Reproductive seasonality of the Egyptian fruit bat (*Rousettus aegyptiacus*) at the northern limits of its distribution

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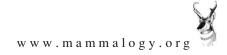* Correspondent: radek.lucan@natur.cuni.cz

We collected and analyzed data on the annual course of reproduction of the Egyptian fruit bat (*Rousettus aegyptiacus*) in 2 climatically distinct areas, the Mediterranean and the Egyptian desert, located at the northern limits of the species' distribution. In both regions, reproductive seasonality was characterized by distinct bimodality in birth timing regardless of climatic differences. A low incidence of simultaneous pregnancy and lactation indicated that both seasonal bimodal polyestry with and without postpartum estrus may occur in both regions, with a possibly lower incidence of postpartum estrus in females from the Mediterranean population. Observed shifts in birth timing between the Mediterranean and the desert study area corresponded to regional differences in fruiting phenology of major dietary plants. The male reproductive cycle was synchronized with that of females. The period of testicular recrudescence occurred during the peak pregnancy period. Because testis size was related to body mass irrespective of body size, we hypothesize that food abundance is an important trigger of male sexual activity. *R. aegyptiacus* is the sole species with seasonal bimodal polyestry among Palearctic bats.

Key words: Chiroptera, desert, Mediterranean, phenology, Pteropodidae, reproduction, reproductive pattern

Synchronization of reproduction with periods of high availability of food resources is often considered to be the driving force behind the annual course of mammalian reproduction (Bronson 1985). This is entirely true for temperate zones where food availability greatly varies due to pronounced climatic seasonality. In the tropics, where food resources are distributed relatively evenly in time, animals tend to reproduce several times a year, and synchronization of reproductive cycles within their populations is often indistinct. In the temperate zone, by contrast, strong synchronization and pronounced seasonality of reproduction are typical (Bronson and Heideman 1994).

Bats (Chiroptera), the second largest mammalian order (> 1,250 species), represent an ideal model group for studying the dynamics of these relationships in detail (Jones et al. 2009). Bats inhabit almost all climatic zones and provide numerous handy examples for testing the effects of extrinsic factors upon

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patterns of the annual cycle and patterns of reproduction. The most comprehensive survey of this topic, compiled by Racey and Entwistle (2000), reports 10 major types of bat reproductive patterns covering a relatively smooth gradient from strict seasonal monoestry, through seasonal polyestry, to aseasonal polyestry. Although all types of reproduction cycles, including diverse forms of polyestry, occur in bats living in tropical and subtropical regions, temperate bats exhibit strict seasonal monoestry.

A particular species may exhibit either a sole type of reproductive pattern throughout its distributional range, or there can be different reproductive patterns in different populations, typically as a response to climatic regimes of the regions they live in (Happold and Happold 1990). Furthermore, populations of the same species living in different latitudes may differ in the timing of their reproduction due to latitudinal shifts in phenology. However, few studies aimed to compare reproductive patterns of bat populations living under different climatic regimes (Happold and Happold 1989, 1990; Bernard and Tsita 1995; Bernard and Cumming 1997).

Here we report on our results of research focused on the annual course of reproduction in the Egyptian fruit bat, *Rousettus aegyptiacus* (Geoffroy 1810) in the northernmost part of its distributional range, including the southern part of the temperate zone of the western Palaearctic. *R. aegyptiacus* is a medium-sized pteropodid bat (100–200 g) distributed from South Africa in the south, throughout Africa and the Arabian Peninsula, to Turkey in the north and to Pakistan in the east (Kwiecinski and Griffiths 1999). Its large polytopic distributional range encompasses a latitudinal gradient covering several climatic zones, including the tropics and subtropics. With its occurrence in the eastern Mediterranean region (Benda et al. 2011) it represents the sole offshoot beyond the tropical zone of the otherwise tropical family Pteropodidae. A significant geographic variation in reproductive chronology has been reported for *R. aegyptiacus* (Kwiecinski and Griffiths 1999). Bimodal seasonal polyestry without postpartum estrus has been described in populations living at the equator in Uganda (Mutere 1968). Seasonal monoestry has been reported from South Africa (Jacobsen and Du Plessis 1976; Herzig-Straschil and Robinson 1978; Penzhorn and Rautenbach 1988). No study has looked at the reproductive seasonality of the northernmost populations in detail, and the information published so far is often contradictory and generally inconclusive (Spitzenberger 1979; Madkour et al. 1983; Qumsiyeh 1985; Korine et al. 1994; Benda et al. 2006, 2007; Albayrak et al. 2008; Nicolaou 2010).

The present paper summarizes field data on the course of reproduction of *R. aegyptiacus* in the eastern Mediterranean region (Cyprus, Turkey, Lebanon, and Jordan) and the Sahara Desert (Dakhla Oasis, Western Desert, Egypt). In accordance with hitherto published data, we expected a single reproductive period to occur in these populations. We further tested the hypothesis that populations inhabiting climatically different regions (Mediterranean versus desert climates, in the sense of Peel et al. 2007) essentially differ both in the timing and the
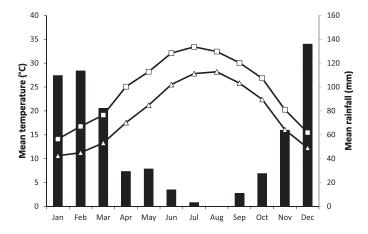

FIG. 1.—Annual course of mean monthly temperatures (Egypt, squares; Mediterranean, triangles) and precipitation (Mediterranean, vertical bars) in the 2 study areas based on data from 2009–2012. Data from the Mediterranean are based on least-square means obtained from 3 weather stations located less than 10 km from bat roosts studied and covering a latitudinal gradient of the Mediterranean study area. Note there was no rainfall in the Egyptian study area.

annual course of their reproduction. Against our expectations, we found that the bimodal pattern of reproduction is retained in both climatic regions and that females are capable of actual polyestry (with postpartum estrus) even in the northernmost populations.

MATERIALS AND METHODS

Study areas.—The data analyzed in this paper were collected between 2005 and 2013 in five countries: Cyprus, Turkey, Lebanon, Jordan, and Egypt (see Benda et al. 2011 for a detailed list of particular sites). All study populations of *R. aegyptiacus* from Cyprus, Turkey, Lebanon, and Jordan (hereafter referred to as the Mediterranean) occurred in areas with a typically Mediterranean climate (thermo-Mediterranean, sensu Blondel and Aronson 1999; warm Mediterranean, sensu Peel et al. 2007). The Egyptian study population inhabited a large isolated desert oasis (Dakhla Oasis, Western Desert) with a warm desert climate (Peel et al. 2007). The climatic characteristics of the regions (average values for 2009–2012) are summarized in Fig. 1. We averaged the mean monthly temperatures and rainfall for the Mediterranean region from 3 stations located close to (< 10 km) the bat roosts under study. A latitudinal climatic gradient runs through the study area (Mersin, Turkey; Tripolis, Lebanon; and Amman, Jordan). The mean monthly temperatures and rainfall for the Egyptian study site were measured at the weather station in Al Qasr in the Dakhla Oasis. All climatological data were obtained from a public database (Tutiempo Network 2014). The mean monthly temperature was 4–5°C higher in Egypt than in the Mediterranean region. The annual precipitation was 0 mm at the Egyptian site but varied from 138 to 1,355 mm in the Mediterranean. In the latter region, rain typically falls from September to April, after which comes a 3–4-month dry summer period. There is no rainfall year-round in the Egyptian

desert, but water in the oasis is continuously available from local springs and managed by an extensive irrigation system. The vegetation period of plants producing fruit eaten by *R. aegyptiacus* is therefore not restricted by a lack of water. Instead, plant fructification is largely controlled by temperature and the annual course of farming activities.

Bat populations and sampling design.—All but 1 roost of the Mediterranean population of *R. aegyptiacus* were located in caves or similar underground shelters, whereas the Egyptian study population roosted exclusively in old abandoned buildings (Benda et al. 2011). We sampled *R. aegyptiacus* either in their roosts using hand nets, or by mist netting at roost entrances (216 samples, 3,786 individuals), or at feeding and drinking sites (44 samples, 570 individuals). Most roosts were sampled repeatedly (1–11 times, $\bar{X} = 3$).

Altogether, we examined 4,356 individuals captured during 260 sampling occasions at 88 sites. Of these, 1,521 individuals were sampled in the Mediterranean region and 2,835 in Egypt. For each captured bat we ascertained the sex, age, and reproductive state. We weighed most bats except most juvenile–mother pairs, using a Pesola spring balance and measured their forearm length using a caliper. We measured the length of testicles in adult males exhibiting a scrotal position of the testes. We followed a protocol for handling animals conforming to the guidelines of the American Society of Mammalogists (Sikes et al. 2011) that has been approved by the Institutional Animal Care and Use Committee of the Faculty of Science, Charles University in Prague.

Reproductive status of females.—Females of *R. aegyptiacus* carry their nonvolant pups (< 2–3 months old) attached to their nipples, and only volant but still suckled juveniles fly separately from their mothers. We therefore identified lactating females on the basis of attached juveniles or enlarged nipples without fur around them that secrete milk when gently pressed. Postlactating status was determined on the basis of enlarged dry nipples not secreting any milk when pressed. Pregnant females were identified by gentle palpation of their abdomen. In a subsample of 408 lactating females, we palpated the abdomen and checked for the presence of a fetus, indicating postpartum estrus (Happold 2013).

Postnatal age and estimation of parturition dates.—We estimated the age of juvenile bats on the basis of the growth curve of forearm length published by Mutere (1968) using the following categories: 51 to 60 mm, 1 month; 61 to 70 mm, 2 months; 71 to 80 mm, 3 months; 81 to 85 mm, 4 months; 86 to 90 mm, 6 months. We used this rough age estimation for backward calculation of the date of parturition of each measured juvenile with forearm length of ≤ 90 mm. Of 1,118 juvenile bats captured (both volant and nonvolant), the birth date was estimated for 691 individuals (Mediterranean: 358, Egypt: 333).

Statistical analyses.—The structure of the total sample does not allow direct testing of between-year variation in selected reproductive parameters, among reasons, because the samples for particular months were collected in different years. Thus, to reveal the general pattern of seasonal variation, we pooled data from different calendar years. For similar reasons, we pooled data from different countries of the Mediterranean and different roosts in the Dakhla Oasis in Egypt. We tested all data for normality using the Kolmogorov–Smirnov test; for subsets departing from the normal distribution, we used nonparametric tests. The criterion proposed by DeCarlo (1997) (kurtosis −3), < −1.2, was applied as a simple confirmation statistic for hypotheses concerning the bimodal distribution. We used a nested-design analysis of variance and a linear regression to examine the effects of seasonal variation, forearm length (as a measure of body size), and body mass upon the reproductive state of males (represented by the length of testes). To examine monthly variation in frequencies of particular reproductive categories of females, we applied a chi-square test. We then examined the relationship between the proportions of pregnant and lactating females within particular months using Spearman's correlation, similarly as the relationship between the mean testis size of males and the proportion of pregnant and lactating females. We performed all computations with the aid of STATISTICA 6 software (StatSoft Inc. 2001).

RESULTS

Female reproductive condition.—Adult females made up 33.1% and 22.8% of the total sample in the Mediterranean ($n = 504$ females) and Egypt ($n = 645$ females), respectively.

The summary of the seasonal variation in the reproductive condition of females is given in Table 1. Overall, reproductive females (pregnant, lactating, and postlactating) made up 90.3% and 85.3% of the total sample of females in the Mediterranean and Egypt, respectively.

The frequencies of pregnant and lactating females were nonrandomly distributed among different months of the season in both regions (Mediterranean, pregnant females: $\chi^2 = 149.908$, $d.f. = 7$, $P < 0.001$; lactating females: chi-square $= 94.925$, $d.f. = 7$, $P < 0.001$; Egypt, pregnant females: $\chi^2 = 124.286$, $d.f. = 8$, $P < 0.001$; lactating females: $\chi^2 = 86.041$, $d.f. = 8$, $P < 0.001$). In the Mediterranean region, the highest proportions of pregnant females occurred in late winter/early spring (February–March) and in summer (July–August). Lactating females were abundant from May until October with more or less evident peaks during late spring/early summer (June–July) and autumn (August–October).

In Egypt, the highest proportion of pregnant females occurred during late spring (April) and autumn and winter months (October–January). However, in contrast to Mediterranean populations, we encountered pregnant females in Egypt in all months from which we have data. The highest proportion of lactating females occurred in late winter (February) and summer (July–August), but they were recorded in all months except for December and January. The proportions of pregnant and lactating females within individual months were correlated negatively (Mediterranean: $r_s = -0.71$, $n = 8$, $P < 0.05$; Egypt: $r_s = -0.74$, $n = 9$, $P < 0.05$).

Altogether, we examined in detail 408 reproductive females for the simultaneous presence of lactation and pregnancy by

TABLE 1.—Proportions of adult females in different reproductive states examined during the study. Abbreviations: Grav, gravid; Lact, lactating; PL, postlactating; NR, nonreproductive.

	n	Grav	Lact	PL	NR
Mediterranean					
February	8	87.5	0.0	0.0	12.5
March	159	81.8	2.5	1.3	15.7
May	38	15.8	68.4	0.0	15.8
June	11	0.0	90.9	9.1	0.0
July	54	20.4	44.4	29.6	5.6
August	79	31.6	51.9	11.4	5.1
September	61	8.2	65.6	19.7	6.6
October	94	2.1	37.2	52.1	8.5
Egypt					
January	59	78.0	0.0	1.7	20.3
February	36	2.8	72.2	22.2	2.8
March	43	7.0	18.6	18.6	11.6
April	147	52.4	27.2	10.9	2.7
July	43	18.6	46.5	34.9	0.0
August	136	2.2	47.1	41.2	5.9
October	105	27.6	20.0	21.0	25.7
November	24	33.3	8.3	12.5	12.5
December	52	46.2	0.0	0.0	53.8

gentle palpation of the abdomen. In the Mediterranean, of 180 reproductive females examined, we confirmed 4 positive cases (i.e., 2.2% incidence). We recorded all 4 cases in July in Lebanon. In Egypt, we recorded simultaneous lactation and pregnancy in 20 females of 227 (8.8% incidence). Of these, we recorded 10 cases in April, 3 in July, and 7 in October.

Birth dates.—On the basis of our estimates of birth dates, a vast majority of juveniles in the Mediterranean region were born either between March and April or between September and November (Fig. 2). By contrast, most juveniles from the Egyptian study population were born either between January and February or between May and July (Fig. 2). We estimated that some 67% and 70% of juveniles were born within 1 of the 2 major peak periods in the Mediterranean and Egypt, respectively; the remaining proportion of juveniles were born outside these periods.
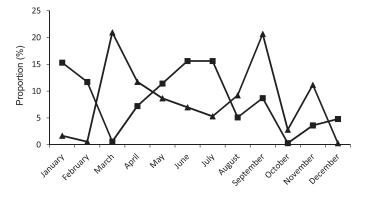

FIG. 2.—Estimated annual distribution of birth timing of juvenile Egyptian fruit bats (*Rousettus aegyptiacus*) based on backward age estimation using their forearm length (Mediterranean: $n = 358$, triangles; Egypt: $n = 333$, squares).
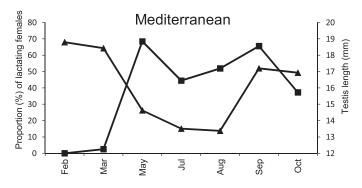

FIG. 3.—Seasonal changes in the length of testes in male (triangles) as related to the proportion of lactating female (squares) Egyptian fruit bats (*Rousettus aegyptiacus*) in the Mediterranean study population. Least-square means are shown.

Male reproductive condition.—Adult males comprised 32.6% of the total sample in the Mediterranean ($n = 496$) and 56.3% in Egypt ($n = 1,596$). Testis size was examined in 874 males (Mediterranean: 421, Egypt: 453).

The length of testes differed between different months in both study areas (Mediterranean: $F_{(6, 414)} = 70.301$, $P < 0.0001$; Egypt: $F_{(8, 444)} = 33.166$, $P < 0.001$). Males in both regions generally tended to have larger testicles during autumn and winter months (September to March) than in spring and summer. The length of testes was not correlated with body size (Mediterranean: $R^2 = 0.00006$, $F_{(1,420)} = 0.022$, $P = 0.881$; Egypt: $R^2 = 0.003$, $F_{(1,452)} = 1.283$, $P = 0.258$), but it was positively correlated with body mass (Mediterranean: $R^2 = 0.074$, $F_{(1,420)} = 31.565$, $P < 0.001$; Egypt: $R^2 = 0.022$, $F_{(1,452)} = 10.302$, $P < 0.001$). Body mass differed between months (Mediterranean: $F_{(7, 414)} = 6.088$, $P < 0.001$; Egypt: $F_{(8,445)} = 6.40$, $P < 0.001$). It was highest in winter, decreased during spring and early summer, and increased again from late summer. In the Mediterranean, the mean monthly testis size was negatively correlated with the proportion of lactating females ($r = -0.82$, $n = 7$, $P < 0.05$, Fig. 3). There was also an indication of a positive correlation with the proportion of pregnant females ($r = 0.68$, $n = 7$, $P = 0.093$). We also found similar correlations with the proportion of lactating females and with the proportion of pregnant females in the Egyptian sample: viz. $R = -0.79$, $n = 9$, $P < 0.01$ (Fig. 4) and $r = 0.78$, $n = 9$, $P < 0.01$, respectively.

Annual cycles in particular regions.—The annual distributions of parturitions and female reproductive states exhibit significant bimodal patterns (negative kurtosis), both in the Mediterranean and in Egypt (except for the proportion of nonreproductive females, which shows a nearly uniform distribution in the Mediterranean and a unimodal distribution in Egypt). The respective cycles in both regions are mutually shifted by approximately 3 months (see above). Despite the bimodal pattern, the synchronization of individual cycles within populations is relatively faint, and pregnant or lactating females are present in relatively high percentages almost throughout the year except winter months (Table 1).
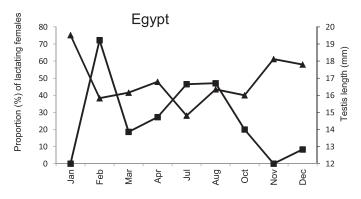
Fig. 4.—Seasonal changes in the length of testes of male (triangles) as related to the proportion of lactating female (squares) Egyptian fruit bats (*Rousettus aegyptiacus*) in the Egyptian study population. Least-square means are shown.

DISCUSSION

In spite of spatiotemporal gaps in the sampling design, our large data set enabled us to analyze basic reproductive patterns of populations of *R. aegyptiacus* living in two climatically distinct regions, the Mediterranean and the Egyptian desert. In both regions, the annual course of reproduction was characterized by distinct bimodality in birth timing regardless of the distinct differences in the climatic regime under which the populations lived. On the basis of the low incidence of simultaneous pregnancy and lactation, which typically indicates postpartum estrus, we assume that both seasonal bimodal polyestry with and without postpartum estrus (cf. Racey and Entwistle 2000) occur in both regions, with a possibly lower incidence of postpartum estrus in females from the Mediterranean population. Furthermore, postpartum estrus may occur after every parturition in Egypt, though it is probably absent after autumn births in the Mediterranean population. In line with our observations, albeit based on a small sample size ($n = 4$), Korine et al. (1994) reported that 100% of females sampled in summer in Israel were simultaneously lactating and pregnant.

Populations from the two study regions differed in the timing of parturitions. The peak birth periods were shifted by roughly 2–3 months between the Mediterranean and the Egyptian study population. Timing of reproduction in bats is typically dictated by food availability, which is usually controlled by the climate (Heideman 2000). The 2 study populations live under different environmental conditions. Moreover, both literary data and our unpublished observations imply clear differences in their diets. Some 15–20 food plant species are known to be consumed by fruit bats in the Mediterranean, but the major bulk of their diet consists of several species of figs (*Ficus* sp.), carob (*Ceratonia siliqua*), Persian lilac (*Melia azedarach*), mulberry (*Morus nigra*), and loquat (*Eriobotrya japonica*—Korine et al. 1999). In contrast to the situation in the Mediterranean, no detailed information on the diet of *R. aegyptiacus* is available from Egypt. Madkour (1977) and Qumsiyeh (1985) reported that bats in the region feed on sycamore, mulberries, figs, and dates. Our pending

radiotracking study of more than 100 *R. aegyptiacus* in the Dakhla Oasis suggests that the Egyptian study population is almost entirely dependent on dates (*Phoenix dactylifera*) and fruits of mango (*Mangifera indica*), with another 3–4 plant species being consumed occasionally. In the Mediterranean region, *R. aegyptiacus* consumes the highest quantity and diversity of food in autumn and spring (Herrera et al. 2008), i.e., at the beginning and end of the rainy period. The reproductive cycles of local fruit bat populations are thus synchronized with precipitation seasons. Peaks of parturition and early lactation coincide with rainy periods. In Egypt, the periods of peak food abundance (fruiting of date palms and mango trees) occur from September to December and from May to July. Thus, only summer births are well synchronized with highest food abundance. The 2nd peak birth period (late winter) occurs shortly after the peak food abundance period, however. In contrast to the Mediterranean, plant fruiting phenology in the Egyptian study site is not linked to the annual course of precipitation. The water supply is unlimited thanks to continuous artificial irrigation. Plant phenology is instead affected by the ambient temperature and, to a lesser extent, by agricultural practices. Hence, despite the common bimodal pattern of reproductive cycles of *R. aegyptiacus* in both regions, the modes of synchronization and its proximate drivers may differ considerably between these regions.

The male reproductive cycle in polyestrous species typically copies that of females, although it may not be its direct consequence (Krutzsch 2000). Likewise, our data show that, in both study populations, the testis size dynamics correlated with the female reproductive cycle. Basically, the period of testicular recrudescence was synchronized with peak pregnancy in females. Such a pattern may indicate that mating takes place shortly after parturition. An analogous pattern has been observed in *Cynopterus brachyotis* in Thailand by Bumrungsri et al. (2007). Although testicular recrudescence in males is typically related to increased mating activity (Racey and Entwistle 2000), mating may obviously occur even outside these periods, as indicated by our estimates of birth dates in juveniles. In any case, seasonal variation in testis size is actually only minute (less than 30% of testis length), and adult males obviously remain fertile throughout the year. Similarly, Madkour et al. (1983) reported year-round presence of living spermatozoa in the male reproductive tract in Egyptian populations of *R. aegyptiacus* despite profound seasonal dynamics in testis size.

Several factors, including the photoperiod, food availability, and female reproduction, have been proposed as regulators of the male reproductive cycle in pteropodid bats (Heideman 2000; Krutzsch 2000). In our study, males of *R. aegyptiacus* showed seasonal changes in testis size, which in turn was significantly related to body mass. Since changes in body mass are directly linked to food consumption, we assume that the male reproductive cycle is ultimately regulated by food availability. Racey and Entwistle (2000) and Bumrungsri et al. (2007) have already suggested that the food supply is a

major factor determining the reproductive timing in male pteropodid bats.

Last but not least, the bimodal reproductive pattern is typical of bats living in tropical latitudes, whereas temperate bats reproduce during a single season (Racey and Entwistle 2000). Due to its reproductive phenology, *R. aegyptiacus* is the sole exception among all Palaearctic bats, which are strictly monoestric. Although rousettes may be capable of monoestric reproductive phenology in higher latitudes, as indicated by the situation reported from southern Africa (Jacobsen and Du Plessis 1976; Herzig-Straschil and Robinson 1978; Penzhorn and Rautenbach 1988), populations living at the northern limits of the species' distributional range have retained the reproductive mode typical of tropical bats. Given the generally higher reproductive output of polyestric populations as compared with monoestric ones, we suggest that this extraordinary pattern may be an indication of the phenotypic plasticity and adaptability of *R. aegyptiacus* to locally specific conditions. It might be a key qualitative trait that facilitated the species' Quaternary range expansion and colonization of areas far beyond the distributional range of other pteropodid bats (Benda et al. 2011, 2012; Hulva et al. 2012).

Acknowledgments

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