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## Sex ratio, population structure and roost fidelity in a free-ranging colony of Indian false vampire bat, *Megaderma lyra*

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**We studied sex ratio, population structure and roost fidelity in Indian false vampire bat, *Megaderma lyra* for four years using mark-recapture method, in a free-ranging colony at Pannian cave, Madurai, South India. Jolly–Seber analysis of mark-recapture data showed variable fluctuation in population size of both sexes. The population size from 2001 to 2004 varied from 138 to 37 for males and 213 to 61 for females. In all the years, females outnumbered males and sex ratio ranged between 0.2 and 0.3. Compared to males, females exhibited low roost fidelity, and also showed high percentage of emigration across four years. However, there is no significant difference in percentage of immigration between the sexes. We predict that bats exhibit sexually dimorphic dispersal behaviour that depends on time and space, similar to other mammals and we hypothesize a few reasons for this dispersal, including population density, habitat destruction and inbreeding avoidance.**

**Keywords:** Dispersion, *Megaderma lyra*, population structure, roost fidelity, sex ratio.

EVOLUTIONARY theory predicts that most populations should consist of roughly as many males as females. Females in relatively good physiological condition should produce offspring of the more expensive sex, if the increased allocation is likely to benefit the fitness of offspring more than it would benefit the cheaper sex<sup>1</sup>. Thus, the ability to control the sex of her offspring could be of survival value to a mother. Sex ratio variation is observed in many mammals such as red deer, soay sheep, rhesus monkeys and rodents. In ungulates, the maternal condition is one of the important factors determining the sex ratio of a population<sup>2,3</sup>. For example, in polygynous red deer *Cervus elephus*, maternal dominance governs the sex ratio of offspring, where the dominant mothers produce significantly more number of sons than their subordinates<sup>2</sup>. However, increasing population size decreases number of males born to them<sup>4</sup>. Similarly, in soay sheep *Ovis aries*, sex-ratio variations are due to maternal condition and are independent of ecological variables such as population growth rate and weather conditions<sup>3</sup>.

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In majority of bat species, there is an unbalanced sex ratio with females far outnumbering males, whereas the sex ratio is even during the juvenile life<sup>5</sup>. A few studies have described the reasons for unbalanced sex-ratio in bats<sup>6</sup>, but most reports are fragmentary. In general, sex-ratio studies in bats are relatively difficult due to their high potential for rapid movement over long distances and recaptures are often low<sup>7</sup>. However, studies on population structure and sex-ratio variations, consecutively for several years, help to understand the social organization and dispersal behaviour of bats<sup>8</sup>. Data, particularly on this aspect are scanty for bat species in India.

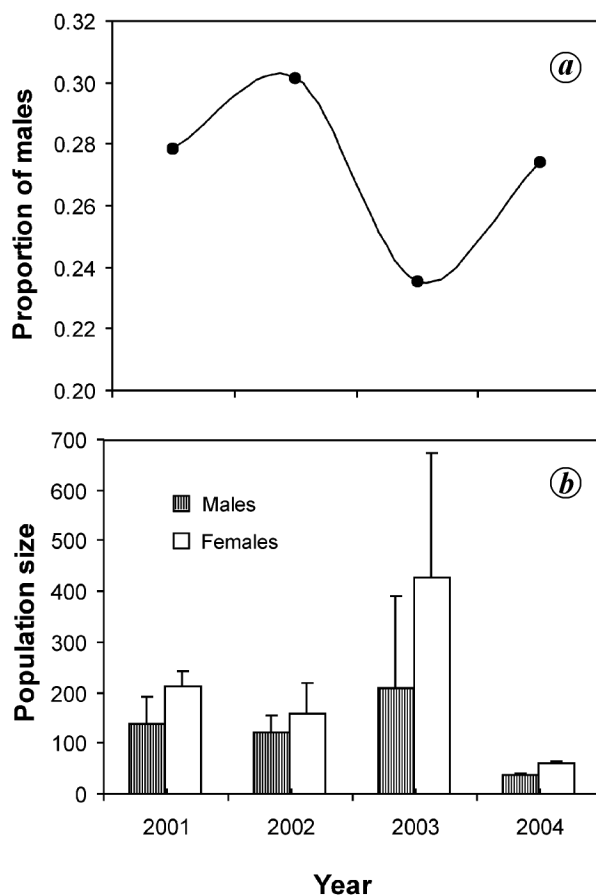
Although we have adequate information on diet, echolocation and foraging ecology of Indian false vampire bats<sup>9-11</sup>, knowledge about population structure and demography is still scanty<sup>12</sup>. Indian false vampire, *Megaderma lyra* preferentially roosts in caves, but also can easily exploit man-made structures such as temples, unused buildings, etc. as stable roost sites<sup>13</sup>. They breed once a year, the period of parturition falls between January and May, and females produce a single young<sup>14</sup>. Several studies have documented the sexual segregation in this species, but the exact reasons for this are still unknown<sup>13,15</sup>. The present study addresses sex ratio and population size conducted for four years. Since rainfall correlates with the abundance of insects and frogs, a prime food resources for *M. lyra*<sup>9</sup>, we tested whether this ecological factor influences any changes in population size during these four years, and also is a cause for dispersion.

The study was carried out in a colony of *M. lyra* roosting in a cave at Pannian hill complex (lat. 9°58'N, long. 78°10'E) situated ca. 10 km northwest of the Madurai Kamaraj University campus. The colony at Pannian cave denotes a single large population of *M. lyra*, where they share the roost with three other smaller microchiropteran species<sup>12</sup>. Since only one portion of the population could be captured at any one time from this large colony, we used mark-recapture method to estimate the population size of bats. Mark-recapture studies were conducted during four breeding seasons (2001–04). Each year, bats were captured and marked from February through May at fortnightly intervals. We trapped bats using a nylon mosquito net by covering the mouth of the cave during their return after foraging. Adults and sub-adults of both sexes were tagged with neck collars containing coloured beads, different colours representing 0 to 9. The young ones attached to their mothers are not banded. The number of recaptures was counted for both males and females each year. The mark-recapture data were analysed using Jolly–Seber method to estimate population size<sup>12</sup>. Jolly–Seber analyses were performed using Krebs/Win ver. 1.02. The proportions of males were calculated for each year.

We used chi-square goodness-of-fit test to check whether the number of males versus females deviated from a 1 : 1 ratio, and one-way ANOVA to test the difference in total population size and sex ratio between years. Differences among sexes in percentage of immigration and emigration

for all four years were also tested with chi-square test. General linear model (GLM) multivariate analysis was performed to test whether ecological variable of rainfall affects population size during these four years. Ecological data were obtained from the Regional Meteorological Station, Chennai.

Jolly–Seber estimates of population size of *M. lyra* at Pannian cave, show variable fluctuation in total number of both sexes for all the four years (Figure 1 b). The population size in 2001 varied from 102 to 176 for males and 193 to 234 for females, but the numbers decreased precipitously in 2004, 35 to 39 for males and 40 to 62 for females. Population size was maximum in 2003, due to high percentage of immigration (Table 1). Females show significantly high percentage of emigration than males ( $\chi^2 = 17.92$ ,  $df = 2$ ,  $P < 0.05$ ), but there is no significant difference in percentage of immigration ( $\chi^2 = 1.97$ ,  $df = 2$ ,  $P = 0.37$ ) between the sexes for all years (Table 1). Furthermore, percentage of recapture of same individuals for more than one year is high for males (Figure 2), and therefore males showed high roost fidelity than females



**Figure 1.** Demography data of Indian false vampire bat *Megaderma lyra* at Pannian cave, Madurai for four consecutive years after Jolly–Seber analysis: (a) sex-ratio and (b) population size.

**Table 1.** Mark-recapture data of *Megaderma lyra* in matrix of years (2001–04), representing percentage of recapture, emigration and immigration. Emigration and immigration result using Jolly–Seber analysis (Sripathi *et al.*<sup>12</sup>)

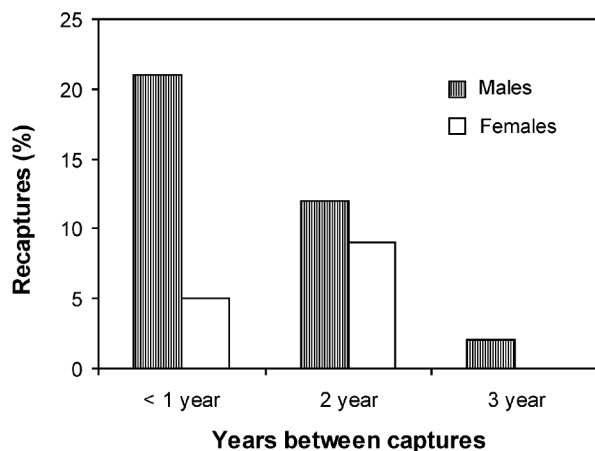
Year	Total marked	Total number of recaptures (% of recaptures in parenthesis)				Emigration (%)	Immigration (%)
		2001	2002	2003	2004		
2001	74	4 (11)*	–	–	–	–	
2002	47	22 (26)**	7 (14) *	–	2	11	
2003	45	13 (17) <sup>#</sup>	15 (18)**	7 (15) *	32	17	
2004	12	3 (6) <sup>¶</sup>	7 (14) <sup>#</sup>	9 (18)**	10 (42) *	8	
2001	45	3 (18)*	–	–	–	–	
2002	42	17 (23)**	6 (12)*	–	26	22	
2003	35	7 (12) <sup>#</sup>	16 (27)**	4 (15)*	33	17	
2004	22	2 (5) <sup>¶</sup>	4 (10) <sup>#</sup>	4 (9)**	11 (55)*	18	

\*Number of bats recaptured in the same year after marking (i.e. capture session at fortnightly intervals in the same year).

\*\*Number of bats marked in the first year and recaptured in the second year.

<sup>#</sup>Number of bats marked in the first year and recaptured in the third year.

<sup>¶</sup>Number of bats marked in the first year recaptured in the fourth year.



**Figure 2.** Comparison of roost fidelity between males and females based on repeated recaptures of same individuals.

( $\chi^2 = 14.03$ ,  $df = 2$ ,  $P < 0.001$ ). Mark-recapture study shows that 44% of those recaptured were male, which does not differ significantly from a sex ratio of unity ( $\chi^2 = 9.66$ ,  $df = 1$ ,  $P = 0.56$ ). However, from the estimated population size using Jolly–Seber analysis, the sex ratio is female-biased and ranges between 0.2 and 0.3 (Figure 1 a), and differed significantly from unity ( $\chi^2 = 30.58$ ,  $df = 11$ ,  $P < 0.05$ ) across all the years. Between years, total population size differed significantly (one-way ANOVA;  $F_{3,8} = 7.04$ ,  $P < 0.05$ ) but not sex ratio (one-way ANOVA;  $F_{3,8} = 0.26$ ,  $P = 0.85$ ). Rainfall did not explain significant variation in population size ( $F_{1,4} = 1.068$ ,  $P = 0.30$ ), when this ecological factor was compared for each year with population size (GLM multivariate analysis; population size vs ecological factor  $\times$  year).

The present study suggests that both males and females had long-term associations for more than one year within the same roost site as evident from the continuous recaptures of the same individuals between successive years. Adult males and females exhibited both immigration and emigration, and this implies that both sexes use alternative roosts, where they can mix with other colonies. A few individuals (~ 10%) of the marked population were observed to roost along with unmarked bats in a nearby cave (Tiger cave), situated < 1 km towards west of the native roost Pannian cave. However, we could not rule out the possibility of the remaining migrated population having moved to other caves. The availability of food resource is an important factor limiting the population size and causes dispersion from the natal roost<sup>9</sup>. Nevertheless, the ecological factor of rainfall that governs food availability remains constant throughout the study years. The most plausible reason that we could ascertain were population density and habitat destruction that influence an individual's decision to disperse at any particular time<sup>12</sup>. On the other hand, physiological factors, including neuroendocrine, metabolic and energetic variables also influence the probability or timing of dispersal behaviour<sup>16</sup>.

The population size of *M. lyra* lacks a temporal inter-annual periodicity and sex ratio is always skewed with females outnumbering males for all the years. This implies that they exhibit a sexually dimorphic dispersal pattern that depends on space and time similar to other mammals<sup>16</sup>. Adult *M. lyra* males exhibit seasonal dispersal after mating<sup>13,15</sup> by forming an all-male group away from the natal roost during August through October within a short distance of < 1 km. Our previous report<sup>12</sup> suggests that *M. lyra* males preferentially disperse to avoid competition with pregnant females for food resources in the same foraging

grounds and thereby increasing female survival rate. The skewed sex ratio may also be due to the differential mortality of males during the growth period<sup>5,6</sup>, and human poaching of bats for food and medicine in the study area<sup>12</sup>.

Although males prefer to disperse after mating, the timing of dispersion of female *M. lyra* is obscure. The daily migratory activity for foraging is different between sexes, females prefer to forage long distances of more than 4 km, away from the roost and males have a relatively short home range<sup>10</sup>, within 500 m. Therefore, females have a greater chance to discover new roosting sites since their home range is large, thereby forming small groups. Yet another reason for female dispersion involves the maternal care of their young ones<sup>13,14</sup>. *M. lyra* shows a high degree of between-litter siblicide<sup>17</sup>, where a first-year born sub-adult kills the newly born pup, born to its own mother. In order to avoid siblicide, pregnant females may leave the roost to form new maternity colonies away from their natal roosts. It is clear in both the sexes that dispersion occurs mainly by fission, where the parent group divides into a few distinct daughter groups as in many mammals<sup>16</sup>.

Studies of variation in wing morphology and its correlations with population size of several vespertilionid bat species have shown that wing morphology is closely associated with migration and dispersal abilities of bats<sup>18,19</sup>. Entwistle *et al.*<sup>18</sup> suggested that species with slow, manoeuvrable flight which are specialized as gleaners (act of taking prey from surface) are more likely to form the small groups, with some degree of population structuring when compared to species specialized for long-range aerial foraging. *M. lyra* is a gleaning carnivorous species which has similar wing morphology and slow manoeuvrable flight, reflecting a tendency of forming small groups and presumably resulting in high degree of gene flow between populations. This is corroborated with studies on genetic relatedness within and between colonies, suggesting that *M. lyra* is an interbreeding unit, where females apparently seek mating partners from outside the native colony<sup>20</sup>. Low roost fidelity and high percentage of emigration by females compared to males further substantiates that female *M. lyra* disperse to avoid inbreeding. It was proved in *Rhinolophus ferrumequinum* that outbreeding increases offspring survival thereby promoting population stability and growth<sup>21</sup>. Further studies are required to understand the dispersal abilities of both sexes in *M. lyra* with large number of population samples between colonies from long distances and extensive genetic analysis is necessary to prove inbreeding avoidance.

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