations, on the other hand, were emitted mainly in an aggressive context and, in 94% of cases, were related to the male's activity – sexual or approach.

The nightly and hourly fluctuations in the number of vocalizations recorded *ad libitum* during the first mating season are presented in Figure 3. The female vocalized most often in the middle of the observation period (days 8–10), and the peak frequency of the female vocalizations coincided

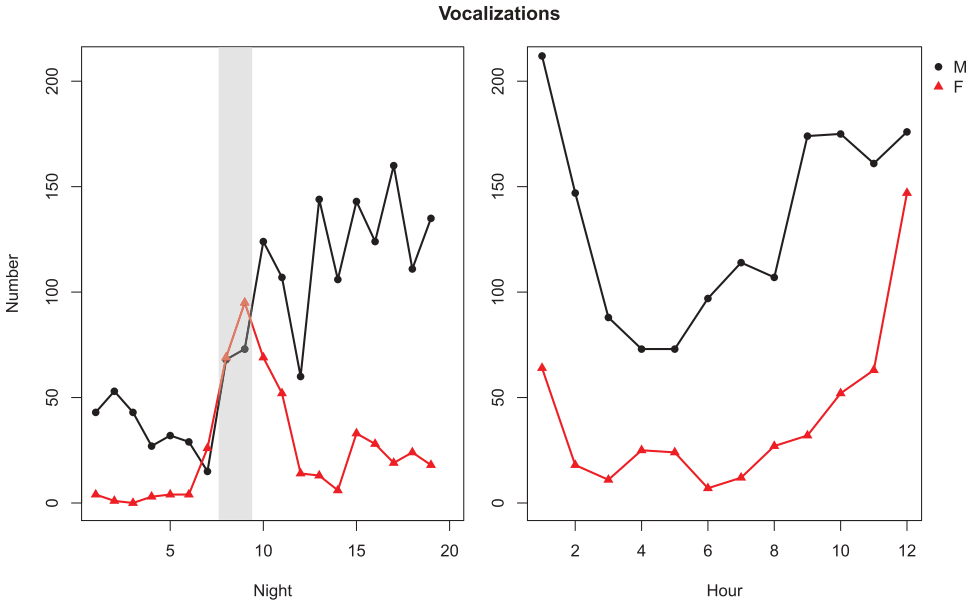


Figure 3. Nightly (N = 19) and mean hourly (N = 12) fluctuations in the number of incidences of vocalizations emitted by the male (M) and female (F) Philippine tarsiers during the 2015 mating season. The gray bar indicates days of copulation occurrence.

with days when copulations (and estrus) occurred. The male started emitting more vocalizations at the same time as the female but continued this up until the end of the observation period. Both sexes vocalized more often at the beginning (in the first hour) and at the end of the night.

Discussion

Sociality and social interactions

The reproducing pair of captive Philippine tarsiers did not allocate much of their overall awake time to social behavior (for activity budget see Wojciechowski et al., 2019). The results obtained that ca. 4% of the time budget during the mating seasons was allocated to social, including sexual, interactions – need to be interpreted cautiously, however since the pair were in captivity, and thus "forced" to be in close proximity to each other.

The social interactions of the Philippine tarsier over two mating seasons studied were mostly affiliative and sexual, with significantly more time allocated to sexual activity during the 2015 than the 2016 season, and somewhat, though insignificantly, more time allocated to affiliative than sexual interactions during the second season. We propose the following to account for this difference between the mating seasons: It may be that male Philippine tarsiers exhibit increased sexual interest toward a new, unfamiliar female. This behavior was cited by Evans and Poole (1983) for common marmoset (*Callithrix jacchus*). However, the sexual behavioral data for the tarsiers during the second mating season could also have been slightly underestimated, as on some days, the animals started their activity before observation had begun.

Allogrooming comprised most of the Philippine tarsier affiliative interactions, which was initiated with almost equal frequency by both sexes. The allogrooming activity may serve several functions: reduce ectoparasite-borne disease and improve hygiene (Clark, 1985; Wiens & Zitzmann, 2003), serve to establish and maintain social bonds (Ramanankirahina, Joly, & Zimmermann, 2011; Wolovich, Tapanes, & Evans, 2017), and play a role in mate-guarding strategy (Lewis, 2010). For our pair of captive tarsiers, as there were no grooming differences between the sexes and, as it was performed mainly on the unreachable parts – head and ears, so we suspect that it may primarily serve a hygienic function.

The proportion of time allocated to agonistic behavior observed in the Philippine tarsier was on average ca. 17%. Being captive may cause an increase in agonistic behaviors, as the means to prevent an escalation of conflicts are limited in the captive setting (Gartlan, 1968; Hosey, 1989; Radespiel & Zimmerman, 2001). Mild agonism, however, is widely observed in animals as a part of the courtship ritual (Lindburg & Fitch-Snyder, 1994), and was commonly observed for the captive pygmy loris (*N. pygmaeus*) (Fitch-Snyder & Jurke, 2003) and the two species of galago (*G. senegalensis* and *G. crassicaudatus*) (Welker & Welker, 1989). The studied female Philippine tarsier initiated the majority of the agonistic interactions and won all conflicts by forcing the male to retreat, which is associated with female dominance in the Strepsirhini species (e.g., Dammhahn & Kappeler, 2005; Kappeler, 1989; Ramanankirahina et al., 2011).

Female dominance and agonistic behavior may result from unintended meetings at the limited food resources (Schülke & Kappeler, 2003), ecological limitation, or as an instrument of active female mate choice (Radespiel & Zimmerman, 2001). We did not observe agonistic interactions in the feeding context in our study. The majority of the observed agonistic events resulted from the sexual activity of the male, like in the slender loris where males always submit to females, except for the copulation events when males do not retreat (Radhakrishna & Singh, 2002). Because of the captive Philippine tarsier affiliative interactions were performed equally by the opposite sexes, while agonistic interactions mainly by the female, we could not conclude that there was any clear-cut evidence of female dominance.

Copulatory behaviors

The copulatory behavior of the wild-caught captive western tarsier (Wright, Izard, & Simons, 1986a; Wright et al., 1986b) and spectral tarsier (Hidayatik, Yusuf, Agil, Iskandar, & Sajuthi, 2018a) is quite well documented. In the above-mentioned studies, copulations were observed once per estrus, which for the western tarsier species lasted 1–3 days. Copulatory behaviors can, apparently, be more complex in the wild – one spectral female tarsier was observed copulating once with one male and then, 11 days later, 3 times on the same day with a different male (Gursky, 2007).

During the 2015 season, the female Philippine tarsier was sexually receptive for 3 days, during which the individuals mated once per day (the copulation events were observed on the first and third day during her estrus). The Philippine tarsiers mated immediately after their activity began, while the other tarsier species mated later during their activity periods – yet still within/at the first hour, and, in case of the western tarsier, after ca. an hour-lasting courtship (Wright et al., 1986b). Duration of copulations for *T. syrichta* was ca. 5 min, while in other tarsier species this was shorter – in the western tarsier 1–2 min (Wright et al., 1986b), and in the spectral tarsier 3–4 min (Hidayatik et al., 2018a). In all tarsier species, copulations occurred in the vertical position. Hidayatik et al. (2018a) reported that for the spectral tarsier it was the females who vocalized during the copulation, but not so the males, while for the western tarsier, males signaled females with courtship calls before mating (Wright et al., 1986b). In our study, both male and female tarsiers emitted a few calls before the second (last) mating event and the female vocalized most during the whole estrus period.

The western tarsiers displayed interplay courtship behavior before copulation (Wright et al., 1986b); this comprised of a repeated sequence of the male approaching the female and her jumping away, which occurred every 10–15 min until female did not jump away and copulation started. The spectral tarsier females actively avoided the males, jumping away ca. 40 times more frequently after than before copulation, which, according to Hidayatik et al. (2018a), may be an indicator of the occurrence of copulation during estrus. The average number of agonistic behaviors for the Philippine tarsier female toward the male (rejecting him) happened only at a slightly lower rate before than after copulation. In the Philippine tarsiers, agonistic interactions were only increased for three consecutive days after the last copulation. In addition, the animals, in 2015 spent 1.5 times more time at further distances (>2–7 m) to each other after mating events than before them.

For the Philippine tarsiers, a rapid decline after the increased number of sexual interactions might indicate the end of the female's estrus: after the last copulation in the 2015 season, sexual interactions between male and female conspicuously declined and never raised again. The first offspring of our reproducing pair of captive Philippine tarsiers was born after 187–185 days of gestation (from copulations to birth). Other published gestation lengths are: for a captive western tarsier – 178 days (Izard et al., 1985), and for a wild spectral tarsier – ca. 195 days ($N = 4$) (Gursky, 2007). Only Hidayatik, Agil, Heistermann, Iskandar, Yusuf, & Sajuthi, (2018b) based on endocrine data gave much shorter, and inconsistent with other, gestation lengths for one captive spectral tarsier female – 128 and 131 days, while for a second female – 164 days.

Sleeping patterns

The tarsiers shared a sleeping site for about half of the study period (being either in a direct contact or near each other). In the semi-wild setting, Jachowski and Pizzaras (2005) also observed a group of the Philippine tarsiers (a female with a juvenile and another tarsier) on the same sleeping tree for a period of over 2 months. In contrast, in the wild, sharing a sleeping site is rare. Albeit that Rickart, Heaney, Heidman, and Utzurrum (1993) once reported hunters' observations from Leyte, that tarsiers were seen in pairs. According to Dagosto et al. (2001), only one out of four studied Philippine tarsiers was seen sharing a sleeping tree with another adult individual on 3 out of 8 nights, but no closer than 1 m from each other. On Bohol, the tarsiers were either observed to sleep solitarily (Neri-Arboleda et al., 2002), or, occasionally, in pairs (Řeháková, pers obs).

Several hypotheses for the communal sleeping pattern in Strepsirhini were proposed: thermoregulatory, reduction of predation risk, male mating strategy to control access to females, and limitation of high-quality sleeping sites (e.g., Kappeler, 1998; Radespiel, Cepok, Zietemann, & Zimmermann, 1998; Weidt et al., 2004; Schmid, as cited in Dammhahn & Kappeler, 2005). In our study, despite the availability of several potential sleeping sites in the enclosure, the tarsiers slept on only three trees of two genera, which may be indicative of their sleeping trees preferences (such preferences have been described for spectral tarsiers [Gursky, 2007]). A few agonistic interactions were also observed at the sleeping trees, which may be a sign of inter-individual (male-female) competition for the sleeping place on a tree.

Vocalization

In nocturnal prosimians, both sexes vocalize more intensely during the mating season (Zimmermann, 1995), as was the case in our study. The male tarsier emitted the majority of the vocalizations. The male vocalized more often during the first mating season, which could be attributed to being paired with the new female for the very first time and him expressing increased sexual interest toward her. Řeháková-Petrů et al. (2012) suspected that the most common tarsiers' vocalization – loud calls – may serve a territorial or mate attraction function. During our study, a wild Philippine tarsier, presumably male, had been approaching the enclosure vocalizing frequently, which might have caused competition between the males for the female. The female vocalizations were emitted mainly in an aggressive context and might have reflected the mate choice strategy. She also vocalized at an increased rate during the time of her receptivity, which might be interpreted as a form of signaling of her reproductive status. Both the Philippine tarsier individuals vocalized the most during the first and the last hour/hours of the night, which agrees with the pattern observed in the wild (Řeháková-Petrů et al., 2012), where the Philippine tarsiers exhibited peaks of acoustic activity around sunset and sunrise.

Husbandry and welfare implications

Species-specific housing and husbandry practices allowing an optimal level of animal contact and performance of natural behavior related to sexual reproduction such as courtship and mating are crucial in captive management (Farmer, Plowman, & Leaver, 2011; Swaisgood & Schulte, 2010). Welker and Welker (1989) remarked that pairs of some nocturnal primates that either do not get on well together or are supposedly compatible may not breed. Excessive aggression or stress could compromise the well-being and affect reproduction. Separation of compatible pairs for several months before being brought together again during the female's fertile periods has been then suggested (Swaisgood & Schulte, 2010; Welker & Welker, 1989). For species of the Callitrichidae, on the other hand, it was suggested that young females be paired with sexually experienced adult males to improve their chances of successful breeding (Evans & Poole, 1983).

We paired the male and the female tarsier for only a few weeks during their mating season (Philippine tarsiers are once-a-year seasonal breeders [Wright, Pochron, Haring, & Simons, 2003]) after which they were separated for the rest of the year until the next mating season. The separation after mating seemed important in order to eliminate all possible factors that could cause failure of the breeding, such as aggression and associated stress during the female pregnancies, and also to avoid the possibility of the male harassing the infants, as was observed in the western and eastern tarsier species (Roberts, 1994; Severn, Dahang, & Shekelle, 2008). Separation resulted in successful breeding, and thus seems to be a suitable housing method for the species.

The female gave birth after both mating seasons with the second offspring surviving, indicating that despite some observed agonism welfare was not compromised and that agonism may be a natural element of courtship. Surviving the critical period after birth and beyond the first few months of life was a significant success, as this is the time of very high infant mortality, not only

in captivity (Roberts, 1994; Roberts & Kohn, 1993) but also in the wild (Gursky, 2007). In the first mating season (animals unfamiliar to each other) some associations between behaviors and the time of female receptivity were found: increased rate of female vocalization and increased distances between the individuals, while decreased number of sexual interactions after copulations. We suggest that these indicators may be used to determine the time of receptivity and the time at which copulation occurs (if not actually observed).

The sleeping association of the captive Philippine tarsiers and the occurrence of some agonistic interactions on the sleeping sites may be due to the limited number of preferred sleeping trees. As the tarsier pair used only two tree genera (*Swietenia* sp. and *Tabernamontana* sp.) for this purpose, we recommend special attention be paid to their quantity and arrangement when designing and maintaining the enclosure for the mating of the tarsiers.

Conclusions

We have described the social interactions for a reproducing pair of the Philippine tarsier during their mating season. Despite the small sample size, our results are the first data on the social behavior of the species in captivity, information which would otherwise be difficult to gather in the wild. We were able to demonstrate what proportion of the tarsier activity budget was constituted by social interactions, and, of these, that sexual and affiliative interactions prevailed. Analysis of sexual interactions and, to some extent, the distance between the individuals might be useful in estimating the time of copulation occurrence. We also witnessed the growth and development of an offspring that survived the critical period around birth and within the first few months of life. We suggest the results presented be taken into account to improve husbandry practices for the Philippine tarsier if we are to successfully breed this threatened species in captivity.

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Author contributions

FJW and MŘ designed the experiments; FJW collected the data; FJW and KAK analyzed the data, wrote the paper, and revised the text; MŘ submitted comments.

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VIII. MANUSCRIPT 3:

Utilizing local community knowledge of the Philippine tarsier in assessing the Bilar population endangerment risk, and implications for conservation.

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Name of author	WOJCIECHOWSKI FILIP J. https://orcid.org/0000-0002-3598-9109
Affiliation	• Institute of Human Biology and Evolution, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland • Wings of Serenity Inc., Tagbilaran City, 6300 Bohol, Philippines
Contribution	• Obtained funds; • Conceived the project; • Conducted fieldwork; • Analysed the data; • Wrote the paper.
Contribution %	**70%**
Date and signature	19.06.2021 .....

Name of author	KASZYCKA KATARZYNA A. https://orcid.org/0000-0003-1348-1037
Affiliation	• Institute of Human Biology and Evolution, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland
Contribution	• Conceived the project; • Performed statistical analyses; • Analysed the data; • Provided comments and editorial advice (review and editing).
Date and signature	1.06.2021 .....

Name of author	OTADOY JULIE B.
Affiliation	• University of San Carlos Biology Department, Arnoldus Science Complex, Talamban Campus, Nasipit, Cebu City 6000, Philippines
Contribution	• Conducted fieldwork
Date and signature	22.06.2021 .....

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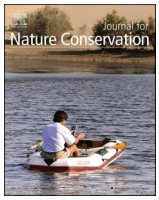

Utilizing local community knowledge of the Philippine tarsier in assessing the Bilar population endangerment risk, and implications for conservation

Filip J. Wojciechowski [a,b,*], Katarzyna A. Kaszycka [a], Julie B. Otadoy [c]

[a] Institute of Human Biology and Evolution, Adam Mickiewicz University, Poznań, Poland
[b] Wings of Serenity Inc., City of Tagbilaran, Bohol, Philippines
[c] University of San Carlos Biology Department, Cebu City, Cebu, Philippines

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ABSTRACT

Investigating the local people's perception of the primate species in question, as well as the impressions of and experiences with conservation measures in their neighbourhood, is important in order to devise an appropriate conservation strategy. Here, we provide our findings on the knowledge of the Bilar local community about the Philippine tarsier (*Tarsius* [*Carlito*] *syrichta*) and its population endangerment risk. From October 2016 to November 2017 we conducted interviews with 325 residents from five villages in Bilar, Bohol Island, the Philippines. Tarsiers, though correctly recognized as such by the majority of interviewees, were infrequently sighted in the area, mainly by men, local resource suppliers and villagers in forested areas. Despite a high general knowledge of the species, its ecology and conservation are less well known, with word-of-mouth and personal experience being important sources of information. The species is generally not perceived by locals as endangered, and positive conservation attitudes prevail. Nevertheless, hunting in the area is widespread, and tarsiers are captured either for sale, to be kept as pets or trafficked to tourist facilities or foreigners. The Philippine tarsier, as a charismatic animal, has the potential to be an effective 'flagship species' for promoting conservation efforts. To strengthen the species' conservation, we recommend involving forest resources suppliers in research activities and wildlife tour services, continuing teacher training to ensure that school education emphasizes the ecological and aesthetic values of the Philippine tarsiers, and enhancing the image of this primate, particularly in the digital context, to improve tarsier welfare in captivity.

1. Introduction

The recent statistics of the IUCN Red List of Threatened Species (2020) showed that ca. 65 % of all primate species are threatened with extinction. Simultaneously, 75 % of primate species populations around the world are decreasing (Estrada et al., 2017). This crisis is the result of unsustainable human practices and is driven by two major causes, i.e., habitat shrinkage (agriculture, logging and harvesting, livestock farming and ranching) and direct loss of animals (hunting and trapping) (Estrada et al., 2017). These threats usually occur in tandem and primate conservation is best achieved when multiple approaches are applied. At the same time, the world's human population is increasing (it is estimated to have reached almost 7.8 billion people as of March 2020 [*Worldometers*, 2020]), especially in lower income countries, leading to the niche overlap of non-human and human primates. It is, therefore, crucial to include human needs and concerns into the development of a conservation strategy. Local communities share the ecosystem with wildlife, interact with it and bear the costs of its protection, therefore their incorporation in decision-making processes and evidence-based management is important (Kansky & Knight, 2014; Nepal, 2002). It is even recognized that local people better manage the resources they have been surrounded by for generations than "fortress conservation" and top-down approaches imposed on local communities without consulting and incorporating them, which may lead to even further biodiversity loss (Domínguez & Luoma, 2020; Kamoto, Clarkson, Dorward, & Shepherd, 2013). Studies reveal a link between the success of the wildlife conservation projects and the supportive participation of local communities (Fiallo & Jacobson, 1995; Heinen, 1993; Parry & Campbell, 1992).

Understanding the factors which influence the extent of local participation and attitudes towards management in already existing protected areas is of utmost importance (Alexander, 2000; Gillingham &

* Corresponding author at: Institute of Human Biology and Evolution, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614, Poznań, Poland.
E-mail address: philip.wojciechowski@gmail.com (F.J. Wojciechowski).

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Lee, 1999; Sekhar, 2003). Local people's perceptions and experiences with conservation measures in their vicinity is one aspect for consideration, but assessment of their perception of the primate species in question is of equal importance in devising an appropriate conservation strategy. Such information can be obtained via the field of ethnoprimatology, which Fuentes (2012) defines as: "theoretically and methodically interdisciplinary study of the multifarious interactions and interfaces between humans and other primates" (p. 102). McKinney and Dore (2017), however, frame this more broadly, to involve any research focused on the human-primate interface itself, regardless of whether social, biological, or both sciences are applied.

Ethnoprimatology is built on the notion that humans and other primates live in integrated and shared ecological and social spaces, which they co-shape, thus anthropological approaches must be incorporated in behavioural, ecological and conservation studies on non-human primates (Fuentes & Hockings, 2010; Lee, 2010; Malone et al., 2014). Since the term was first introduced (Sponsel, 1997), its theoretical consideration and practical use have grown and it is recognised for having an important role in primatological research (see Fuentes, 2012). Even though the assessment of human attitudes towards, perceptions of, or beliefs about primates until 2016 were subject of 21 % papers overall, more work needs to be carried out and published to incorporate the human dimension in primate conservation (McKinney & Dore, 2017; McLennan, Spagnoletti, & Hockings, 2017). These studies have shown that the knowledge and perception of local people vary across the globe and various factors come into play in shaping these. Some of the most important variables are sex/gender (Ellwanger, Riley, Niu, & Tan, 2015; Torres Junior, Valença-Montenegro, & Castro, 2016; Xu, Chen, Lu, & Fu, 2006), age (Nekaris, Boulton, & Nijman, 2013; Sousa, Vicente, Gippoliti, Casanova, & Sousa, 2014), socioeconomic profile (Gillingham & Lee, 1999), proximity to wild areas and encounter rate with animals (Reibelt et al., 2017; Sousa et al., 2014), length of residency in the area (Riley, 2013; Torres Junior et al., 2016), level of education (Liu, Ouyang, & Miao, 2010; Nekaris, Boulton et al., 2013), and prevailing beliefs and taboos in the area (Etiendem, Hens, & Pereboom, 2011; Jones, Andriamarovololona, & Hockley, 2008). Knowing what underlies the perception of local people in the area of interest is important for both determining conservation measures and identifying crucial stakeholders to be involved.

The Philippines, with its over seven thousand islands, is considered as one of the "hottest biodiversity hotspots" based on the numbers of endemics, endemic species/area ratios, and habitat loss (Ambal et al., 2012; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). The country is home to at least 214 mammal species with 58 % of them endemic (Heaney et al., 2010). One of these is the Philippine tarsier (*Tarsius* [*Carlito*] *syrichta*), a small primate inhabiting the young secondary lowland rainforest on several islands of Mindanao, Samar, Leyte, Bohol, Dinagat, Siargao, Basilan, Biliran, and Maripipi (Gursky-Doyen, Salibay, & Cuevas, 2011; Neri-Arboleda, 2010; Neri-Arboleda, Stott, & Arboleda, 2002). The Philippine tarsier is one of the main tourist attractions in Bohol, with almost every advertisement for the island incorporating mention of this primate. At the time of the study two establishments in Bohol were legally permitted to display tarsiers: the "Philippine Tarsier and Wildlife Sanctuary" of Corella and the "Bohol Tarsier Conservation Area" in Villa Aurora, Bilar. After the completion of the survey, a third establishment in Bilar was opened (Burlace, pers. comm.).

The Philippine tarsier is not adequately understood in terms of taxonomy, ecology and conservation status owing to its nocturnality, small body size and the difficult habitat it occupies. Its IUCN Red List categorization has changed a number of times: from Endangered (EN), through Lower Risk/ Conservation Dependent (LR/CD), Data Deficient (DD), to its current Near Threatened (NT) status, last assessed in November 2015 (Shekelle, 2020). More recently Gursky, Salibay, Grow, and Fields (2017) suggested that their conservation status should be changed to Vulnerable (VU), based on population size reduction and density fluctuation of the Philippine tarsiers in Corella. Finally, in the updated "National list of threatened Philippine fauna and their categories", it is listed as Other Threatened Species (OTS) – i.e., under threat from adverse factors, such as, e.g., over collection throughout its range (DENR, 2019), and its acquiring and possession without a permit is punishable under Republic Act No. 9147 (2001). These different threat categories clearly highlight the lack of knowledge of the species and the need for further scientific investigation. The main threats to the Philippine tarsiers are deforestation (habitat loss), hunting for the illegal pet trade, as well as natural disasters, such as typhoons (Shekelle, 2020; Shekelle, Gursky, Merker, & Ong, 2015; Wright, Simons, & Gursky, 2003). The situation is exacerbated by the difficulty of tarsier breeding and thus the non-existence of long-term captive populations (Fitch-Snyder, 2003). Immediate action needs to be taken and the following areas were suggested: taxonomy clarification of the Philippine tarsier; assessment of suitability of non-forest habitats to sustain tarsier populations; impact evaluation of catastrophic disturbances on the extinction risk of tarsiers and the development of a means to enhance the position of tarsiers as a 'flagship species' for conservation (Shekelle et al., 2015). There has only been one ethnoprimatological fieldwork study which provided qualitative data on the cultural status of the Philippine tarsier among the residents of the town of Corella, and its shift from "an *inconsequential* species to an *important* animal" (Aure & Escabi-Ruiz, 2005: 92). However, there have not been quantitative accounts of the knowledge of the species and perceptions of its conservation among local communities.

In this study we aimed to increase our knowledge of conservation of the Philippine tarsier in Bohol by better understanding its use as an effective 'flagship species' among the local community. Our specific goals were to investigate the knowledge of this primate in the local community, attitudes towards its conservation and the variables responsible for shaping them, as well as the most suitable channels for knowledge transmission regarding the species. Based on the endangerment risks to the tarsier population in Bilar emerging from the results, our final objective was to formulate recommendations for the planning of a tarsier species conservation strategy in the area.

2. Material and methods

2.1. Study area

The research was conducted in Bilar Municipality of Bohol Island in the Philippines (9°40′–9°45′ N and 124°03′–124°11′ E), approximately 40 km from the island's capital – City of Tagbilaran, in the vicinity of two conservation areas: the Rajah Sikatuna Protected Landscape and the Loboc River Watershed Forest Reserve (Fig. 1). The total municipality land area is 129.71 km^2 and inhabited by ca. 17,590 people scattered across 19 villages (*Philippine Statistics Authority*, 2015). The municipality's landscape comprises of a mixture of distinctive flat rural areas near human settlements, used as rice fields and plantations for various crops, steep karst hills covered by brush and secondary forest, and primary rainforest in protected areas (Bogdan, Jůnek, & Jůnková Vymyslická, 2016).

This study was conducted as a research project of the Subayon Conservation Center for the Philippine tarsier (located in Subayon [Fig. 1c] and operational between 2014 and 2019). It was purely a research centre, not open to visitors, or promoted locally. Its focus had been behavioural research on captive Philippine tarsier (Wojciechowski, Kaszycka, Wielbas, & Řeháková, 2019; Wojciechowski, Kaszycka, & Řeháková, 2020) and the improvement of the guidelines for the husbandry of the species, as well as community environmental outreach. The staff of the Subayon Conservation Center conducted several environmental education programs at local schools at all levels engaging tens of pupils as well as teachers. The project was carried out by Wings of Serenity Inc., a local non-profit conservation organization (of which FJW was a member), which also established the Habitat Bohol

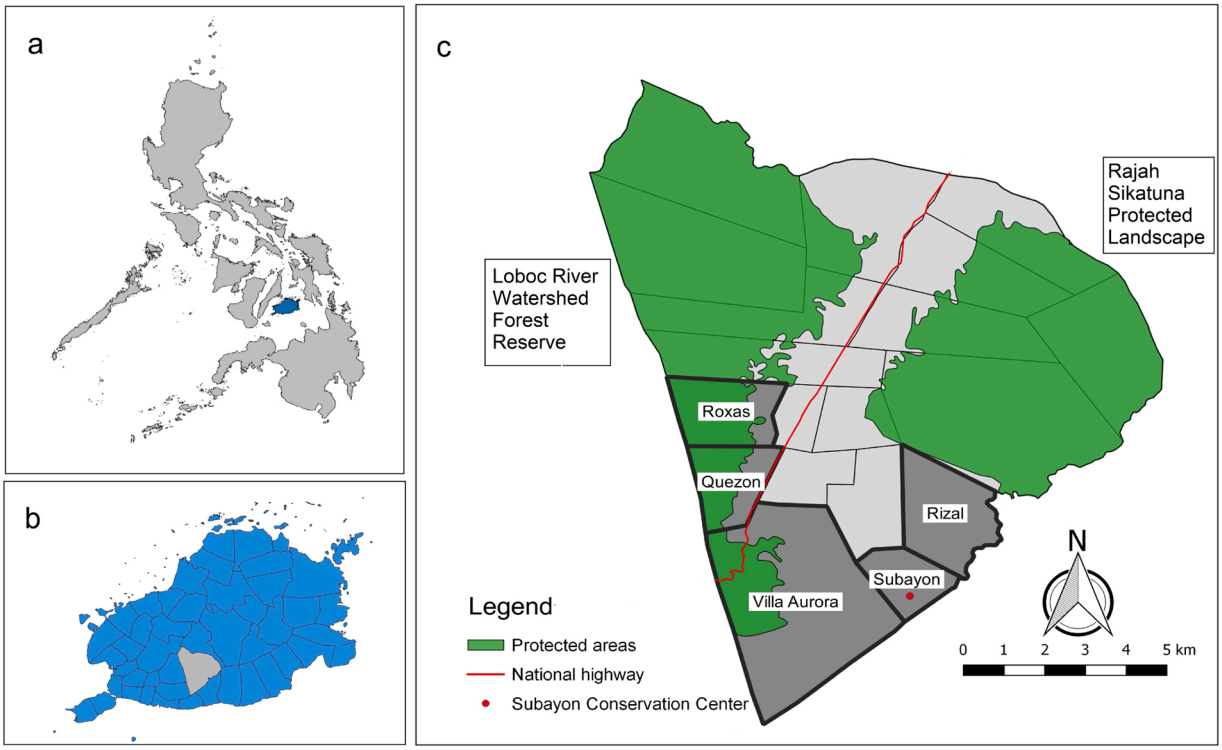

Fig. 1. Overview maps showing the location of the study area: (a) national – Bohol Island on map of Philippines, (b) regional – Bilar municipality on map of Bohol, and (c) local – villages, surveyed between the period October 2016 – November 2017, on map of Bilar.

Conservation Center, a butterfly garden and tourist centre in Bilar, Bohol. Habitat Bohol was one of the biggest employers in Bilar and initiator of livelihood projects, mainly handcrafting, to local women. It was also the first to run "Night Safaris" on Bohol, where tourists could view the wildlife of the Philippines tracked by former hunters who were trained to lead the tours. The residents of Bilar associated the Subayon Conservation Center with Habitat Bohol, therefore it unlikely that they realised that the interviewers might be key stakeholders in tarsier conservation, increasing the reliability of the data collected.

2.2. Data collection

Studies were conducted among the local people of five villages: Rizal, Subayon, Villa Aurora, Quezon, and Roxas (Fig. 1, Table 1) during October 2016 to November 2017 using interviewer-administered questionnaires. These included a mixture of fixed-response and open-ended questions, the content of which is given in the Appendix (Supplementary data). In total, we surveyed 325 persons, on average 32.7 % of households per village (SD = 6.46; SE = 2.89). Selection of participating households was done by random sampling, and, where circumstances permitted, two persons per household were interviewed (23 % of such households). We chose the villages based on proximity to the Subayon Conservation Center of the Philippine tarsier, the terrain, locality relative to the forest, and size of their human populations. Two of the villages (Subayon and Roxas) lie almost entirely within the forest, whereas the remaining three are located in areas only adjacent to the forest patches.

To compare differences in the knowledge of the local people, we surveyed two groups of respondents. The first of these were local "resources suppliers", i.e., people who visit the forest regularly to gather natural resources for income, such as hunters, honey collectors or any other forest resource gatherers. Respondents within this group were assembled in consultation with village captains and informal conversations with local communities. All other villagers – "other residents" who do not visit the forest to gather its resources for financial purposes constituted the second group of interviewees. All respondents were ≥18 years old.

The interviews were conducted in the local language – Visayan, as translated from the English. The survey was carried out by two of the current authors (FJW, working at the time at the Subayon Conservation Center and locally known in the village and the municipality, and JBO, a university lecturer from the nearby Cebu Island proficient in the Visayan language) and a local research assistant (born and living locally in Subayon). We tested the structure of the interview, as well as participants' understanding of the questions, in a preliminary survey in May 2016 in Subayon village with 15 participants prior to the actual data collection. (The data from the preliminary survey was not included in the final data set). Upon introduction, we began interviews by asking interviewees about their demographic variables (i.e., age, sex, religion, education level, occupation, years spent at the village, and the frequency

Table 1
Population characteristics, number of households and respondents interviewed in each village selected for this study (Bilar, Bohol, Oct 2016 – Nov 2017).

Village	Location	Population Size	Households	Respondents- total	Resources suppliers	Other residents
Subayon	Forest	1303	300	93	15	78
Roxas	Forest	1159	233	75	15	60
Villa Aurora	Non-forest	737	124	58	15	43
Quezon	Non-forest	618	128	52	12	40
Rizal	Non-forest	425	90	47	15	32
Total		4242	875	325	72	253

of visits to the forest). Once the participant demographic variables were noted, the interviewer showed pictures and played vocalization recordings of a few animal species to the respondents in order to assess their recognition rate for the Philippine tarsiers. Four images of animals present in Bilar were shown on a rotating basis: the Philippine tarsier, Philippine colugo (*Cynocephalus volans*), Philippine long-tailed macaque (*Macaca fascicularis philippensis*) and Asian palm civet (*Paradoxurus hermaphroditus*), mixed with two decoy species occurring in the Philippines, but not in Bohol: the Mindanao tree shrew (*Tupaia everetti*) and Philippine slow loris (*Nycticebus menagensis*). The vocalization recordings to be identified were of four animals present in the area (loud call and chirp of the Philippine tarsier, Everett's scops owl [*Otus everetti*] and cricket [*Gryllus* sp.]).

The main part of the questionnaire followed with a mix of 20 closed and open-ended questions (see Appendix in Supplementary data). This comprised of three themes: (1) Sightings of Philippine tarsiers in the area and knowledge of the species, (2) Attitude towards conservation of the species, and (3) Species exploitation. At the end of the interview, the respondents could ask interviewers additional questions about the research and carry on an informal conversation. We did not provide incentives for participation in the survey.

2.3. Ethical statement

The methods employed in this research complied with ethical standards as specified by University of San Carlos Biology Department, Philippines. We obtained prior verbal informed consents from the Barangay Captains of all the study villages, and then informed consents from all the participants. We familiarized the participants with the topic, objectives, and procedures of the study, dispelled any doubts on our alleged ties with governmental offices, allowed them to withdraw anytime they wished and/or decline to answer any question they felt uncomfortable with, maintained anonymity and confidentiality.

2.4. Data analysis

We used descriptive statistics to analyze the survey participant characteristics. The remaining results are shown as response frequencies for the entire sample and, where necessary, categories based on the respondents' answers were created. The interviewees were permitted multiple responses on the question pertaining to channels for knowledge transmission (these results are presented as the percentage of respondents giving each response).

To examine whether there was a relationship between demographic variables (i.e., sex, age, level of education, occupation, respondents' profile, residency relative to the forest, frequency of forest visits) and the respondent's answers, we employed the Chi-square test of independence (χ^2). We created three generational age categories: young generation (20–39 years), middle-aged people (40–59 years), and older generation (>60 years), also taking into account active employment age, the number of respondents, and past opportunities for education. Respondent occupation was divided into four categories: (1) farmers, (2) physical labourers and basic services (carpenters, drivers, daily helpers, gardeners) (3) professionals (government employees, teachers, company-employed), and (4) non-employed (housewives and job seekers). We analysed data using *Statistica* 11 software package (Statsoft Inc.) and Microsoft Excel. For all tests, $P < 0.05$ (two-tailed) was taken as statistically significant.

2.5. Data availability

The data collected and analyzed in the current study is available from the corresponding author upon reasonable request. The questionnaire used in the study (Appendix Supplementary data) is available online in the supplementary material.

3. Results

3.1. Socio-demographic profile

Of the 325 interviewees, 185 (57 %) were males and 140 (43 %) females. Their ages ranged from 20 to 89 years, with a mean of 50 years. Nearly half of the survey participants were middle-aged – 40–59 years (46.5 %, $N = 151$), followed by 60–89 years old group – mostly retired (27.7 %), and the youngest generation – 20–39 years old (25.8 %). The youngest respondents were the least encountered, because many of them study or work in cities and were not present during the data collection. Among the villagers interviewed, 11 % (37 respondents) had completed only the first three years of education (primary school), approximately half – all years of elementary school (49 %, $N = 160$), one-third had graduated from high school (31 %, $N = 101$), while those who had completed higher education amounted to only 8% ($N = 27$).

The majority of the villagers declared themselves as farmers (34 %, $N = 111$), unemployed (34 %, $N = 109$), or engaged in physical labour and basic services (25 %, $N = 82$), whereas a minority claimed to be professionals (7%, $N = 23$). Most local people were Roman Catholics (97 %, $N = 314$), and the remaining 3% ($N = 11$) Protestants. The vast proportion of the interviewees were local, i.e., born and living in a village for their entire life (88 %, $N = 287$), with only 12 % ($N = 38$) being immigrants. The majority of Bilar residents visited the forest either often, i.e., a few times a week (45 %, $N = 147$), or every day (36 %, $N = 116$), while the minority visited wild areas rarely – i.e., a few times a month or less (19 %, $N = 62$).

3.2. Recognition of local species

Of all the animal images shown to the respondents, the Philippine long-tailed macaque was identified by all but two, and the Philippine tarsier by 98 %. The other local species were less often recognised – the Philippine colugo in 74 % of cases, and the Asian palm civet cat in 50 %. Most of the Bilar residents correctly identified the decoy species as not being present in the area: 83 % in the case of the Philippine slow loris and 54 % for the Mindanao tree shrew. Respondents were less familiar with animal vocalizations than the images. The cricket sound was correctly identified by 60 % of the interviewees and the Everett's scops owl's by 41 %. Tarsier vocalizations turned out to be very difficult for the local people to recognize, with the loud call correctly identified by 23 %, while the chirp by only 1%.

3.3. Encountering tarsiers in the area and knowledge of the species

Overall, 45 % of all respondents either saw or heard the Philippine tarsiers in the area. We found statistically significant relationships between:

- The respondents' profile and their answers, with more local resource suppliers answering in the affirmative (63 % yes : 38 % no) than non-suppliers (40 % yes : 60 % no) ($\chi^2 = 11.14$, df = 1; $P = 0.0009$);
- Respondents' residency and their answers, with more residents from forest villages answering in the affirmative (55 % yes : 45 % no) than those living in non-forested villages (34 % yes : 66 % no) ($\chi^2 = 14.52$, df = 1; $P < 0.001$); and
- Respondents' sex and their answers, with more males answering in the affirmative (57 % yes : 43 % no) than females (30 % yes : 70 % no) ($\chi^2 = 23.47$, df = 1; $P < 0.001$).

In addition, we found a statistically significant relationship between the respondents' occupation and their answers ($\chi^2 = 20.49$, df = 3; $P<0.001$), where farmers and people engaged in physical labour & basic services stated that they had seen and/or heard tarsiers in the area, more often than professionals and unemployed.

Most of the respondents (81 %) knew the tarsier's diet, and correctly

identified it as an insect and/or spider eater. The rest of the interviewees incorrectly pointed to fruits (15 %) and charcoal (3%), while one mentioned crops. Despite the high number of correct answers, when we asked interviewees to elaborate further on the specific insects tarsiers ate, only 59 % could provide an answer and all but two of these claimed this to be crickets only. The rest of the answers were: worms (10 %), katydids (4%), meat (3%), grasshoppers (3%), prey mantis (1%) and cockroaches, house lizards, dragonflies and mice (each mentioned once). We found statistically significant relationships between:

- Respondents' sex and their answers about tarsier diet, where there were more knowledgeable males (92 %) than females (65 %) ($\chi^2 = 36.80$, df = 1; $P < 0.001$); and
- Respondents' profile and their answers, with local resource suppliers being more familiar with what tarsiers feed on (99 %) than all other respondents (76 %) ($\chi^2 = 26.40$, df = 1; $P < 0.001$).

We also found statistically significant relationships between:

- Responses and interviewees' age ($\chi^2 = 6.24$, df = 2; $P = 0.04$) and
- Responses and interviewees' occupation ($\chi^2 = 26.91$, df = 3; $P < 0.001$).

Respondents knowledge of the tarsier's diet decreased with age, with the youngest villagers knowing more than the oldest, and those engaged in any income-generating activities having greater knowledge than the unemployed who spend most of their time at home.

A great majority of the respondents (90 %) stated that they had never seen Philippine tarsiers in their neighbourhood, whereas the remaining 10 % observed them on some occasions (a few times a month to a few times a year). Residents of the forested villages, however, encountered tarsiers significantly more often (18 % yes : 82 % no) than the inhabitants of non-forested areas (2% yes : 98 % no) ($\chi^2 = 14.52$; df = 1; $P < 0.001$). The majority (99 %) of all the respondents gave the correct, or a partially correct answer regarding the occurrence of the Philippine tarsier. Yet, as many as 97 % of the interviewees stated the species occurring nowhere else other than in Bohol, and none of the survey participants could mention all of the islands inhabited by the species. A minority of the interviewees (6%) said that they had seen or heard about tarsiers being the prey of another animal. The predators mentioned were snakes ($N = 11$) or cats ($N = 10$), with one villager mentioning both, while another stated it was the civet cat.

Local people's knowledge of the Philippine tarsier had come from several sources (Fig. 2). The most important knowledge source mentioned by interviewees was family and friends (37 %), followed by the media (34 %) and school (29 %). Training and seminars were mentioned least often (16 %), as also the category "others" (13 %), which included the knowledge gained by the local people themselves (e.g., through forest visits) or via tourist facilities.

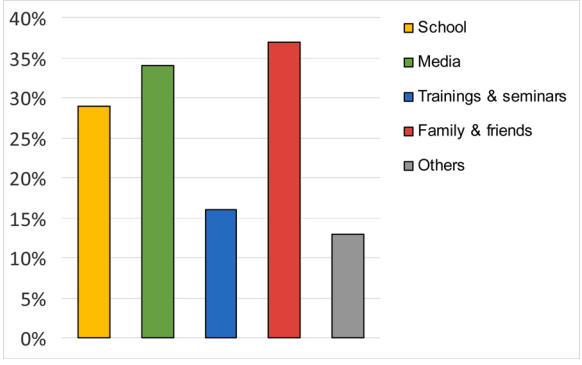

Fig. 2. Tarsier knowledge transmission channels for local people in Bilar, Bohol ($N = 325$) (Oct 2016 to Nov 2017 study). Multiple-choice question, where 42 % of respondents chose one answer only, while the rest, more than one.

3.4. Attitudes towards tarsier conservation

The majority of all respondents (87 %) stated that they found the Philippine tarsier useful – males significantly more so than females (91 % vs. 81 %, respectively) ($\chi^2 = 5.47$; df = 1; $P = 0.02$), with its usefulness justified by economic reasons, followed by ecological and aesthetic (Table 2).

Regarding the opinion on the number of tarsiers in the area over the past 10 years, more than half of interviewees (57 %, $N = 186$) believed their numbers had increased, about one-third (31 %, $N = 102$) thought it had stayed the same, while a minority (11 %, $N = 35$) stated it had decreased (2 villagers did not answer). Of the respondents stating an increased population, 164 supported their answer by saying, among others: "they keep breeding" (74 %), followed by "they are protected" (12 %). A population decline, on the other hand, was declared by 27 people, stating as their reasons: "they are captured by people" (44 %), "I have not seen them recently/ there are not so many of them" (41 %), followed by "they die in tourist facilities from stress" (7%), and the "forest is being depleted/they are being eaten by snakes" (7%).

The vast majority of the local Bilar residents (89 %) did not consider the Philippine tarsier as endangered. The reasons for this given by 94 out of 290 interviewees were: "they keep breeding/ they do not decrease in numbers" (40 %), "the species is protected" (27 %), and "there are many of them here" (23 %). Nonetheless, 97 % of respondents ($N = 312$) believed the species should be protected and many ($N = 260$) justified their answers. Among the reasons given for supporting the protection of tarsiers compassion/concern was pre-eminent, followed by economic, ecological and aesthetic (Table 3).

3.5. Species exploitation

There were no reports of traditionally held beliefs related to tarsiers in the area, although two respondents recited the view that "tarsiers always go together at night". None of the interviewees knew whether tarsiers were being eaten or used for any other purpose, such as for medicines or aphrodisiacs. Over half of all the respondents affirmed they had seen (54 %), and a similar number (53 %) that they had heard about, people hunting the Philippine tarsiers. When such sightings and hearing were taken together as a joint category (seen and heard about), the number of respondents who knew about the presence of the hunters increased to 62 %. Only a minority of Bilar interviewees (17 %) stated they had captured tarsiers themselves. Those who had seen or heard about the hunters, or had hunted the animals themselves, were significantly more often local resource suppliers and men (Table 4).

Table 2
Reasons given by the local people in Bilar, Bohol ($N = 257$) (Oct 2016 – Nov 2017 study) for why the Philippine tarsier is a useful species.

Justification	No. of mentions	%
Economic	**213**	**82.8**
- tourist attraction	198	77.0
- sellable	15	5.8
Ecological	**27**	**10.5**
- eats insects	16	6.2
- helps to balance the ecosystem	10	3.9
- pollinator	1	0.4
Aesthetic	**10**	**3.9**
- enjoyable/ nice to see	7	2.7
- God's gift	1	0.4
- treasure at the forest	1	0.4
- only seen in Bohol	1	0.4
Other	**7**	**2.8**
- good as pet	4	1.6
- endangered species	1	0.4
- doesn't bite	1	0.4
- doesn't destroy plants	1	0.4

Table 3
Reasons given by the local people in Bilar, Bohol ($N = 260$) (Oct 2016 – Nov 2017 study) for why the Philippine tarsier should be protected.

Justification	No. of mentions	%
Compassion/concern	**177**	**68.1**
- so they do not decrease in numbers	168	64.6
- we should protect all wild animals in the forest	5	1.9
- should be preserved for future generations	2	0.8
- endangered species	2	0.8
Economic	**32**	**12.3**
- tourist attraction	30	11.5
- sellable	2	0.8
Ecological	**29**	**11.1**
- helps to balance the ecosystem	23	8.8
- useful for the environment	4	1.5
- eats insects	2	0.8
Aesthetic	**13**	**5.0**
- symbol of Bohol\they're native	8	3.1
- it's nice to see and adds beauty to the place	5	1.9
Other	**9**	**3.5**
- they are protected by DENR	5	1.9
- harmless	3	1.2
- because they are small	1	0.4

Seeing or hearing about people who hunted tarsiers was also dependent on occupation. Villagers who were engaged with income-generating activities (farmers, physical labourers and basic services, and professionals) stated that they had seen or heard about human hunters more often than people staying mostly at home [($\chi^2 = 20.30$, df = 3; $P < 0.001$) and (χ^2=19.80, df=3; $P = 0.0002$) respectively]. Tarsier capture carried out by the respondents themselves also correlated with level of education – those with only primary or elementary education, stated having done so more frequently (21 % yes: 79 % no) than high school or university graduates (10 % yes: 90 % no) (χ^2=6.82, df=1; $P = 0.009$).

Interviewees who answered that they knew about the presence of hunters, when asked about the frequency of seeing or hearing about them stated "many times" (>10), followed by "once" and a "few times" (between 2–10). On the other hand, among those respondents who had captured tarsiers themselves, 76 % stated they had caught only one individual, while for the rest it was a "few", but never "many". Over half (56 %) of the Bilar respondents gave the reasons for the capture of tarsiers: the most frequent was "for sale" (76 %, $N = 138$), while the second most frequent was "as pets" (20 %, $N = 37$). When the interviewees who stated the purpose of capture was for sales were asked where the tarsiers were being sold, the majority (70 %, $N = 61$) indicated "tourist facilities", followed by "to foreigners" (21 %, $N = 18$) or "to local people" (4%, $N = 4$).

4. Discussion

4.1. Knowledge of the Philippine tarsier

The majority of respondents recognized the images of the Philippine tarsier at a rate higher than that for other nocturnal species in the area, however, tarsier vocalizations were much more rarely identified. This could be due to the fact that local people are exposed to the species through commercial and promotional materials (e.g., tourist adverts, T-shirts and food products with tarsier labels found everywhere in Bohol), but that they do not see tarsiers on a daily basis and are, consequently, not familiar with their calls. As expected, tarsiers were observed more often in villages within forested areas, and more often encountered by men, local resource suppliers, and people engaged in income-generating activities working in the field or visiting wilderness areas, than women and other respondents, who are usually focused on daily household chores or office duties.

Initial impressions are that the knowledge of local people on the Philippine tarsier in Bilar seems high. However, on closer examination of the data, this conclusion is not straightforward, as despite the very high rate of correct answers about the species' diet and occurrence, there were far fewer completely correct ones. This was especially seen in the answers to occurrence of the species, which, according to the respondents, inhabited only Bohol. This perception may be a consequence of the great popularity of tarsiers as a main tourist attraction on the island. Tarsiers are depicted as primates from Bohol in commercial and school materials which easily reach local residents and influence their knowledge.

Reibelt et al. (2017) drew attention to the link between the frequency of encountering an animal and the knowledge of it (as well as the greater likelihood of concern about its future). In our study, less than half of the local residents had seen or heard about tarsiers in Bilar, but only a minority of these said they had encountered the animals themselves in the neighbourhood. This may explain why, despite their high overall knowledge, local people lack detailed information about the species. The group of respondents who encountered and knew more about tarsiers were males and local resource suppliers, confirming that people who visit wild areas more often, like fishers (Reibelt et al., 2017) or hunters (Ceballos-Mago & Chivers, 2010) possess greater knowledge about wildlife. Greater contact with nature is likely also a reason why farmers and physical labourers had more knowledge of the species. On the other hand, the better insights into the tarsiers' diet by professionals and younger respondents may be a consequence of greater access to and use of more reliable sources of information (e.g., websites, online databases, better equipped libraries) by these groups.

Word-of-mouth (family and friends) combined with own experience of the local people constituted half of all responses pertaining to the channels of knowledge, thus being the most important factor in transmission of information about the Philippine tarsier, followed by the media. Knowledge passed on in this way, however, may be unreliable and consequently mislead local residents, which appears to have occurred, for example, with the casual reports that tarsiers eat charcoal. Aure and Escabi-Ruiz (2005) mention that tarsiers eating charcoal is a traditionally held belief in the Visayas, while the animals may actually be retrieving insects from sometimes burned wood.

4.2. Conservation attitudes towards the species

Conservation perceptions among local residents were somewhat inconsistent as most of them did not perceive tarsiers as an endangered species, yet the vast majority expressed the opinion that they should be

Table 4
The number and frequency (percentage) of local Bilar people who had seen or heard about the Philippine tarsier hunters and villagers who had captured tarsiers themselves with results of the Chi-square test (χ^2) (Oct 2016 - Nov 2017 study).

Response	Respondent profile					Sex				
	Resource suppliers		Other villagers		χ^2	Males		Females		χ^2
	N	%	*N*	%		*N*	%	*N*	%	
Seen hunters	59	82	118	47	30.05*	125	68	52	37	29.46*
Heard about hunters	57	79	117	46	25.63*	120	65	54	39	21.79*
Captured themselves	36	50	18	7	63.5*	50	27	4	3	39.79*

* $P < 0.001$.

protected. Over half of the respondents reported an increase in the number of tarsiers in the area, due mainly to the belief that the animals keep breeding, and, to some degree, that the species is already sufficiently protected. The high proportion of local people stating that the tarsier population is on the rise is nonetheless surprising when compared with other Asian (Devi & Radhakrishna, 2013; Nekaris, Boulton et al., 2013; Quinten, Stirling, Schwarze, Dinata, & Hodges, 2014) or South-American (Freire Filho, Pinto, & Bezerra, 2018; Stafford, Alarcon-Valenzuela, Patiño, Preziosi, & Sellers, 2016) findings, where local people reported that primate populations were declining rather than increasing. However, results similar to ours were obtained in Madagascar, where local people believe that the risk of extinction of various lemur species (due to hunting) is low, despite solid evidence to the contrary (Gore, Lute, Ratsimbazafy, & Rajaonson, 2016).

Ross et al. (2008) found that people were less likely to perceive chimpanzees as endangered compared to other great apes, because they often appear on television, in movies and printed materials such as greetings cards and advertisements. The Philippine tarsiers are the most common feature on the various sources promoting the island and, in addition, the live individuals are showcased at tourists facilities in Bohol. This could possibly give the impression to the local populace that if these animals are famous and shown to tourists, their number are not in jeopardy. At the same time, promotional materials did not contain any information about the species' conservation status, which might further deepen the impression of the local residents that the tarsier population is not threatened, or in decline. Their belief that the tarsiers "keep breeding" is, however, without any solid evidence. There is no data available for tarsier population size or trends in the area, except from one study in Corella, Bohol (Gursky et al., 2017), which showed their decline in numbers from 157 individuals/km^2 before typhoon Haiyan struck Bohol in 2013, to 36 individuals/km^2 after the typhoon.

As our data shows, there were fewer respondents who had actually encountered the tarsiers themselves than expressed the opinion that the number of animals has increased over the past years, which renders such claims doubtful. On the one hand, views on population growth might be exaggerated because local people perceive wildlife as an inexhaustible resource, undisturbed by human activities such as e.g., hunting (Aiyadurai, 2011). Alternatively, it may be that local people wish to maintain the reputation of Bohol Island as the top tourist destination for viewing tarsiers. The perception that tarsiers are growing in number, even while the species is threatened with extinction, may foster a belief that the species is not in need of special conservation efforts (Torres Junior et al., 2016). However, this notion has not yet found root in Bilar, where villagers still advocate for protection of the tarsiers.

Most of the respondents of this study, and especially men, found the Philippine tarsier useful. Around the Selous Game Reserve in Tanzania it was also noted that males were more likely to express similar positive wildlife conservation attitudes than females (Gillingham & Lee, 1999), which was linked to the marginalized status of women in the predominantly Muslim villages. Bilar women respondents being mostly housewives, are thus also likely to be less engaged with discussions on environmental issues and less informed about public issues concerning wildlife management. They do not hold relevant positions in environmental offices in the surrounding protected areas, nor are they greatly involved in village councils (all the staff and village captains were males [FJW pers. obs.]). In our study, the tarsiers were considered useful largely for economic reasons (83 %), which also was the second major argument in support of their protection. However, the association of wildlife species and tourism-generated income, found across Africa (Gillingham & Lee, 1999; Newmark, Leonard, Sariko, & Gamassa, 1993; Sousa et al., 2014), may be a dangerous trap. If the expectations of local people are not fulfilled, i.e., they gain less revenues than anticipated, or benefits are unequally distributed within the community, this can result in local residents withdrawing from their sanctuary membership pledges, or in violent conflict between local communities and authorities, visitors and outside investors (Alexander, 2000; Harcourt, Pennington, & Weber, 1986; Sekhar, 2003; Sousa et al., 2014).

4.3. Threats and endangerment risks to the tarsier local population

We found no shared beliefs or folklore about the Philippine tarsier in Bilar. This is perhaps due to the limited contact with the species, as evidenced for other elusive primates, e.g., the Guizhou snub-nosed monkey (*Rhinopithecus brelichi*) (Ellwanger et al., 2015), or the night monkey (*Aotus vociferans*) (Mere Roncal, Bowler, & Gilmore, 2018). The absence of folklore or beliefs may also explain why tarsiers are not used for medicinal purposes, as people do not associate these primates with any health benefits. Aure and Escabi-Ruiz (2005) attributed tarsier hunting in Corella, Bohol rather to external demand for live specimens, taxidermy mounts, for public showcasing or for luring tourists. The Bilar residents, however, did not report on the tarsiers' being used for taxidermy, which may indicate a variation in the demand for this across the species range.

While we did not aim to quantify the rate of tarsier capture, the knowledge of local people nonetheless may indicate that hunting is widespread in the area: as many as 62 % respondents reported having seen or heard about the hunting of tarsiers in the Bilar area, although only a minority admitted to capturing tarsiers themselves. One of the authors of this paper (FJW) was informed about the capture of five tarsiers by local villagers over a two-year timeframe in Subayon only, confirming the interviewees' statements. While the low capture rate among the respondents may initially seem to contradict the interviewers' statements, when local resource suppliers are considered alone, up to half of them reported catching tarsiers. Tarsiers quickly traverse their dense and harsh habitat at night, thus making them very difficult for amateurs to catch, which explains why the majority of those people who captured tarsiers are forest resources suppliers. Most inhabitants of non-forested areas (including women) only go to collect firewood in the areas near their homes, where there is a smaller chance of capturing a tarsier. They are also generally less skilled and agile than the forest resources suppliers and thus less able to catch this small primate, though there is always a possibility of some dishonest answers. The Bilar residents, being aware of the illegal hunting, consistently stated that tarsiers are being caught for sale and, less often, also as pets. At the same time, tourist facilities and, less commonly, foreigners, were identified as destinations where the animals are being trafficked.

Tourism seems to be a vital threat to the Philippine tarsier, a problem shared with other iconic primate species, such as catta lemurs (*Lemur catta*), which are kept in businesses for income generation in Madagascar (LaFleur, Clarke, Reuter, Schaefer, & terHorst, 2019), and slow lorises (*Nycticebus* spp.), which are used as photo props in Thailand (Osterberg & Nekaris, 2015). Currently, three tourist establishments in Bohol are legally permitted to display tarsiers: one in Corella, and two in Bilar. Animals there are showcased during the day, sometimes photographed with flash, and, although not permitted, hand held by tourists. However, other, more private places where tarsiers are kept as props for tourist photos operate illegally across Bohol (FJW pers. obs.). Although there are still too few data on the Philippine tarsier's longevity, Fitch-Snyder (2003) and Shekelle and Nietsch (2008) reported it as a dozen or so years (12, 10–14, ~16) in captivity/ zoo conditions. On the other hand, two of our respondents mentioned during the interviews that the lifespan of the tarsiers in tourist facilities are about one month which sheds some light on the plight of these animals in the Bilar area.

Establishments of this kind have a negative impact on animals welfare, as the individuals are exposed to severe stress, an unsustainable diet, flash photography and unnatural surroundings, which can eventually lead to their death (Orams, 2002; Osterberg & Nekaris, 2015; Rehnus, Wehrle, & Palme, 2013). This type of environment is even more detrimental to tarsiers, who do not thrive well in captivity and where successful breeding colonies have not been achieved (Fitch-Snyder, 2003). Exploitation of tarsiers is further exacerbated by the illegal pet trade, which appears to be local and/or regional. In recent years,

though, eleven live Philippine tarsiers were confiscated before they could be smuggled abroad (Mayuga, 2016), corroborating similar statements from the residents of Bilar, and indicating that the illegal wildlife trade is still very much ongoing, although the exact scale of this practice is not known.

Camera traps in Bilar have revealed the presence of feral cats in heterogenous habitats where tarsiers are known to be present (Bogdan et al., 2016). Domestic cats were mentioned as tarsier predators by only a few respondents. However, quite a number of recorded deaths within the Philippine Tarsier Sanctuary in Corella were attributed to these predators (Aure & Escabi-Ruiz, 2005). One of the authors of this paper (FJW) has heard about domestic cat predation in Subayon village, where in one instance, five tarsiers had been brought to the doorstep of one household over only two years. However, implementing any intervention with just this level of knowledge could create a conflict situation that may jeopardize the relationship between conservationists and the local residents. Therefore careful planning and communication on an appropriate strategy is crucial (Waters, Watson, Bell, & Setchell, 2018). To enable this further investigation into cat predation on tarsiers and other wildlife should be conducted. Such a study could be a complex undertaking, and possibly not resolvable through quantitative techniques, but which may require a more ethnographic approach. Qualitative methods have been proven effective in the past in uncovering nuances required to guide conservation strategies that align with the interests of local people who are directly involved with the conservation actions (Setchell, Firet, Shutt, Waters, & Bell, 2016; Waters, El Harrad, Bell, & Setchell, 2019).

4.4. Implications for conservation

The local residents of Bilar associate the Philippine tarsier primarily with tourism and the expectation of revenue generation through foreign money exchange. At the same time, this notion is the main driver of tarsier capture which threaten its local population numbers. It is therefore crucial to decrease the demand for the captive viewing of these primates and the desire to own them as pets – both very difficult to achieve. We have demonstrated here the high environmental knowledge of local forest resources suppliers, who should be the main stakeholders in the conservation strategy: Firstly, they should be included in any research activities, by which the researchers would benefit from their knowledge. This could also help to build close relationships with local resource suppliers, which might bring benefits beyond improved scientific outcomes. In a related example, positive engagement and sharing of information between conservationists and shepherds (Waters et al., 2019) led to changing the attitude of the latter, some of whom stopped hunting for Barbary macaques. At the same time, these authors provided proactive conflict mitigation initiatives focusing on livestock and human health in the villages affected by crop-foraging macaques to reinforce the shepherds' change in behaviour. This could be applied in our case, where incentives such as sustainable tourism opportunities might be offered to forest resources suppliers to further encourage them to limit their hunting activities. Involvement of these individuals would be beneficial both for tourists, who would gain information about the animals from those most knowledgeable, and the local residents, who would derive additional income from this as an alternative to hunting. Such tourism field trips could thus potentially decrease the demand for the viewing of tarsiers in captivity and, consequently, their capture in the wild.

Simultaneously, the complementary conservation education proposed could reinforce the perception of tarsiers as an integral part of the ecosystem having aesthetic value, rather than simply as a magnet for revenues. The Subayon Conservation Center has worked closely with Department of Education, Philippines (DepEd) in conducting several programmes for students and developed environmental training programs for teachers in schools. The latter activity has proven to be effective in expanding teachers' knowledge and appreciation of the surrounding wildlife and beneficial for conservation owing to the teachers' influence on generations of pupils throughout their careers. We suggest increasing such training sessions for teachers in areas where tarsiers are naturally found, conducted initially by NGOs or conservation establishments such as Habitat Bohol, in collaboration with local Universities, until the staff of DepEd are trained to conduct these seminars on their own. This would be the most cost-effective strategy as DepEd conducts seminars for local teachers several times a year, where conservation content could be easily incorporated.

Tourism is also an unreliable source of income owing to its dependency on seasonal occurrences and the prevailing regional or national situation (Stem, Lassoie, Lee, & Deshler, 2003), which, if adverse, may trigger negative sentiments among local residents. Appropriate education aimed at expanding local appreciation and associating tarsiers and other wildlife with intrinsic values, on the other hand, is important in the longer term to prevent possible disappointments among local residents related to possible failure in generating financial benefits. Finally, decreasing the demand for captive tarsiers and improving of their welfare in tourist facilities is of high importance. Studies revealed a link between primates being shown next to a human or in a non-natural setting with the desirability of owning one as a pet and belief that the animal is not endangered (chimpanzees [Ross, Vreeman, & Lonsdorf, 2011]; capuchin monkeys (*Cebus* sp.), squirrel monkeys (*Saimiri* sp.) and ring-tailed lemurs (*Lemur catta*) [Leighty et al., 2015]). Content on YouTube and social media may impact perceptions of wild animals as well. The wish to keep a pygmy slow loris as a pet increased after a video of this primate being tickled was uploaded on YouTube (Nekaris, Campbell, Coggins, Rode, & Nijman, 2013), or a desire to keep a ring-tailed lemur after just a short clip of a habituated individual was posted on Twitter (Clarke, Reuter, LaFleur, & Schaefer, 2019). It is likely that the Philippine tarsier shown in the media or commercial material triggers similar perceptions among tourists and local people alike and increases the demand to view them.

We further recommend that researchers work with the Bohol Tourism Office, tour operators and online users (e.g., bloggers) to promote tarsiers shown in their natural settings and, where possible, to delete images in which they are shown in contact with humans. In instances where several places illegally keep tarsiers as photo props to attract tourists monitoring of such activities can be costly and time-consuming. There have, however, been effective practices implemented elsewhere to tackle this problem. In Morocco, *Barbary Macaques Awareness and Conservation* was launched on the Rif Facebook page to raise awareness of the threats to the wild Barbary macaques (*Macaca sylvanus*), especially in relation to the pet trade (Waters & El-Harrad, 2013). This resulted in the engagement of Moroccans, who started reporting illegal pet macaques to page administrators, helping with confiscation of the animals. The Philippines ranks first in the world for social media penetration (99 %), with 75 out of 76 million social media users registered on Facebook (Gonzales, 2019). We therefore, propose the active use of social media to strengthen public conservation education (e.g., inform responsible tourist behaviour) and engagement with the netizens in the Philippines, who might become important stakeholders in illegal activities reporting.

Last, but not least, the Subayon Conservation Center has been instrumental in broadening the understanding of the Philippine tarsiers' captive behaviour and husbandry guidelines (Wojciechowski et al., 2019, 2020) and, also, in achieving reproductive success (Wojciechowski et al., 2020). These lessons should be passed to legal tourist destinations to help foster close collaboration between the staff of these centres and researchers and NGOs. Improved husbandry and reduction of the stress of human visitation (keeping safe distance and forbidding contact with animals) would significantly improve tarsier welfare and their survival rate, while simultaneously drive a decrease in the demand for these wild individuals.

5. Conclusions

We were able to demonstrate the knowledge of the local community in Bilar, Bohol of the Philippine tarsier. These primates are not frequently encountered by the residents in the area, which explains the low familiarity with the behavioural ecology and conservation status of the species. We showed that local people rely primarily on word-of-mouth, personal experience, and the media to learn about tarsiers. Forest resources suppliers are the individuals who encounter tarsiers and possess the most knowledge about them, but also capture them and know the most about other hunters. Positive conservation attitudes towards the species prevail amongst the local people, both as a desire to maintain population numbers and for economic reasons. Yet, most residents do not consider the Philippine tarsier as endangered and believe its population is increasing. We also showed a high endangerment risk to the tarsier population of Bilar which may be inferred based on the accounts of local respondents, who frequently noticed the presence of human hunters in the area. Undoubtedly, the animals were being hunted – for selling or keeping as pets, and for trafficking to tourist facilities or to foreigners. In our opinion, because of favourable attitudes towards the Philippine tarsier by the local people, the species has potential to be a flagship species for conservation in the area. This potential, however, depends on the implementation of a carefully designed conservation strategy, which, if not appropriately actualized, could generate unintended consequences. We recommend promoting the involvement of forest resource suppliers in wildlife research and tourism, furthering teacher training to ensure emphasis of the ecological and aesthetic values of the Philippine tarsiers in schools, and enhancing the perception of this primate, particularly in the digital context, to improve tarsier welfare in captivity.

Author contributions

FJW obtained funds, conceived the project, conducted fieldwork, analysed the data, and wrote the paper. JBO conducted fieldwork. KAK conceived the project, performed statistical analyses, analysed the data, and provided comments and editorial advice (review and editing).

Permits and clearances

This study was conducted as a research project of the Subayon Conservation Center for the Philippine tarsier, and adhered to the legal requirements of the Republic of the Philippines. We received a permit to operate from the Department of Environment and Natural Resources (DENR) VII, based on the Memorandum of Agreement (MoA) granted for the period 2014–2019, and Mayor's Clearance (dated March 15, 2016).

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Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jnc.2021.126028.

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Appendix 1:

Study Questionnaire – English Version

Introduction:

We are conducting this interview to collect information for a research project being conducted in several villages in Bilar. Your answers will help us to gather data on your knowledge about wildlife, forest usage and attitudes towards the area and its animals. We will not at any stage record your name or affiliations, which will not allow you to be identified by anyone, thereby making you anonymous. your participation is entirely voluntary. We are asking you to be a respondent only if you are willing to do so. However, no gifts or compensation for participation will be offered. We will not force you to provide answers to all of the questions if you do not wish to as this is entirely voluntary on your part. But if you have any additional questions along the course of the interview, do not hesitate to ask. We are not tied to any governmental office and our research project has absolutely nothing to do with law enforcement. Its aim is only to obtain information on the perceptions of residents of the barangays in Bilar.

Type of interviewee: Hunter / hunter's family Random

Date:

Part I . Background/demographic

a) Barangay:
b) Year the village was established
c) Population size
d) Number of households
e) Age
f) Sex
g) Occupation/livelihood
h) Religion
i) Level of education a. part elementary b. elementary c. high school d. higher
j) Local/immigrant (no. of years spent in the village)
k) How often do you go into the forest

a. every day c. few times a month e. few times a year

b. few times a week d. once a month f. never

Part II . Reliability

Animals – showing of pictures to recognize the local animals – 6 photos to be shown

Sounds – producing sounds of animals to recognize the vocalisation of the tarsiers - 4 sounds to choose from.

Part III . Tarsiers

1. Have you heard or seen any tarsier/s in the area?

    a) Yes, where
    b) No

2. Have you seen tarsiers close to your house or heard about their presence in your neighborhood?

    a) Never
    b) Sometimes
    c) Frequently

3. What do tarsiers eat?

    a) Fruits
    b) Insects
    c) Charcoal
    d) Crops
    e) Birds
    f) Arachnids

4. Where do the tarsiers live?

    a) Cebu
    b) Bohol
    c) Camiguin
    d) Leyte
    e) Samar
    f) Siquijor
    g) Mindanao
    h) Dinagat
    i) Siargao
    j) Basilan

5. How would you describe tarsiers?

    a) Harmful (Why?)
    b) Useful species (Why?)
    c) Neutral

6. In your opinion, the number of the tarsiers in past 10 years has:

    a) Increased (Why?)
    b) Decreased (Why?)
    c) Stayed the same

7. Have you seen or heard tarsiers being predated by animals in the area?
    a) Yes, how many times and by which animal
    b) No

8. Are there any beliefs related to tarsiers in the area?

    a) Yes, (describe)
    b) No

9. Do you know if tarsiers are eaten or used for any other purpose?

    a) Yes, (How?)
    b) No

10. Have you seen people hunting tarsiers within the area?

    a) Yes, (How many times?)
    b) No

11. Have you heard of people hunting tarsiers within the area?

    a) Yes, (How many times?)
    b) No

12. What is the purpose of this?

13. Have you hunted/captured any tarsiers in your life?

    a) Yes, (How many?)
    b) No

14. Do you know where tarsiers are sold after capturing?

15. Do you think that the tarsiers are endangered?

    a) Yes (Why?)
    b) No (Why?)

16. Do you think Tarsiers should be protected?

    a) Yes (why?)
    b) No (why?)

17. Where did you get your knowledge about tarsier?

    a) School
    b) Media (newspapers, TV, internet, cellphone)
    c) Trainings and seminars
    d) Family and friends
    e) Others (specify)_____

18. What forest resources are the most useful for you?

a) Lumber
b) Firewood
c) Water
d) Medicine
e) Fruits
f) Honey
g) Swiflets nests
h) Others (specify):_____

19. Have you collected them in the forest? (simultaneous question to 17)
    a) Yes, how often?
        i. Frequently
        ii. Sometimes
    b) No

20. In your opinion have the forest resources been depleted in the past 10 years?
    a) Yes - what resources in particular?
    b) No

Appendix 1:

Study Questionnaire – Visayan Version

Among gihimo kining maong pakisusi aron sa pagpangolekta sa mga impormasyon alang sa proyektong pagtuon nga himuon dinhi sa mga pinili nga barangay sa lungsod sa Bilar. Ang imong tubag may ikatabang alang sa among pagpangolekta og mga datus kabahin sa mga ihalas nga mananap, saktong paggamit sa kalasangan, ug kinaiya nga gibuhat ug gipakita ngadto sa mga lugar ug sa mga mananap nga namuyo niini. Dili namo isuwat ang imong pangalan aron sa paglikay nga mailhan ka sa uban. Ang imong pagpanginlabot boluntaryo lamang. Kami nagahangyo kanimo nga mahimo kang hingtungdan kana kung ikaw interisado. Sa laing bahin, sa imong pagpanginlabot wala kami ikahatag nga bugti niini sanglit boluntaryo man kini. Dili ka namo pugson sa pagtubag sa mga pangutana nga dili nimo kayang tubagon kay kini boluntaryo lamang sa imong bahin. Pero kun ikaw adunay wala hisabti samtang gihimo ang mga pangutana, ayaw pagmakuli sa pagpangutana. Kami wala malambigit ngadto sa bisan unsang organisasyon sa gobyerno ug ang among gihimo nga Proyektong Pagtuon walay kalambigitan sa mga tinugyanan sa balaod. Ang tumong lamang niini, mao ang pagkuha sa mga impormasyon kabahin sa panglantaw sa mga residente sa mga barangay dinhi sa lungsod sa Bilar.

Type of interviewee: Hunter / hunter's family Random

Date:

a) Barangay:
b) Tuig namugna ang lugar:
c) Edad:
d) Kasarian:
e) Trabaho/ Panginabuhian:
f) Relihiyon:
g) Edukasyon nga naabot:

   a. part elementary b. elementary c. high school d. higher

h) Gidugayon sa pagpuyo sa maong lugar:
i) Kapila muadto sa lasang?

a. kada adlaw

b. panagsa sa matag simana

c. panagsa sa matag bulan

d. kausa sa usang bulan

e. panagsa sa matag tuig

f. Wala gyud

Part II . Reliability

Animals – showing of pictures to recognize the local animals – 6 photos to be shown

Sounds – producing sounds of animals to recognize the vocalisation of the tarsiers - 4 sounds to choose from.

Part III . Tarsiers

1. Nakadungog naba ka o nakakita ug mawmag dinhing dapita?

   a) Oo, diin man b) Wala

2. Nakakita ka na ba ug mawmag duol sa inyung balay o sa silinganan?

   a) Wala gyud b) Panagsa c) Kanunay

3. Asa man nga lugar sa Pilipinas makita ang mga mawmag?

   a. Cebu
   b. Bohol
   c. Camiguin
   d. Leyte
   e. Samar
   f. Siquijor
   g. Mindanao
   h. Dinagat
   i. Siargao
   j. Basilan

4. Unsay kan-unon sa mawmag?

   a. Prutas
   b. Insekto
   c. Oling
   d. Lagutmon
   e. Langgam
   f. Gamba

5. Unsaon nimo paghulagway ang usa ka mawmag?

   a) Makadaot (Nganu man?) b) Mahimuslan (Nganu man?) c) Wala Lang

6. Sa imung pagtuo sa nanglabay nga napulo ka tuig ang gidaghanun sa mawmag ni:

   a. Nisaka (Nganu man?) b. Niubos (Nganu man?) c. Mao lang gihapun

7. Nakadungog ka na ba nga adunay mawmag nga gikaun sa lain nga mananap sa maong lugar?

   a. Oo, kapila ug unsa nga mananapa? b. Wala

8. Aduna bay mga tinuohan kabahin sa mga mawmag dinhing dapita?

   a. Oo, unsa man? b. Wala

9. Aduna ka bay nahibaloan nga ang mawmag gikaon sa tawo o gigamit sa bisan unsang tumong (sama pananglit: sa tambal o handumanan)?

    a) Oo (Gi unsa man?) b) Wala

10. Nakakita ka ba ug mga tawo nga nanakop ug mawmag dinhing dapita?
    a) Oo, kapila man? b) Wala

11. Nakadungog ka ba ug mga tawo nga nanakop ug mawmag dinhing dapita?
    a. Oo, kapila man? b. Wala

12. Unsay tumong niini?

13. Nakakuha/nakadakop ka na ba ug mawmag sa imung kinabuhi?

    a) Oo (Pila man?) b) Wala

14. Nakahibalo ka ba ug asa ibaligya ang mga mawmag human madakpan?

15. Sa imung hunahuna hapit na ba mahurut/mapuo ang mga mawmag?

    a) Oo (Nganu man?) b) Wala (Nganu man?)

16. Sa imung hunahuna angayan ba nga protektahan ang mga mawmag?

    a. Oo (Nganu man?) b. Dili (Nganu man?)

17. Diin nimu nakat-onan ang mahitungod/kabahin sa mga mawmag?

    a) Eskwelahan
    b) Pahayagan/newspapers, Radyo, Telebisyon, internet, cellphone
    c) Trainings ug seminars
    d) Pamilya ug amigo
    e) Ug uban pa (i-klaro)_____

18. Unsa nga mga kaayuhan sa lasang ang gamit para nimu?

    a) Kahoy
    b) Sugnod
    c) Tubig
    d) Tambal
    e) Prutas
    f) Dugos
    g) Salag
    h) Ug uban pa (i-klaro)

19. Nakolekta mo ba kini sa lasang?

    a) Oo, kapila?
        i. Kanunay
        ii. Usahay
    b) Wala

20. Sa imung hunahuna nahurot ba ang mga bahandi sa kalasangan sa nilabay nga napulo ka tuig?

    a) Oo - unsa nga mga bahandi man pananglitan?
    b) Wala