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Source: Acta Chiropterologica, 6(1) : 145-154

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/001.006.0111

Acta Chiropterologica, 6(1): 145–154, 2004
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS

Population size and survival in the Indian false vampire bat *Megaderma lyra*

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We used the Jolly-Seber method to analyze mark-recapture data and estimate both survival and population size in the Indian false vampire bat *Megaderma lyra* in Madurai (South India). Population size of bats from 2001 to 2003 varied from 379 to 476, and showed fluctuation in numbers for both sexes. The mean (±SE) survival rate of females (1.26 ± 0.33) exceeded that of males (1.02 ± 0.16) although the differences were not statistically significant. We observed a gradual decline in reproduction as indicated by the number of pups born in each year. This was consistent with a declining trend in population size from 1995 to 2003. We hypothesize a few reasons for this fall in population size, including habitat destruction and human poaching of bats.

Key words: mark-recapture, Jolly-Seber, population estimation, survival rate, *Megaderma lyra*

INTRODUCTION

Changes in the abundance of mammalian populations depend upon four parameters: birth, death, immigration and emigration (Usman, 1986; Feldhamer *et al*., 1999). These parameters serve as the currency for studies of life history theory (Sterns, 1992), quantitative population ecology (Renshaw, 1991), and evolutionary ecology (Futuyma, 1998). For species conservation accurate information on abundance and population dynamics are necessary. Given the essential importance of these four parameters, capture-recapture techniques were developed for the design and analysis of population dynamics of animals (Lindberg and Rexstad, 2002).

Estimation of population size of bats is extremely difficult due to their high potential for rapid movement over long distances, the complex and unpredictable distribution pattern of the roost, and the tendency for individuals to hide inside inaccessible places even within roosts (Ransome, 1989). Moreover, it is also difficult to estimate population parameters of nocturnal animals within a short span of time (Usman, 1986). Heideman and Heaney (1989) suggested that capturing bats was often difficult, marking them presents some unique problems and recapture rates are often low. Therefore, population numbers of bats could not be estimated by other methods because populations were open and the bats are not equally catchable (Krebs, 1989; Happold and Happold, 1996). The most common method used for 'open' populations is the Jolly-Seber model which helps in estimating both mortality and population size (Seber, 1982).

In bats, mark-recapture was first used by Allen (1921) to study migration. Observations on recaptures of banded individuals make up samples of the banded subset and from these samples, population properties such as movement, survival, fecundity, growth rate, and exploitation may be estimated (Keen, 1988; Balasingh *et al*., 1992). Mark-recapture experiments help to determine the longevity (Heideman and Heaney, 1989) and relative abundance of bats (Gaisler and Chytil, 2002), and they also provide information about the activity (Kunz and Brock, 1975), social behaviour (Fleming, 1988), reproductive status (Nathan *et al*., 2001), and roost fidelity and habitat selection (Whitaker and Gummer, 2000).

Early mark-recapture analyses used ad hoc methods aimed at estimating age-specific mortality with actuarial approaches (Keen, 1988). Some studies followed simpler approaches to predict rough estimates of annual and sex specific survival rates (e.g., Keen and Hitchcock, 1980; Hitchcock *et al*., 1984; Gerell and Lundberg, 1990). In the past 50 years, methods with significant advantages over these life-table analyses have been developed. Hoyle *et al*. (2001) applied the Cormack-Jolly-Seber model to estimate the survival rate of *Macroderma gigas*. They mainly focused on demography concerned with age-specific survival and also the influence of climatic conditions such as rainfall and temperature. Seasonal variation in the survival rate of *Pipistrellus pipistrellus* was studied recently with sophisticated modelling, suggesting that hibernation does not apparently entail a survival cost for bats (Sendor and Simon, 2003).

Data on population size, density, and survivorship are scanty for bats and are essentially non-existent for most species, especially in India. Therefore, we conducted a mark-recapture census on the largest population of *M. lyra* in Madurai during four breeding seasons. The data were analyzed through the Jolly-Seber model. Our main objectives were to (1) document changes in the size of the adult population and determine its present status and (2) estimate what changes have occurred in survival and reproduction and relate these to the changes in population size.

Materials and Methods

Study Animal

Megaderma lyra is a fairly large carnivorous bat that can be easily identified by its large medially fused pinnae and triple lobed noseleaf. The forearm length of males is 66.9 ± 1.56 mm (n = 50) and that of females is 68.6 ± 1.67 mm (n = 50). The body mass of males is 37.3 ± 1.8 g (n = 30) and that of females is 38 ± 2.1 g (n = 30).

The species is well adapted to caves as well as temples, old buildings, and artificial underground structures (Brosset, 1962). The period of parturition falls between January and May (Emmanuvel Rajan and Marimuthu, 1999), and female produce a single young during a reproductive season. This species feeds on large insects and small vertebrates such as frogs, mice, fish, and geckoes (Advani, 1981; Habersetzer, 1983), which are usually taken from surfaces such as tree bark, rock, wall, or water level, therefore the species is thought to be a gleaner (Neuweiler, 1989; Marimuthu, 1997). *Megaderma lyra* also preys on small birds (Green, 1907) and small bats, such as *Pipistrellus mimus* (McCann, 1934; Phillips, 1922) and *Taphozous perforatus* (Prakash, 1959). For prey detection it relies on prey generated sound (Marimuthu and Neuweiler, 1987; Marimuthu *et al*., 2002) and echolocation (Möhres and Neuweiler, 1966; Schmidt *et al*., 2000).

Study Area

In Madurai (South India), *M. lyra* is present in three different regions: Samanar Hills in Keela kuyil kudi village, Thidiyan Hills, and Pannian Hills. Direct counts at daytime roosts indicated that there were about 18 bats (n = 12) in Samanar Cave and 30 bats (n = 3) in Thidiyan Cave. Of the three roosting sites, the largest colony was present in the Pannian Cave. In

1977, roughly 1,600 bats were found there (SK, unpubl. data). The cave is situated in the Pannian hill complex (09º58'N, 78º10'E), ca. 10 km NW of the Madurai Kamaraj University campus. It occupies the southern slope of the hill, about 200 m above the adjacent plain. The cave mouth has a diameter of 2.4 m and faces the zenith. The internal passage goes on both west (up to 69 m) and east (ca. 62 m) from the entrance of the cave. The daylight penetrates to a distance of about 10 m on either side of the cave entrance. The cave has numerous labyrinthine ramifications, and the bats use several of them as their roosting sites (Koilraj, 1998). A stable temperature of 27 ± 0.5ºC and a relative humidity of 85 ± 5% prevails inside the cave throughout the year (Habersetzer, 1983).

Three species of microchiropterans (*Hipposideros speoris*, *H. bicolor*, and *Rhinopoma hardwickei*) are associated with *M. lyra* there. *Rhinopoma hardwickei* roosts at the entrance, *H. speoris* occupies the middle part, *M. lyra* roosts deep inside, and *H. bicolor* inhabits all parts of the cave.

Mark-Recapture Census

Mark-recapture censuses were conducted in the Pannian Cave during four breeding seasons (1995, 2001, 2002, and 2003). Each year bats were captured and marked from February through May at fortnightly intervals. The study was restricted to the breeding season because of sexual segregation by males; males disperse after mating during August through October (Balasingh *et al*., 1994). Therefore, it is not possible to perform mark-recapture censuses throughout the year to obtain total population estimates.

Bats were captured on their return from foraging during the pre-dawn hours from 0300 hr to 0630 hr. Nylon net was used to cover the cave mouth for trapping bats. The adults and subadults of both sexes were tagged with coloured bands as described by Balasingh *et al*. (1992). The mass of tags was 0.4 g, which was equal to ca. 1% of the body mass of adult bats. The bats showed no adverse reaction to the tags and appeared to become accustomed to their tags with minimal stress.

Jolly-Seber Analysis

Population estimates were calculated using a Jolly-Seber stochastic method. Separate analyses were conducted for males and females, excluding pups. The notations follow that of Jolly (1965) and Seber (1982). The basic equation of the Jolly's method is:

$$\widehat{N}_i = \frac{\widehat{M}_i n_i}{r_i}$$

where, $\widehat{N}_i$ = the estimate of population on day i; $\widehat{M}_i$ = the estimate of the total number of marked animals in the population on day i; r_i = the total number of marked animals recaptured on day i; and n_i = the total number captured on day i.

The field data were tabulated according to the date of initial capture and the date on which the animal was last captured. The respective column was summed to give the total number of animals released and subsequently recaptured (R_i). Another table was derived giving the total number of animals recaptured on day i, bearing marks of day j or earlier; this was done by adding rows in the original table from left to right and entering the accumulated total. The number marked before time i, which are not caught in the i^{th} sample but are caught subsequently (Z_i) is found by adding all but the top entry in each column.

The total number of marked animals in the population on the sampling day is estimated using:

$$\widehat{M}_i = \frac{a_i Z_i}{R_i} + r_i$$

(where, a_i is total released)

The proportion of marked animals (α_i) in the population at the moment of capture on day i is found by:

$$\alpha_i = \frac{r_i}{n_i}$$

The total population was then estimated for each day by:

$$\widehat{N}_i = \frac{\widehat{M}_i}{\alpha_i}$$

The probability that an animal alive ($\widehat{\Phi}_i$) at the moment of release of the i^{th} sample will survive till the time of capture of the $i + 1^{th}$ sample was found as:

$$\widehat{\Phi}_i = \frac{\widehat{M}_{i+1}}{\widehat{M}_i - r_i + a_i}$$

The survival rate estimates of slightly over 1.0 may arise from sampling effects, but 'rates' greatly above this indicate a major error. Frequently it will be found that the marks of one occasion have been lost or were not recognized. Therefore, this survival rate converted to a loss rate (the effect of death and emigration):

$$\widehat{\gamma}_i = 1 - \widehat{\Phi}_i$$

This formula corrects for all accidental death or removals at time i.

The number of new animals joining ($\widehat{B}_i$) the population in the interval between the i^{th} and $i + 1$ samples and alive at time $i + 1$ is given by:

$$\widehat{B}_i = \widehat{N}_{i+1} - \widehat{\Phi}_i (\widehat{N}_i - n_i + a_i)$$

This may be converted to the dilution rate (β), which includes both additions by births and immigration:

$$\frac{1}{\beta} = 1 - \frac{\widehat{B}_i}{\widehat{N}_{i+1}}$$

Thus when there are no losses ($\widehat{\Phi} = 1.0$) and no additions ($\beta = 1.0$) the population remains constant.

Powerful software like MARK (White and Burnham, 1999), SURGE (Pradel and Lebreton, 1991), POPAN (Arnason, *et al*., 1998), and RELEASE (Burnham *et al*., 1987) have been developed for both Cormack-Jolly-Seber (see discussion) and Jolly-Seber methods. The analysis in these software packages provide extremely precise results but requires much more patience in loading data, a tedious process since most of the programs run in DOS. We used Krebs/WIN ver. 0.94 and SIMPLY TAGGING ver. 1.3 (PISCES Conservation Ltd, IRC House, Penington, Hymington, SO 41 8 GN, UK) programs, both of which are windows based and also give accurate results. The data for captures, recaptures, and releases were entered as matrices. Results were tabulated as population size and probability of survival, with their 95% confidence interval limits (Manly, 1984).

The Jolly-Seber analysis was done separately for year 1995 using five random sampling days. The result was used as a control to verify the population size in subsequent sampling years (2001 to 2003). Results were interpreted by occurrence or non-occurrence of any violation of the assumptions described by Jolly (1965) and Seber (1965). The major assumptions were: (1) all individuals, marked or unmarked, have equal probabilities of capture, (2) between sampling periods, all marked individuals have equal probabilities of survival, (3) markers do not affect the behaviour of the marked individuals and markers are not lost or overlooked, and (4) sampling time is negligible compared to the time between samples.

We used chi-square goodness of fit tests to check the first assumption of ‘equal catchability’, i.e., the population was sampled randomly with respect to its mark status, age, and sex. The test was applied to the table of marked, non-recaptures and recaptures of both sexes (Southwood, 1978; Keen, 1988; Hoyle *et al*., 2001; Hoffmann *et al*., 2003). Probability of survival is an age-dependent parameter and the rapid turnover of the colony was evaluated with respect to the maximum longevity recorded in this species (15 years — Badwaik, 1992). We used Wilcoxon signed rank test (non-parametric) to compare survival rates of males and females.

The number of pups produced per year was used as an index to measure reproductive success. During the course of the study, number of pups born was obtained by counting the number of females with pup and combining them with lactating females. Some mothers leave their pups inside the cave while going outside to forage. These females were identified by means of swollen teats.

RESULTS

General Observations

Megaderma lyra exhibited a typical pattern of flight by swooping down suddenly into the cave after foraging. On some occasions, we observed a few bats circling over the cave mouth and this behaviour was associated with rigorous wing beats. This served us as a key for identification of this species while flying. Flying back to day roost after foraging started at 03:20 hr with a maximum around 05:45 (n = 15). On all sampling days, females returned or were captured earlier than males. The timing of the end of activity ranged from 05:55 to 06:32 (n = 10).

Jolly-Seber Estimates

There was yearly variation in the colony estimates for both sexes. In 1995, being a control year, a total number of 681 females and 438 males was estimated from five sampling days. In 2001, the total number of females was 221, but in 2002 this number decreased steeply to 85 due to emigration. With an increase of 239 bats in 2003 thanks to immigration, the population increased steadily and attains a constant size of 212 bats. In contrast male population numbers were very low compared to females, with 158 bats in 2001, increasing to 233 due to immigration, and decreasing to 48 bats in 2003 (Table 1). The standard errors for some sampling days (see Tables 1 and 2)

TABLE 1. Summary of the results of Jolly-Seber analysis for three consecutive years 2001 to 2003. In the new animals joining column negative values indicate emigrants and the positive values indicate immigrants. na — no value could be computed

Year	Date	Proportion marked (α_i)	Size of marked population	Population estimate ($\widehat{N}_i$)	SE of population estimate		Probability of survival ($\widehat{\Phi}$)	SE of survival		New animals joining ($\widehat{B}_i$)
					low	high		low	high	
					♂♂					
2001	04.03.01	0.000	0.0	na	na	na	1.250	0.612	2.546	na
	18.03.01	0.222	35.0	157.5	51.7	891.6	0.643	0.300	1.416	-8.4
	06.05.01	0.286	26.4	92.3	47.1	271.6	1.075	0.636	1.803	11.6
2002	24.02.02	0.333	35.9	107.6	60.2	273.4	0.686	0.417	1.133	27.7
	09.03.02	0.300	29.4	98.1	46.4	318.2	1.656	0.689	4.088	-84.6
	31.03.02	0.765	57.0	74.5	37.1	242.4	1.429	0.304	7.488	144.0
	14.04.02	0.300	70.0	233.3	68.5	1552.9	0.373	0.108	1.422	53.6
	10.05.02	0.200	28.0	140	60.1	536.1	1.553	0.713	3.462	-61.8
2003	24.02.03	0.387	59.0	152.4	80.4	438.6	0.552	0.128	2.674	-30.0
	22.04.03	0.769	37.0	48.1	18.3	298	na	na	na	na
	14.05.03	0.381	na	na	na	na	na	na	na	na
					♀♀					
2001	04.03.01	0.000	0.0	na	na	na	1.030	0.558	1.929	(a)
	18.03.01	0.200	44.3	221.4	96.9	812.3	0.427	0.239	0.782	114.7
	06.05.01	0.118	24.5	208.0	76.8	1003.8	1.664	1.150	2.369	-129.1
2002	24.02.02	0.297	64.0	215.3	133.5	460.2	0.407	0.312	0.533	111.9
	09.03.02	0.167	32.6	195.4	48.4	1666.4	2.402	1.324	4.381	-288.9
	31.03.02	0.500	90.3	180.5	91.8	517.3	0.778	0.261	2.539	-42.7
	14.04.02	0.769	71.0	92.3	44.8	293.8	0.582	0.210	1.727	36.6
	10.05.02	0.444	37.8	85.1	45.7	224.4	3.216	1.326	8.082	60.4
2003	24.02.03	0.395	128.0	324.3	153.6	1065.1	0.861	0.132	6.678	-54.8
	22.04.03	0.556	118.0	212.4	56.3	2046.8	na	na	na	na
	14.05.03	0.474	na	na	na	na	na	na	na	na

TABLE 2. Summary of the results of Jolly-Seber analysis for year 1995. Standard errors calculated according to Manly (1984). na — no value could be computed

Sample	Probability of survival ($\widehat{\Phi}_i$)	SE of survival	
		low	high
	♂♂		
1	1.352	0.450	4.367
2	0.411	0.070	2.815
3	0.571	0.053	7.184
4	0.217	0.040	1.291
5	na	na	na
	♀♀		
1	0.651	0.327	1.351
2	1.035	0.357	3.250
3	1.848	0.236	17.266
4	0.077	0.012	0.574
5	na	na	na

were large due to a low recapture rate. The population trend from 2001 to 2003 followed a constant probability of total numbers with a slight fluctuation between years. But the number of bats were reduced in 2001 when compared to 1995. Females were most abundant on all sampling days except in 2002, when the males outnumbered females due to immigration of some individuals.

The data for males and females showed a reasonably good fit for equal catchability. There was no difference between marked, non-recaptured and recaptured bats for both males (χ^2 = 0.907, *d.f.* = 3, *P* = 0.82) and females (χ^2 = 4.64, *d.f.* = 3, *P* = 0.20), suggesting statistically equal catchability among the marked sample of animals. Between sampling periods, all marked individuals also had equal probabilities of survival (χ^2 = 0.272, *d.f.* = 3, *P* = 0.96).

The average yearly survival rates from 2001 to 2003 were 1.02 (±0.16 SE) for males and 1.26 (±0.33 SE) for females (Table 1). Nevertheless, there was no statistical difference in survival between both sexes (*Z* = 1.83, *n* = 4, *P* = 0.07) across all sampling years although there was an apparent fluctuation from negative to positive log-values of survival rates during the study period (Fig. 1).

In 1995, 110 pups were born. There was a decline to 50 pups in 2001, an increase to 60 in 2002, and again decline but to 40 in 2003. This suggests that there was a marked decrease in reproductive success over the study period, and fluctuations in pup production closely mirrored estimates for adult population.

DISCUSSION

Jolly-Seber Estimates

There is no statistical difference in survival of male and females of *M. lyra*. Nevertheless, significant differences in survival rates between sexes, were reported in other species of bats, e.g., *Pipistrellus abramus* (Funakoshi and Uchida, 1978) and *Myotis lucifugus* (Keen and Hitchcock, 1980). In *Pipistrellus pipistrellus*, sexual differences in survival rates were due to energy constraints imposed on territorial males by the resource defense polygyny mating system (Gerell and Lundberg, 1990). Sexual segregation in *M. lyra* (Balasingh *et al.*, 1994) confirms that males occupy separate roosts away from their natal sites. It appears that male dispersion after mating helps to avoid competition with pregnant females for food resources in the same foraging grounds and therefore, female survival rate exceeded that of males.

A simple model of trap dependence did not alter survival estimates (3rd assumption) and suggested positive rather than negative response to trapping. Trap-shyness (i.e. the bats learn to avoid nets following capture) was found to be more evident in males. Thus, the male population size was likely underestimated. Moreover, males suffer more tag losses than females, due to behavioural differences between the

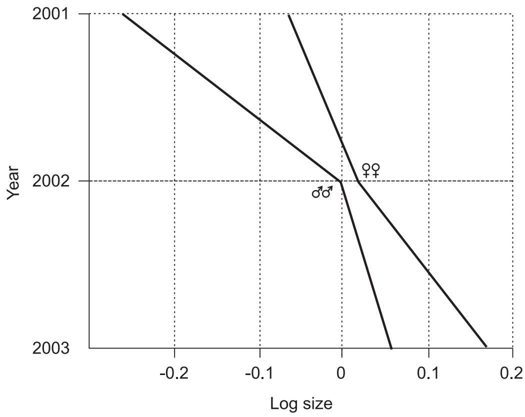

FIG. 1. Survivorship curves of males and females predicted through the results of Jolly-Seber estimates over the study periods 2001 to 2003. *x*-axis represents the log-number of survival rate and *y*-axis represents the study period

sexes, including a higher level of conflict. In all capture sessions, females were captured earlier than males. We suggest that males avoided traps by using alternative roosts, whereas females are restricted to a narrower range of roosting options (Hoyle *et al*., 2001).

Many bat biologists dealing with mark-recapture analyses (e.g., Keen and Hitchcock, 1980; Hitchcock *et al*., 1984; Keen, 1988; Gerell and Lundberg, 1990; Hoyle *et al*., 2001; Sendor and Simon, 2003) recommend the use of the Cormack-Jolly-Seber (CJS) method — a conditional Jolly-Seber design (Lindberg and Rexstad, 2002). The CJS method works very well for winter-banding data (Keen, 1988). Nevertheless, the present study describes the use of traditional Jolly-Seber model. In the CJS method the first captures are treated as uninformative constants and therefore they only allow the estimate of survival and capture rates. In the Jolly-Seber model the first captures are random variables that provide information on colony size; in addition to estimates of recruitment rate and survival (Schwarz 2001; Schtickzelle *et al*., 2003). Bias in estimates of survival probability is likely to be of minimal concern when using the Jolly-Seber model (Lindberg and Rexstad, 2002).

We limited our study to three breeding years due to constant netting and banding at a single colony may cause some negative effects (Gaisler and Chytil, 2002). Although our sample sizes were relatively small, the statistical treatment and high degree of internal consistency indicate that these data may provide the first good approximation of the population of *M. lyra* under study.

Present Population Status

Compared to 1995, the number of bats was reduced considerably by 2001. From 2001 onwards, the Jolly-Seber estimates showed some stability in probabilities until 2003. In our research there was a decline in reproductive success, which again was reflected in the colony size. It is obvious that longevity of bats depends on the reproductive success (Wilkinson and South, 2002). There was no significant difference in the survival rate between males and females although year-to-year fluctuations were evident.

The changes in the survival rate and colony size could not be attributed to changes in major climatic conditions, because the mean temperature and humidity were relatively constant and the rainfall was moderate during the entire study period. Numerous potential predators like owls, owlets, falcons, snakes, and cats frequented the roost and its vicinity. Nevertheless, the fluctuation in survival of *M. lyra* does not seem to be influenced by predators (Usman, 1986). We did not observe any predation on this species in the studied area either.

The most plausible explanation that we could ascertain from the present data was habitat destruction. In 1995, the agricultural lands formed large areas around the hill complex. These areas constituted ultimate foraging places for *M. lyra*. From 2001 onwards, the region started to be heavily occupied by human settlements and the construction of new buildings around the roosting site (the foot hills); this likely has led to decrease in the colony size due to non-availability of main prey items. We also observed human poaching on bats as food and medicine.

Overall, the populations of bats seem to be strongly regulated at stable levels over long periods, unless large-scale habitat or climatic changes, or disasters occur. This indicates that homeostatic mechanisms, showing negative feedback, may be involved (Ransome, 1989). Food availability in the habitat surrounding the breeding site is likely to be one of the most significant limiting factors in the case of *M. lyra* (Usman, 1986). Climate may severely reduce or delay the abundance of major food supplies, such as frogs or insects.

Implications for Conservation

Although the IUCN lists *M. lyra* as Least Concerned (LC), the conservation of this species seems to be quite important. Its diet choice, including a variety of insects and rodents (Advani 1981; Habersetzer 1983), may indicate species' importance in biological control for many pests of paddy and wheat crops.

Balasingh *et al*. (1997) have made an attempt to conserve selected colonies of *M. lyra* by transferring some of bats to safer roosts. They detected that 90% of these translocated bats survived in the new environment. This method of rehabilitation could be an effective conservation measure, and a way of conserving this species in disturbed landscapes.

Acknowledgements

We are grateful to two unknown referees for providing valuable comments on the earlier version of the paper. We thank Dr. K. Emmanuvel Rajan, Mr. A. Vivek, Mr. B. Karthikeyan, Mr. B. Singaravelan for their field assistance and Dr. V. Elangovan for statistical analysis. Financial support from DST and UGC (Government of India) to SK are gratefully acknowledged. Krebs/Win software is available free of charge at http://www.gause.biology.ualberta.ca/pub/jbrzusto/krebs. This study was approved by the Institutional Ethical and Bio-safety Committee of MKU and the Forestry Department, Government of India.

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Received 02 March 2004, accepted 28 May 2004