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The Mating System of *Pipistrellus kuhli* (Microchiroptera) in Israel

by Y. BARAK and Y. YOM-TOV

Dept. of Zoology, Tel Aviv University, Ramat Aviv 69978, Israel

Summary. — The mating system of the microchiropteran bat *Pipistrellus kuhli*, was studied in kibbutz Sde Eliyahu, Israel. These bats roost during the day under roofs and in wooden huts and attics and hunt in uncluttered environments (e.g., fields) to which they fly along permanent routes. From the beginning of March the females aggregate, in hundreds, at maternity colonies. Pregnant females are found between March-May and lactating females from May-July. Maximal body weight is reached in autumn (October-November) before hibernation, and in spring, due to pregnancy.

Two types of males were observed : those which roost singly all year round in permanent places located along the females' flying routes, and those which roost in small groups (7-16 individuals), which are located elsewhere. Single males are characterized by attaining maximal body weight in March and minimal body weight in October, having larger testes and exhibiting songflight and false landing displays. In contrast, the body weight of grouped males fluctuates like that of the females. They have much smaller testes and do not exhibit mating displays. It is concluded that the system of *P. kuhli* might be categorized as female resource polygamy, where females are highly social and travel over a large area but along permanent routes, and the reproductive males roost and court along these routes.

Résumé. — La reproduction de *Pipistrellus kuhli* a été étudiée en Israel. Ces chauves-souris se reposent le jour sous des toits et chassent pendant la nuit sur des parcours constants dans un environnement ouvert. Au début de mars, les femelles se réunissent par centaines dans des colonies de maternité. Les femelles gestantes se voient de mars à mai et les femelles allaitantes de mai à juillet. Le poids maximal du corps est atteint en automne (octobre-novembre), avant l'hibernation, et au printemps à cause de la gestation.

Deux types de mâles ont été observés : ceux qui se reposent isolément toute l'année dans le même endroit, près des parcours de vol des femelles, et ceux qui se reposent en petits groupes (7 à 16) qui sont localisés ailleurs. Les mâles solitaires atteignent leurs poids maximal en mars et leur poids minimal en octobre : ils ont des gros testicules et un vol bruyant et des parades de faux atterrissage. Par contre, le poids des mâles groupés fluctue comme celui des femelles. Ils ont des testicules plus petits et ne montrent pas de parades d'atterrissage.

On en conclut à une polygamie des femelles ; les femelles sont hautement sociales et voyagent sur une grande surface, mais selon des parcours constants, et les mâles reproducteurs se reposent et paradent le long de ces routes.

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INTRODUCTION

Bats exhibit a wide variety of social behaviour and organization. Though most of the species tend to aggregate (Kunz 1982) and even form colonies of up to millions (Davis *et al.* 1962), others are solitary (Bradbury 1977 *a*). Their mating system is diverse and ranges from various forms of resource polygamy (Morrison 1979 ; O'Shea 1980) to harems (Wimsatt 1977 ; Williams 1986), leks (Bradbury 1977 *b*) and promiscuity (Thomas *et al.* 1979 ; Wai-Ping and Fenton 1988).

The family Vespertilionidae is the largest among the Microchiroptera and encompasses 319 species, one third of the order (Stebbings 1984). The scant knowledge on the mating systems of this cosmopolitan family has been reviewed by Bradbury (1977 *a*). Recently, O'Shea (1980) and Lundberg and Gerell (1986) studied the mating systems of *Pipistrellus nanus* and *P. pipistrellus*. Although these two species were studied in different latitudes (Kenya and Sweden, respectively), their mating systems are basically similar, based on resource defence polygamy. The two species exhibit sexual segregation throughout the year and form harems during the mating season. Gerell and Lundberg (1985) and Lundberg and Gerell (1986) found six male territories in *P. pipistrellus*, while the females aggregate by the hundreds in maternity colonies (Swift 1980). O'Shea (1980) found an unexplained sex-ratio for *P. nanus* of 1 : 2 in favour of the males. The skewed sex-ratio exhibited in both studies might be a product of an uneven sex-ratio ; yet another possible explanation is that while some males are territorial and breed, others are not, and these two types of males rest in different localities.

We studied the mating system of *P. kuhli* in Israel and our results show basic similarity with the above two pipistrelles. The data collected enable us to give a detailed description of the mating system of *P. kuhli* and may explain the uneven sex-ratio reported in the above two studies.

METHODS

The mating system of *Pipistrellus kuhli* was studied in Kibbutz Sde Eliyahu in the Bet Shean Valley, Israel (35°31'E, 32°27'N, 180 m below sea level). Observations took place between June 1986 and May 1988. We searched the kibbutz for roosting sites of *P. kuhli* which are easily discerned by their strong smell and the remains of feces which are spread on the walls close to their openings. We believe that we identified all the large (over 10 animals) colonies in the kibbutz. Bats were caught at least once a month, mainly by using mist nets at night, but single bats or small groups were caught during the day, using butterfly nets or by hand. All bats caught were banded, weighed with a Pesola spring scale (to the nearest 0.1 g), their forearm length and testis length were measured (to the nearest 0. 1 mm) with a caliper, and their reproductive status (pregnancy, lactation) noted. Ageing and assessment of reproductive status were done according to Racey (1974). Both single and group males were visited at their roosting sites once a week, but handled only once a month to minimize disturbance. The foraging routes of the females were determined by placing observers at various localities in the kibbutz before sunset until one hour after it. We did not notice any route change during the activity season of the bats,

neither was there any foraging activity (which is easily determined acoustically) during the flight of the females to the fields. We also observed the behaviour of males near the roosting sites. Each observation lasted at least 3 hours, and included ultrasonic detection using a Q.M.C. S-200 bat detector. There were approximately 30 observations in each of the two breeding seasons, and they occurred during different hours of the night. The only other species of insectivorous bat present in our study area was *Tadarida teniotis* whose calls are at a much lower frequency than *P. kuhli.*

RESULTS

Kuhl's bats live in uncluttered environments (Schnitzler *et al.* 1987). In our study area, most of their nocturnal activity took place in open fields. Day roost sites were found in wooden huts, under roofs and attics. After emerging, the females flew directly along their permanent routes between the houses to their favourite activity fields (Fig. 1) and used the same routes when they returned late at night.

A high degree of sexual segregation was found throughout the year.

Females : The females aggregate, in hundreds, at maternity colonies at the beginning of March. These roosting sites are perennial and were used during three subsequent years. Pregnant females were found during March, April and

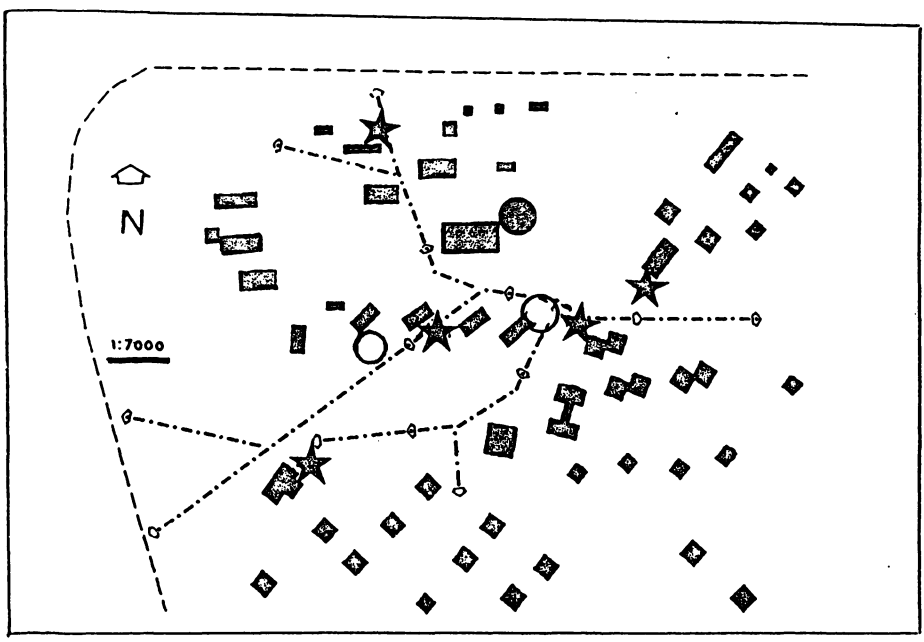

Fig. 1. — A map of the main part of the study area. buildings = Rectangles ; roosting sites of single males = stars ; roosting sites of grouped males = black dots ; breeding females' colony = open circle ; flying routes of females = dotted lines.

May and lactating females during May, June and July (Fig. 2). Flying young were observed from June onwards. *Pipistrellus kuhli* mate in September-October but fertilization is delayed and ovulation presumably occurs during February-March (Andreucetti *et al.* 1984). By the end of October the maternity roosts are deserted.

During February-October, when the females are active, they emerge from their daily roost every day at twilight and fly along permanent routes towards their hunting areas (Fig. 1). Most of the females which emerge from the same site, used the same route. These routes pass between the kibbutz houses, and the bats may fly up to 400 m before reaching their hunting areas in the agricultural fields.

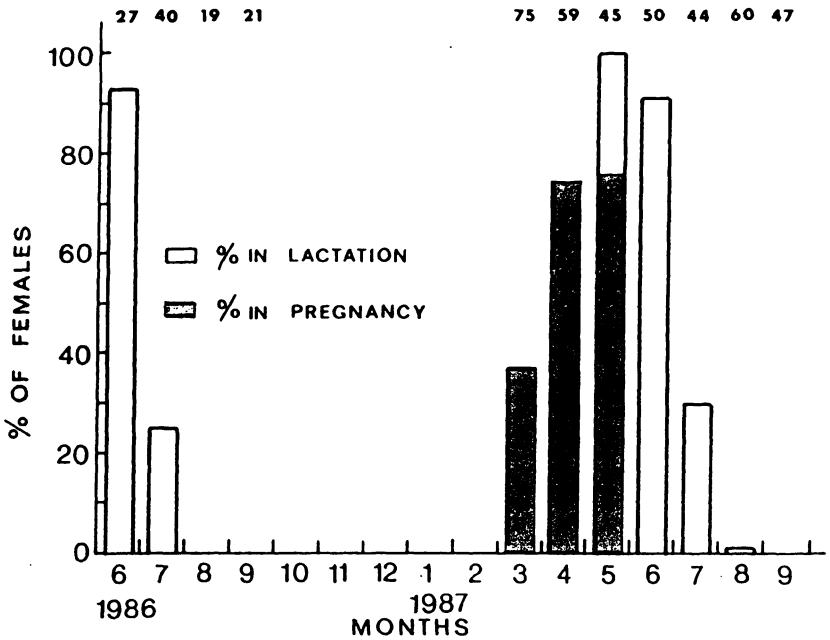

Fig. 2. — Reproductive status of females during the year. Sample size is indicated above each column.

Maximal body weight is reached during autumn (October-November) before hibernation, and during pregnancy (Fig. 3). Minimal body weight is reached in the late winter (February), probably due to exhaustion of fat reserves (Fig. 3).

Males : Two different "types" of adult males were observed, all of which were adults :

A) Single males – solitary individuals which roost alone in permanent places all year round. During our study, we observed 6 such males for periods of 5, 8, 9, 15, 19 and 19 months. All these males kept their roosting sites until they were interrupted by humans (not the authors) who, unintentionally destroyed their sites. Only twice did we see a single male in its roosting site with another individual – in both cases with females, which spent only a few hours there, one at night and the other for a day. Although mating was never observed,

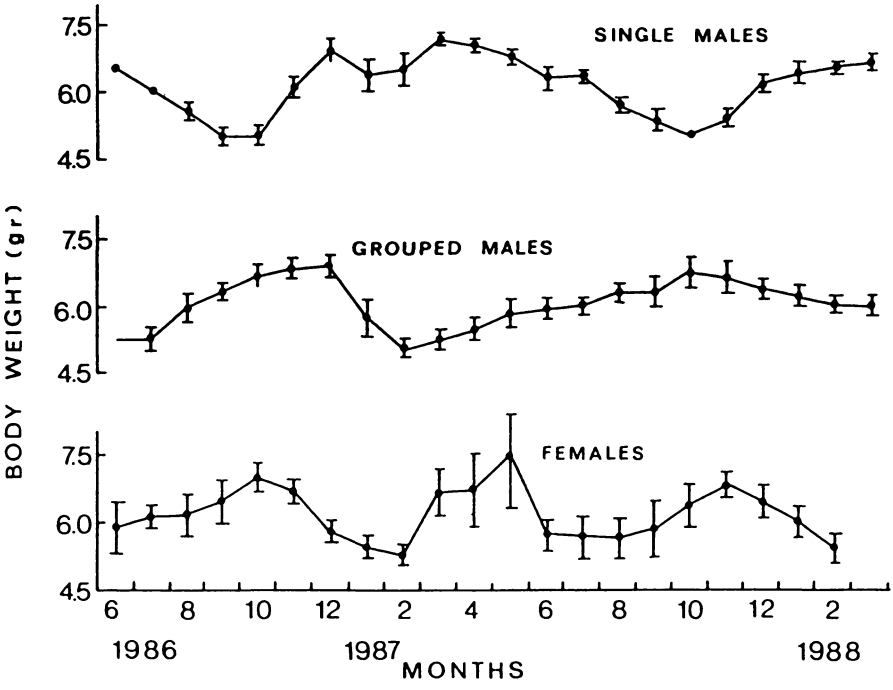

Fig. 3. — Mean (+ SD) body weight of single males, grouped males and females during the study period. The monthly sample size is single males : n = 4 ; grouped males : n = 12-20 ; mean = 18 ; females : n = 8-75 ; mean = 41. .

we believe that it occurs in the single male's roosting sites. This same male courted every observation during the whole reproductive period (mid-September to end of October 1987).

B) Grouped males – adult males which tend to stay in a group. Two day roosts of grouped males were found in the Kibbutz and observed continuously for 10 and 12 months, respectively. The numbers of males in each group varied daily between 7-16 individuals, and the longest period an individually marked male was found in the same group was 3 months. Hence, there was a high turnover rate of males in these roosts. We did not notice any seasonal change in the number of bats in a group.

Several differences were found between the single and grouped males.

1) Body weight : Single males attain their maximal body weight in March and minimal body weight in October, during the mating season (Fig. 3). The grouped males reached their minimal body weight towards the end of the winter, in February. Both maximal and minimal weights achieved by single or grouped males were similar ($t = 1.2$; $p = 0.23$), but they reached these extremes at different times of the year (Fig. 3, $t = 4.45$; $p = 0.001$). The yearly pattern of body weight of grouped males was similar to that of the females except for the period of pregnancy in the spring (Fig. 3), when the body weight of females increased above that of the grouped male.

2) Testes size : All the males had yearly circannual changes in testes size (Fig. 4). The testes are abdominal during spring to mid-summer and become scrotal at the end of July. However, in single males, testes size were much larger than those of grouped males (Fig. 4 ; $t = 4.27$; $p = 0.001$).

3) Behaviour : During September-October, single males exhibit two types of behaviour near their roosts, similar to that of territorial *P. pipistrellus (Lundberg and Gerell 1986). a)* Songflight display, which has a wide range of frequencies (between 30-45 KHZ) compared to normal ecolocation calls (35 KHZ) around their solitary dat roost, probably as a courting, and *b)* False landing display, in which they flew repeatedly towards their day roosts, landed and took off immediately, probably a pointing behaviour towards their day roost. Both types of behaviour took place during late night, after the females returned to their roosting sites from their foraging sites in the fields. It is possible that these behaviours also announce that the territory is occupied.

No songflight display or false landing display was observed near the grouped males' roosting sites.

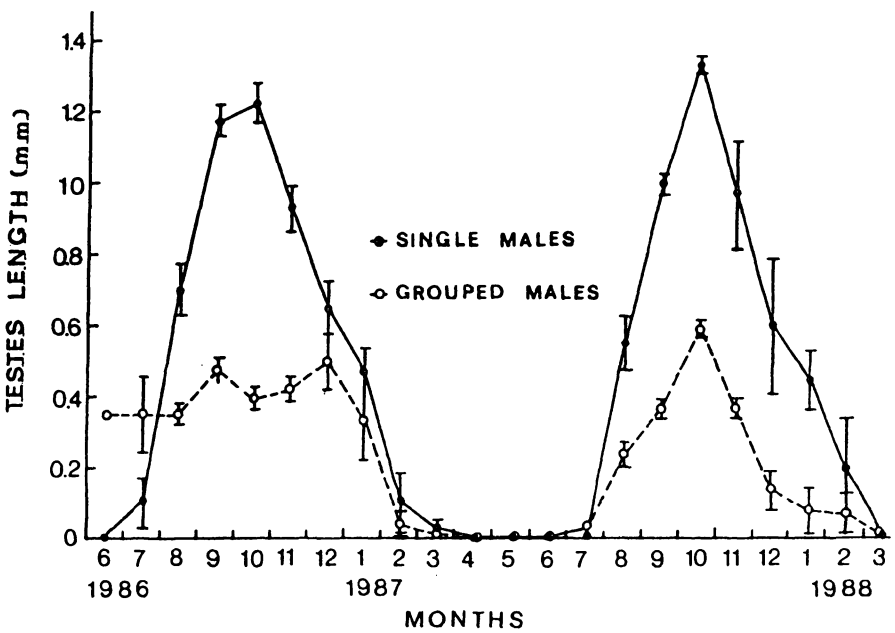

Fig. 4. — Mean testes length (+ SD) of single and grouped males during the study period. Sample size as in figure 3.

4) Day roosts location : The day roosts of single males were located along the routes which the females traversed en route to their hunting areas (Fig. 1). Day roosts of grouped males were not located close to the females' routes and no females' activity was observed along their routes to their hunting areas.

DISCUSSION

The following data indicate that in *P. kuhli* only some of the males, those which roost singly, are reproductive : These males lost weight during the mating season probably due to an increase in their sexual activity which resulted in a decrease in their hunting activity ; their testes size increased towards the reproductive period, and they display courting behaviour and roost near the females' flight routes. The existence of single males in *P. kuhli* was reported by Hanak and Elgadi (1984) and a similar behaviour was observed in both *P. pipistrellus* (Gerell and Lundberg 1985, Lundberg and Gerell 1986) and *P. nanus* (O'Shea 1980). In all three pipistrelle species, the male day roost was found to be a limiting resource. In *P. kuhli*, as was found also for *P. pipistrellus* (Lundberg and Gerell 1986), the position of the male day roost is of primary importance for mating, and only a limited number of roosts are available in the few buildings located near the flying routes of the females. Therefore, only a limited number of males can court the females. In *P. nanus*, O'Shea (1980) claims that only a limited number of roost sites are suitable for establishing harems.

Krebs and Davies (1984) categorized the various forms of female resource polygamy in mammals. According to their categorization, *P. kuhli* belong to those mammals where the females are social and their daily movements are predictable. The females roam over a large range but use regular routes to a particular resource, and the reproductive males defend a territory that is much smaller than the females' range, and attempt to mate with them as they pass through (e.g. topi, *Damaliscus lunatus* and Grevy's zebra, *Equus grevii*). *P. kuhli* clearly belong to this category : females fly along predictable routes to their feeding grounds, and the reproductive males occupy territories along these routes in order to have access to females. The non-reproductive males live in small groups which roost in localities not placed along the females' flying routes. We suggest that all 3 pipistrelles studied are resource defence polygamists. However, male *P. pipistrellus* and *P. nanus* maintain harems where they stay with their females. *P. kuhli* intercept the females en route from their foraging. Our finding of unreproductive, grouped males, if applicable to the other pipistrelles, may explain the uneven sex ratio observed in these species.

Our data also show an interesting annual rhythm in body weight which reached its peak in single males in March, while the reproductive season is in October. This phenomenon can be explained by the fact this is the time of the year when the females form their breeding colonies. The stronger the male is in March, the better territory he can defend and the best ability it gained to approach the females, while courting, 5 months later. This "delayed" behaviour shows that the social behaviour of these bats is more complicated than realized previously.

In addition, our data show *P. kuhli* in Israel are not synchronous in breeding and during May-July the females were observed in different stages of reproduction. This asynchronized breeding differs from other species such as *P. pipistrellus* (Racey and Swift 1981). A possible explanation is that the length of time in which the bats are able to reproduce in Israel is longer than in Europe, Where the summer is much shorter than in Israel.

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