

ORIGINAL ARTICLE

Eclipsed: Emergence-return activity of two pteropodid bat species during lunar eclipse

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ABSTRACT

Lunar eclipses are known to influence flight activity of tropical bats at foraging sites. However, little is known about the onset and offset of flight activity from the roost during lunar eclipses compared to other full moon nights. Emergence from and return to the roost were observed during a total lunar eclipse at a colony of the fruit bat *Rousettus leschenaultii* and during a partial lunar eclipse at a *Pteropus giganteus* colony in southern India. In addition, on the same partial eclipse night, a single male *P. giganteus* was tracked using GPS telemetry. Flight activity in both species was compared between the eclipse night and other full moon nights. In both cases, bats emerged before the eclipse and fewer *R. leschenaultii* individuals returned to the roost during the hours of the total eclipse, compared to the corresponding hours during other full moon nights. No such difference in return activity was observed in the *P. giganteus* colony or in the GPS tracked individual between the partial eclipse and other nights. This is the first attempt to study temporal flight activity of bats during lunar eclipses at their roosting sites. More roosting site observations, especially on species that roost in the open, are required to understand the effects of lunar eclipses on bat activity.

INTRODUCTION

Moonlight influences activity in a range of taxa including bats (Lockard & Owings 1974, Longland & Price 1991, Julien-Laferrière 1997, Fernández-Duque et al. 2010, Appel et al. 2017). Full and new moon phases represent two extremes in light intensities at night, and bat activity in these moon phases have been compared in several species (Elangovan & Marimuthu 2001, Börk 2006, Lang et al. 2006, Riek et al. 2010, Sudhakaran & Doss 2012). Overall, many bat species around the globe show reduced activity on full moon nights compared to new moon nights. Such trends of moonlight avoidance by bats is often hypothesised to be linked to a higher predation risk on brighter nights (Lima & O’Keefe 2013), sensory adaptations, habitat cover (Prugh & Golden 2014) and prey abundance (Lang et al. 2006). However, the effect of moonlight varies considerably between species that differ in diet, roosting or flight capacity (Lang et al. 2006, Saldaña-Vázquez & Munguía-Rosas 2013, Appel et al. 2017, Musila et al. 2019). Non-echolocating fruit bats (Pteropodidae) show reduced flight activity on brighter moonlit nights compared to moonless nights, although brighter nights are better suited for visually guided navigation, foraging and predator avoidance (Morrison 1978,

Nair et al. 1998, Elangovan & Marimuthu 2001, Sudhakaran & Doss 2012, Mello et al. 2013).

Lunar and solar eclipses are known to affect bat activity in a species-specific manner. Observations at the roost during a total solar eclipse showed that flight activity during eclipsed hours was affected to a greater extent for *Balantiopteryx plicata* whose roosts are well lit, compared to *Desmodus rotundus* and *Anoura geoffroyi* which are cave-roosting species (Sánchez et al. 1999). Lunar eclipses occur during full moon nights and are accompanied by a reduction in light intensity during the eclipsed hours. While observations at foraging sites during lunar eclipses have been conducted for a few tropical bat species, the effect of lunar eclipses on flight activity at roost sites has not been studied in most species. Usman et al. (1980) reported reduced flight activity at feeding sites in an insectivorous bat community during the eclipsed period and increased activity during the brighter parts of a partial lunar eclipse night. Foraging site observations in the frugivorous bat *Cynopterus sphinx* in southern India, revealed reduced activity during full moon and greater activity during a total lunar eclipse (Singaravelan & Marimuthu 2002). Two other fruit bats, *Pteropus giganteus* and *Rousettus leschenaultii*,

showed reduced activity at foraging sites on full moon nights compared to new moon nights (Elangovan & Marimuthu 2001, Sudhakaran & Doss 2012). Emergence duration and flight activity were similar across moon phases in colonies of the tree-roosting *P. giganteus* and *C. sphinx*, while emergence activity (proportion of the colony that flew from the roost) varied between full and new moon nights in the cave-roosting species *R. leschenaultii* (Murugavel et al. 2021). However, little is known about how emergence-return flight activity in these species varies during lunar eclipses relative to full moon nights.

In the current study, we examine emergence and return activity of *R. leschenaultii* during a total lunar eclipse and of *P. giganteus* during a partial lunar eclipse. We also examine flight patterns of a GPS tracked *P. giganteus* male during the partial eclipse. *Pteropus giganteus* is a tree-roosting species exposed to bright daylight (>1000 lux), while *Rousettus leschenaultii* is a cave roosting species which prefers dark sites that are not exposed to daylight (<0.1 lux).

MATERIAL AND METHODS

The *Pteropus giganteus* colony we studied consisted of ~5000 individuals, roosting on *Albizia lebeck* and *Ficus benghalensis* trees in the Centre for Biodiversity and Forestry Studies, Madurai Kamaraj University (9°56'N & 78°00'E), India. The *Rousettus leschenaultii* colony consisted of ~10000 individuals roosting within tunnels inside an agricultural spring well (~15 m deep and light levels <0.1 lux during the day) in Theni (9°55'N, 77° 28'E), India.

At both study sites, roost-based observations of flight activity were carried out from 18:00 to 07:00 h during new moon, first quarter, full moon and third quarter phases of five consecutive lunar cycles (January – May 2017 for *R. leschenaultii* (Murugavel et al., 2021) and March – July 2019 for *P. giganteus*). Similarly, whole night observations (18:00 to 07:00 h) were carried out at the *R. leschenaultii* colony during a total eclipse on 27 July 2018 (eclipse time: 22:44 h – 04:58 h) and the *P. giganteus* colony during a partial lunar eclipse on 17 July 2019 (eclipse time: 00:13 h – 05:47 h). These observations were compared with those on full moon nights (N=5 nights for *R. leschenaultii*; N=4 nights for *P. giganteus*) of previous lunar cycles (Table 1).

On each observation night, the time when the first and last bats emerged and the number of bats that emerged or returned at 5-minute intervals were noted. Ambient light levels and viewing conditions at the roost entrance were sufficient for a trained observer to carry out observations from the mouth of the well containing the *R. leschenaultii* roost. In *P. giganteus*, emergence observations during twilight were made by three observers standing ~200 m in the East, North-West and South directions from the roost. It was not possible to count returning *P. giganteus* individuals, as they flew in from multiple directions. Instead, the roosting trees were visually scanned every hour using a flashlight with a red filter to estimate the proportion of the colony that had returned. Since the eclipse observations were from single nights, no statistical tests could be performed with the data.

From February to September 2019, a radio tracking study was carried out at the *P. giganteus* colony in which a few individuals were monitored using solar powered GPS transmitters (15 g Bird Solar, e-obs Digital telemetry, GmbH, Gruenwald, Germany). One of the tracked individuals, an adult male, transmitted data on the partial eclipse night. Its movement was compared between the partial eclipse and other nights (Table 1).

Light levels were measured whenever possible using a photometer (Hagner Universal Radiometer Model S4, Hagner, Solna, Sweden) with a lowest detectable value of 0.01 lux, by placing the sensor facing upwards at a height of 1 m above ground (in *R. leschenaultii* during three lunar cycles from January-March 2017; in *P. giganteus* during two lunar cycles from March – April 2019). Since vegetation was sparse and the habitat was open in the vicinity of the roosts, light measurements were not affected by clutter. Light levels could not be measured on both the eclipse nights due to device malfunction. Hence, for the eclipse nights, relative lunar brightness was calculated from the apparent lunar magnitude. The total and the partial eclipse were simulated at the study locations using the lunar_total.ssc and lunar_partial.ssc scripts in the open source Stellarium software 0.18.2 (Stellarium Developers, www.stellarium.org). Lunar brightness was considered 100 % when the full moon was un eclipsed with a magnitude of -12.13 and 0% at the peak of the total eclipse when the moon was completely covered.

RESULTS

The total eclipse occurred between 22:44 h – 04:58 h, but the lunar brightness decreased only between 23:54 h – 03:49 h, reaching 0% at the peak of the total eclipse (01:51 h). Emergence and return times (marking the onset and end of flight activity) were similar for the *R. leschenaultii* colony on the eclipsed night and other full moon nights (Table 1; Fig. 1 a and c). Flights were initiated 40±12 minutes after sunset (mean ± SD; Range: 28 – 58 minutes) on full moon nights and 36 minutes after sunset on the eclipsed night. The last bat returned to the roost 29 minutes before sunrise during the eclipsed night and 28±4 minutes before sunrise (mean ± SD; Range: 24 – 33 minutes) on full moon nights. The proportion of the colony that emerged or returned was very low (Fig. 1c) during the darkest periods of the eclipse night (00:00 – 03:00 h) in comparison with other full moon nights during the same time interval (Fig. 1a). The number of returning individuals peaked between ~60 - 140 minutes before sunrise (04:00 – 05:00 h) on the eclipse and other full moon nights, but a higher proportion of the colony returned during this period on the eclipse night compared to other full moon nights (Fig. 1 a and c). The mean ± SD return flight time was between midnight (395 ± 93 minutes before sunrise) and civil twilight (28 ± 4 minutes before sunrise) on normal full moon nights, while on the eclipse night, bats started returning to the roost about an hour later (304 minutes before sunrise), and return flights ended during nautical twilight (29 minutes before sunrise) (Table 1; Fig. 1 a and c).

Table 1 - Activity of bats during full moon and lunar eclipse. ^aSunrise and sunset times obtained from www.timeanddate.com for the corresponding nights. ^b Time when the bat reached the first foraging site in a given night; ^c Time when the bat left the last foraging site in a given night. *Overall study period (N=54 nights); ^dData from 16th – 18th June 2019 (Full Moon was on 17th June). ^eData from the week before (10th – 15th July; N=4 nights) and week after (18th – 22nd July; N=4 nights) the eclipse (17th July 2019). (–) Not Available

Species	Nights	Month and date	Emergence time (minutes after sunset ^a)		Return time (minutes before sunrise ^a)		Time spent out (minutes)	Total distance travelled (km)
			Start	End	Start	End		
<i>Rousettus leschenaultii</i> (colony)		January 12th	58	404	400	30	-	-
		February 11th	33	153	540	30	-	-
		March 12th	34	385	408	33	-	-
		April 10th	48	465	331	26	-	-
		May 10th	28	273	299	24	-	-
		Mean±SD	40.2±12.42	336.0±123.62	395.6±92.92	28.6±3.58	-	-
	Total eclipse (27th July 2018)	36	336	304	29	-	-	
<i>Pteropus giganteus</i> (colony)		March 21st	13	37	-	-	-	-
		April 21st	6	42	304	4	-	-
		May 18th	20	44	236	21	-	-
		June 16th	17	42	237	19	-	-
		Mean±SD	14.0±6.06	41.3±2.99	259.0±38.97	14.7±9.29	-	-
	Partial eclipse (17th July 2019)	20	45	364	24	-	-	
<i>Pteropus giganteus</i> (tracking)		*Overall (June – August 2019)	35±9	57±17 ^b	355±46 ^c	336±46	308±42	14.74±2.00
		*Full moon nights	34±3	59±18 ^b	310±18 ^c	299±20	345±18	15.43±1.56
		**Week before eclipse	45±19	65±17 ^b	391±15 ^c	371±13	265±28	14.8±2.33
		**Week after eclipse	31±5	52±11 ^b	372±19 ^c	352±20	300±25	14.53±0.66
	Partial eclipse (17th July 2019)	43	53^c	369^c	349	290	13.4	

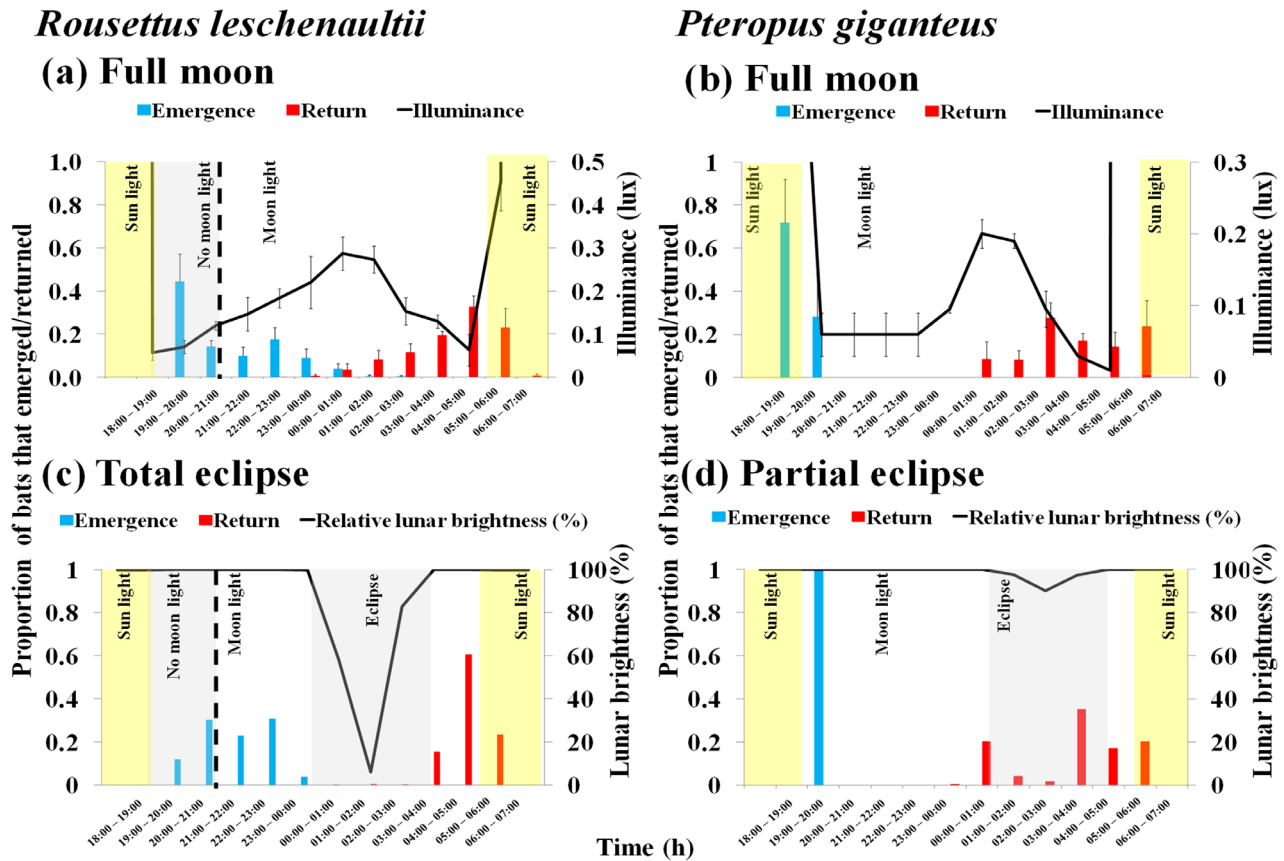


Fig. 1 - Whole night flight activity patterns of pteropodid bats. The blue bars indicate proportions of emerging bats and the red bars indicate proportions of returning bats. *Roussettus leschenaultii* activity during (a) full moon (modified from Murugavel et al., 2021) and (c) total lunar eclipse (27th July 2018). *Pteropus giganteus* activity during (b) full moon and (d) partial lunar eclipse (17th July 2019). The black lines in (a) and (b) indicate mean light levels (lux) measured at the roosts, and in (c) and (d) indicate relative lunar brightness (%). All error bars denote standard errors. The areas shaded in white denote periods when the roost well was exposed to moonlight, grey denotes no moonlight/eclipse and yellow indicates sunlight.

The partial eclipse occurred between 00:13 h and 05:47 h with the relative brightness decreasing from 01:31 h – 04:29 h. Flights were initiated by the *P. giganteus* colony 20 minutes and 14 ± 6 minutes after sunset (mean \pm SD; Range: 6 – 20 minutes) on the eclipse night and on other full moon nights, respectively. Return flights were terminated 24 minutes and 14 ± 9 minutes before sunrise (mean \pm SD; Range: 4 – 21 minutes) on the eclipse night and other full moon nights, respectively (Table 1). During this partial lunar eclipse, the relative lunar brightness decreased by only 3% during the peak of eclipse (03:00 h) compared to uneclipsed hours. However, 37% of the bats returned to the roost during the darkest period of the eclipse between 02:00 – 04:00 h, compared to 30 – 62% during the same time interval on other full moon nights, at light levels of up to 0.2 lux (Fig. 1 b and d).

The tracked *P. giganteus* individual from the same colony emerged at 19:25 h and returned to the roost at 00:15 h when the eclipse was beginning (Table 1). It covered a distance of 13.4 km and spent 290 minutes outside the roost on the partial eclipse night. The flight timing, distance covered per night and time spent outside the roost did not vary much throughout the study period (54 nights; Table 1).

DISCUSSION

The total and partial lunar eclipses coincided with the time when both bat species returned to the roost. We observed slight differences in return flight times between the total eclipse and other full moon nights, for *R. leschenaultii* but not for *P. giganteus*. On the total eclipse night, individuals of *R. leschenaultii* started returning to the roost later than on other full moon nights, and activity was minimal (<1% of individuals) at the roost during the eclipsed time intervals compared to other full moon nights. The proportion of the colony returning to the roost increased after the completion of the eclipse. These differences in flight activity between *R. leschenaultii* and *P. giganteus* may be linked to species-specific responses to a change in ambient light during lunar eclipses. However, it is also possible that total and partial eclipses affect bat flights differently. Since we did not study both species during partial and total eclipses, we are unable to distinguish between these two factors in our study. More comparative studies are required for a better understanding of how eclipses affect flight activity in different bat species.

Previous work reported that lunar eclipses influence nocturnal activity in the lemur *Eulemur fulvus rufus* and in tropical bats (Usman et al. 1980, Donati et al. 2001, Singaravelan & Marimuthu 2002). Foraging activity of cave-roosting insectivorous bats increased during a partial lunar

eclipse compared to other parts of the night (Usman et al. 1980). Flight activity of *R. leschenaultii* decreases with increase in ambient light levels and across moon phases, both at roosting and foraging sites (Sudhakaran & Doss 2012, Murugavel et al. 2021). This species is also known to prefer darker twilight zones and moonless nights when compared to *P. giganteus* and *C. sphinx* in the same area (Murugavel et al. 2021). Hence, reduced return activity of *R. leschenaultii* individuals to the roost may be explained by increased activity (for instance at foraging sites) at low ambient light levels during the eclipse.

The onset and offset of *P. giganteus* flights appeared to be unaffected by moon phase in two previous studies (Sudhakaran et al. 2012, Murugavel et al. 2021). *Pteropus giganteus* typically completes emergence flights within an hour after sunset and returns to the roost between midnight and sunrise. Our observations are consistent with these reports of emergence and return activity in this species. However, we do not know how these patterns change during a total eclipse when the light levels are considerably lower than during the partial eclipse that we studied. On the partial eclipse night, the GPS-tracked adult male was one of the few individuals that returned to the roost by midnight and before the start of the eclipse. However, more tracking studies from multiple individuals are essential to generalise effects of ambient moon light and lunar eclipses on the movement patterns of *P. giganteus*. Although previous studies on bats have shown reduced activity at foraging sites during total and partial eclipses, more roosting site observations, especially on species that roost openly on trees, are required to understand the effect of lunar eclipses and ambient light on their activity. Future studies that simultaneously examine flight activity at multiple roosts during lunar eclipses and across moon phases are needed to better understand their effects on bat activity.

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REFERENCES

- APPEL, G., LÓPEZ-BAUCELLS, A., ERNEST-MAGNUSSON, W. & BOBROWIEC, P. E. D. (2017). Aerial insectivorous bat activity in relation to moonlight intensity. *Mamm Biol*, 85: 37-46. <https://doi.org/10.1016/j.mambio.2016.11.005>
- BÖRK, K. S. (2006). Lunar phobia in the greater fishing bat *Noctilio leporinus* (Chiroptera: Noctilionidae). *Rev Biol Trop*, 54(4): 1117-1123.
- DONATI, G., LUNARDINI, A., KAPPELER, P. & BORGOGNINI TARLI, S. (2001). Nocturnal activity in the cathemeral red-fronted lemur (*Eulemur fulvus rufus*), with observations during a lunar eclipse. *Am J Primatol*, 53(2): 69-78. [https://doi.org/10.1002/1098-2345\(200102\)53:2<69::AID-AJP2>3.0.CO;2-R](https://doi.org/10.1002/1098-2345(200102)53:2<69::AID-AJP2>3.0.CO;2-R)
- ELANGO VAN, V. & MARIMUTHU, G. (2001). Effect of moonlight on the foraging behaviour of a megachiropteran bat *Cynopterus sphinx*. *J Zool*, 253(3): 347-350. <https://doi.org/10.1017/S0952836901000310>
- FERNÁNDEZ-DUQUE, E., DE LA IGLESIA, H. & ERKERT, H. G. (2010). Moonstruck primates: owl monkeys (aotus) need moonlight for nocturnal activity in their natural environment. *Plos One*, 5(9): e12572. <https://doi.org/10.1371/journal.pone.0012572>
- JULIEN-LAFERRIÈRE, D. (1997). The Influence of moonlight on activity of woolly opossums (*Caluromys phillander*). *J Mammal*, 78(1): 251-255. <https://doi.org/10.2307/1382659>
- LANG, A. B., KALKO, E. K. V., RÖMER, H., BOCKHOLDT, C. & DECHMANN, D. K. N. (2006). Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia*, 146: 659-666. <https://doi.org/10.1007/s00442-005-0131-3>
- LIMA, S. L. & O'KEEFE, J. M. (2013). Do predators influence the behaviour of bats? *Biol Rev*, 88(3): 626-644. <https://doi.org/10.1111/brv.12021>
- LOCKARD, R. B. & OWINGS, D. H. (1974). Moon-related surface activity of bannertail (*Dipodomys spectabilis*) and fresno (*D. nitratoides*) kangaroo rats. *Anim Behav*, 22(1): 262-273. [https://doi.org/10.1016/S0003-3472\(74\)80078-3](https://doi.org/10.1016/S0003-3472(74)80078-3)
- LONGLAND, W. S. & PRICE, M. V. (1991). Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology*, 72(6): 2261-2273. <https://doi.org/10.2307/1941576>
- MELLO, M. A. R., KALKO, E. K. V. & SILVA, W. R. (2013). Effects of moonlight on the capturability of frugivorous phyllostomid bats (Chiroptera: Phyllostomidae) at different time scales. *Zoologia (Curitiba)*, 30(4): 397-402. <https://doi.org/10.1590/S1984-46702013000400005>
- MORRISON, D. W. (1978). Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Anim Behav*, 26(3): 852-855. [https://doi.org/10.1016/0003-3472\(78\)90151-3](https://doi.org/10.1016/0003-3472(78)90151-3)
- MURUGAVEL, B., KELBER, A. & SOMANATHAN, H. (2021). Light, flight and the night: effect of ambient light and moon phase on flight activity of pteropodid bats. *J Comp Physiol A*, 207: 59-68. <https://doi.org/10.1007/s00359-020-01461-3>
- MUSILA, S., BOGDANOWICZ, W., SYINGI, R., ZUHURA, A., CHYLARECKI, P. & RYDELL, J. (2019). No lunar phobia in insectivorous bats in Kenya. *Mamm Biol*, 95: 77-84. <https://doi.org/10.1016/j.mambio.2019.03.002>

- NAIR, G. N., ELANGO VAN, V. & SUBBARAJ, R. (1998). Influence of moonlight on the foraging behaviour of the Indian short-nosed fruit bat *Cynopterus sphinx*: radio-telemetry studies. *Curr Sci India*, 74(8): 688-689.
- PRUGH, L. R. & GOLDEN, C. D. (2014). Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J Anim Ecol*, 83(2): 504-514. <https://doi.org/10.1111/1365-2656.12148>
- RIEK, A., KÖRTNER, G. & GEISER, F. (2010). Thermobiology, energetics and activity patterns of the Eastern tube-nosed bat (*Nyctimene robinsoni*) in the Australian tropics: effect of temperature and lunar cycle. *J Exp Biol*, 213(15): 2557-2564. <https://doi.org/10.1242/jeb.043182>
- SALDAÑA-VÁZQUEZ, R. A. & MUNGUÍA-ROSAS, M. A. (2013). Lunar phobia in bats and its ecological correlates: A meta-analysis. *Mamm Biol*, 78(3): 216-219. <https://doi.org/10.1016/j.mambio.2012.08.004>
- SÁNCHEZ, O., VARGAS, J. A. & LÓPEZ-FORMENT, W. (1999). Observations of bats during a total solar eclipse in Mexico. *The Southwestern Naturalist*, 44(1): 112-115.
- SINGARAVELAN, N. & MARIMUTHU, G. (2002). Moonlight inhibits and lunar eclipse enhances foraging activity of fruit bats in an orchard. *Curr Sci India*, 82(8): 1020-1022.
- SUDHAKARAN, M. & DOSS, P. S. (2012). Food and foraging preferences of three pteropodid bats in southern India. *J Threat Taxa*, 4(1): 2295-2303. <https://doi.org/10.11609/JoTT.o2227.2295-303>
- SUDHAKARAN, M. R., SWAMIDOSS, D. P. & PARVATHIRAJ, P. (2012). Emergence and returning activity in the Indian flying fox, *Pteropus giganteus* (Chiroptera: Pteropodidae). *Int J Geogr Geol*, 1(1): 1-9.
- USMAN, K., HABERSETZER, J., SUBBARAJ, R., GOPALKRISHNASWAMY, G. & PARAMANANDAM, K. (1980). Behaviour of bats during a lunar eclipse. *Behav Ecol Sociobiol*, 7: 79-81. <https://doi.org/10.1007/BF00302522>