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BODY SIZE, REPRODUCTIVE BIOLOGY, AND SEX RATIO OF A YEAR-ROUND COLONY OF *EPTESICUS FUSCUS FUSCUS* AND *TADARIDA BRASILIENSIS CYNOCEPHALA* IN EASTERN ALABAMA

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We studied variation in body size, reproductive biology, and sex ratio of a year-round colony of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* located on the campus of Auburn University, Lee Co., Alabama. Females of *E. f. fuscus* had greater mass and length of body than males, there were no differences between genders of *T. b. cynocephala* in mass, but males were larger than females in length of body. Length of testis was greatest in October and least in February for *E. f. fuscus,* and greatest during February and least in June for *T. b. cynocephala.* All females of *E. f. fuscus* examined in May had embryos in both uterine horns; parturition took place in late May-early June. Pregnant *T. b. cynocephala* had embryos only in the right uterine horn; parturition occurred in late May-early June. The number of females in the population of *E. f. fuscus* usually was greater than the number of males; males of *T. b. cynocephala* out-numbered females most of the year. When compared to single-species colonies, there were only slight differences in this mixed colony, which may be attributable to geographic variation in climatic conditions.

Roosts are critical sites that are required for survival of many species of vertebrates, e.g., roost sites may be used for breeding, rearing young, and protection against weather and predators. For bats, roost sites are especially important. Most species spend >50% of their life at one type of roost or another; thus, roosts have influenced behavior and evolution of bats (Kunz, 1982).

Generally, bats form single-species aggregations within a roosting area, but mixed-species use of roosting sites has been observed in many species (e.g., Barbour and Davis, 1969; Eads et al., 1957; Hermanson and Wilkins, 1986; Jennings, 1958; Lowery, 1974; Phillips, 1966; Sherman, 1937). Most mixed-species associations result from bats having similar diurnal requirements and a lack of suitable roost sites (Bradbury, 1977). Graham (1988) investigated use of diurnal roosts by several species of bats and found that some species were more generalized in their requirements and were more likely to share roost sites with other species of bats. Roost sharing may involve costs and benefits. Costs may include increased incidence of disease and parasites, competition for resources, opportunity for detection by predators, and mortality of infants. Benefits may include increased detection of predators and reduced costs of thermoregulation (Bradbury, 1977; Graham, 1988; Kunz, 1982). Nevertheless, most interspecific associations in roosts probably are neutral (Bradbury, 1977; Graham, 1988; Swift and Racey, 1983).

A roost used by both *Eptesicus fuscus fuscus* and *Tadarida brasiliensis cynocephala* was located in the attic of Samford Hall on the campus of Auburn University, Lee Co., Alabama; both of these species had inhabited brick buildings on campus for >50 years (Barkalow, 1939). In 1990, the attic of Samford Hall contained ca. 700 bats of each species, but because of renovation of the structure the colony was destroyed in 1994. Although single-species aggregations of bats were present in the colony, many clusters of bats contained both species in direct contact. Close physical association between *E. f. fuscus* and *T. b. cynocephala* may have been facilitated by partitioning of resources between these taxa. For example, *E. fuscus* primarily feeds upon Coleoptera (Kurta and Baker, 1990; Phillips, 1966), whereas Lepidoptera make up ca. 90% of the diet of *T. brasiliensis* (Ross, 1961; Storer, 1926; Wilkins, 1989). Because differences in diet probably reduce competition for food resources in the area surrounding the roost, this may be a significant factor in allowing these bats to inhabit the same roost site. However, it is unknown whether species inhabiting such mixed-species colonies differ morphologically, reproductively, or behaviorally from other populations of the species that do not share roost sites.

The purposes of our study were to examine patterns of variation in body size between genders, among months, and between species, in reproductive characters among months for each species, and in sex ratio of the population among months for *E. f. fuscus* and *T. b. cynocephala* inhabiting the same roost. Because gestation and lactation are among the most energy demanding periods for females (Kunz, 1974b; Pistole, 1989), we also wanted to document whether temporal adjustments in reproductive activity may have occurred in response to these bats roosting together.

MATERIALS AND METHODS

Samford Hall, located on the campus of Auburn University, Lee Co., Alabama, is a four-story structure with a double-roofed design in the attic, which provided year-round shelter for bats. *E. f. fuscus* and *T. b. cynocephala* were sampled monthly from February through November 1990. A total of 229 bats (31 males, 65 females of *E. f. fuscus*; 74 males, 59 females of *T. b. cynocephala*) was examined to determine body size, reproductive condition, and incidence of parasitism (Durden et al., 1992; Hilton, 1993; Hilton and Best, 2000). Bats were collected by hand, sacrificed with chloroform, and measurements of mass and length of body were taken to the nearest 0.5 g and 1 mm, respectively. Position of embryo in the uterus, number of embryos, length of testis, and sex ratios also were recorded. Specimens were deposited in the Auburn University Museum.

Character heterogeneity (between species, between genders, and among months) was tested with a one-way analysis of variance, and, when statistically significant variation was present ($P \leq 0.05$), a Student-Neuman-Kuels (SNK) a posteriori test for multiple comparisons among means was used to determine maximally non-significant subsets. All statistical analyses were conducted using SPSS/PC+ (Norŭsis, 1990).

RESULTS AND DISCUSSION

Mass.—Burnett (1983) reported that females of *E. fuscus* were slightly larger than males. In Alabama, average mass of nonpregnant females of *E. f. fuscus* (17.1 g) also was greater than that of males (13.6 g; $P < 0.001$; *d.f.* = 1,86; *F*-ratio = 29.4); minimum mass for both genders was attained in April (11.0 and 12.3 g for males and females, respectively; Fig. 1a). This pattern is similar to that reported for females of *E. f. fuscus* in Kansas (Kunz, 1974a). In our study, average mass of males of *E. f. fuscus* decreased from February to April, fluctuated slightly in summer, then increased until maximum mass was reached in November (Fig. 1a), but no statistically significant difference was detected among months by SNK analysis ($P = 0.03$; Table 1). Average mass of females of *E. f. fuscus* declined from February to April; gestation caused mass to increase from its minimum in April (12.3 g) to its maximum in May (20.6 g). After parturition, mass decreased in June, increased from July to September, when average mass almost equaled that during pregnancy, then declined through November (Fig. 1a). When pregnant females were excluded from analyses, there also was significant variation among months ($P < 0.001$);

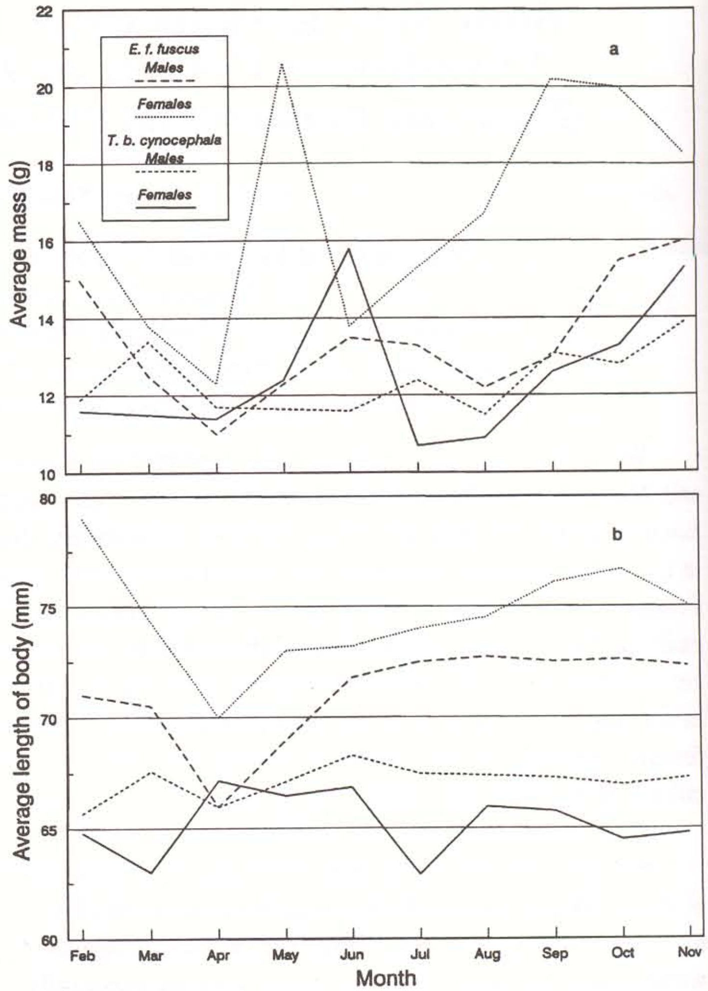

Fig. 1.—Variation in a) average body mass and b) length of body of all males and all females of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* at Auburn University, Lee Co., Alabama, in 1990.

Table 1.—*Results of one-way analysis of variance of morphologic variation for two species of bats occupying the same roost in eastern Alabama. Minimally significant variation among months is assumed where* P < *0.05 (*). Means and results of Student-Neuman-Kuels a posteriori tests for multiple comparisons among means are given for each comparison.*

Character	Sex	*d.f.*	*F*-ratio	Results of Student-Neuman-Kuels analysis									
Eptesicus f. fuscus													
				Apr	Aug	May	Mar	Sep	Jul	Jun	Feb	Oct	Nov
Mass	Male	9,21	2.7*	11.0	12.2	12.3	12.5	13.0	13.3	13.5	15.0	15.5	16.0
				Apr	Jun	Mar	Jul	Feb	Aug	Nov	Oct	Sep	
	Female	8,48	8.8*	12.3	13.8	13.8	15.3	16.5	16.7	18.3	20.0	20.2	
Length of body				Apr	May	Mar	Feb	Jun	Nov	Jul	Sep	Oct	Aug
	Male	9,21	1.3ns	66.0	69.0	70.5	71.0	71.8	72.3	72.5	72.5	72.6	72.7
				Apr	Jun	Jul	Mar	Aug	Nov	Sep	Oct	Feb	
	Female	8,49	1.5ns	70.0	73.2	74.0	74.3	74.5	75.1	76.1	76.7	79.0	
Length of testis				Feb	Apr	Jun	Mar	May	Jul	Sep	Nov	Aug	Oct
	Male	9,17	4.7*	4.0	5.0	5.0	5.5	6.0	6.0	7.0	7.5	7.7	9.0
Tadarida brasiliensis cynocephala													
				Aug	Jun	Apr	Feb	Jul	Oct	Sep	Mar	Nov	
Mass	Male	8,64	6.8*	11.5	11.6	11.7	11.9	12.4	12.8	13.1	13.4	13.9	
				Jul	Aug	Apr	Mar	Feb	Sep	Oct	Nov		
	Female	7,31	8.5*	10.7	10.9	11.4	11.5	11.6	12.6	13.3	15.3		
Length of body				Feb	Apr	Oct	Nov	Sep	Aug	Jul	Mar	Jun	
	Male	8,65	0.9ns	65.7	66.0	67.0	67.3	67.3	67.4	67.5	67.6	68.3	
				Jul	Mar	Oct	Nov	Feb	Sep	Aug	Apr		
	Female	7,31	2.4*	62.9	63.0	64.5	64.8	64.8	65.8	66.0	67.2		
Length of testis				Jun	Jul	Aug	Sep	Nov	Oct	Apr	Mar	Feb	
	Male	8,56	3.4*	3.3	4.0	4.5	5.0	5.0	5.1	5.3	5.6	5.7	

mass of females in April was significantly less than that in August through November, and mass in October and September was greater than that in all other months (Table 1). Pistole (1989) reported that females of *E. fuscus* deposit fat, in anticipation of hibernation, 1 month earlier than do males. This also was shown by the population in Alabama; females had a noticeable increase in mass from August to September, then males showed a similar acceleration from September to October (Fig. 1a).

La Val (1973) and Lowery (1974) reported that average mass of females of *T. b. cynocephala* often was more than that of males in Louisiana, but we found no significant difference in mass between genders in Alabama (average mass: males, 12.5 g, females, 12.1 g; $P = 0.13$; $d.f. = 1{,}110$; F-ratio = 2.4). For males, mass fluctuated from February through October, then increased to the maximum in November (Fig. 1a). Mass of males was significantly greater in March, September, and November than in February, April, June, and August ($P < 0.001$; Table 1), indicating a tendency to add mass following hibernation and before entering hibernation. In February, females of *T. b. cynocephala* had an average mass of 11.6 g. Mass stayed near this level until June when it increased to a maximum of 15.8 g during gestation (Fig. 1a), mass was least in July and August, and then a steady increase occurred from August to November, when mass almost equaled that during pregnancy. Mass of nonpregnant females was significantly greater in November than in any other month, and mass in October was significantly greater than in July and August ($P < 0.001$; Table 1), indicating a pre-hibernation gain in mass. A similar pre-hibernation increase in mass was noted for this taxon in Louisiana (La Val, 1973).

Length of body.—Phillips (1966) and Burnett (1983) reported that males of *E. fuscus* were smaller than females. Likewise, in our study of *E. f. fuscus,* average length of body of males (71.2 mm) was significantly smaller than that of nonpregnant females (74.9 mm; $P < 0.001$; $d.f. = 1{,}87$; F-ratio = 20.0). Average length of body for males ranged from 66.0 mm in April to 72.7 mm in August, but there was no significant difference among months ($P = 0.28$; Fig. 1b; Table 1). Average length of body in females of *E. f. fuscus* was greatest in February and least in April, and there also was no significant difference among months ($P = 0.18$; Fig. 1b; Table 1).

For *T. b. cynocephala,* average length of body of males was larger than females in all months, except April (Fig. 1b); males (66.8 mm) were significantly larger than females for this character (64.9 mm; $P < 0.001$; $d.f. = 1{,}111$; F-ratio = 14.1). For males, length of body was least in February and greatest in June, but there were no significant differences among months ($P = 0.51$; Fig. 1b; Table 1). Average length of body for nonpregnant females was greatest in April and least in July, and measurements for these two months were significant different from each other ($P = 0.05$; Table 1), possibly indicating differences in size of body before and after pregnancy, respectively.

Length of testis.—*Eptesicus fuscus* copulates in autumn (Phillips, 1966). Length of testis of *E. f. fuscus* was least in February, generally increased throughout the year to a maximum in October, then decreased in November (Fig. 2; Table 1). There were significant differences among months ($P = 0.003$; Table 1), and length of testis in February, April, and June was smaller than in August, October, and November. Phillips (1966) also found similar changes in length of testis in Kansas, but maximum size of testes was reached in August. Apparently, *E. f. fuscus* in Alabama breed later in the year than in Kansas, but this probably is related to geographic variation in climate and not the result of sharing a roost with *T. b. cynocephala.*

Length of testis of *T. b. cynocephala* was greatest in February and declined to a minimum in June, increased in September, and varied only 0.1 mm through November (Fig. 2). There were significant differences among months ($P < 0.01$); length of testis in June was significantly smaller than in March and February (Table 1). Previous studies of this subspecies in Florida (Sherman,

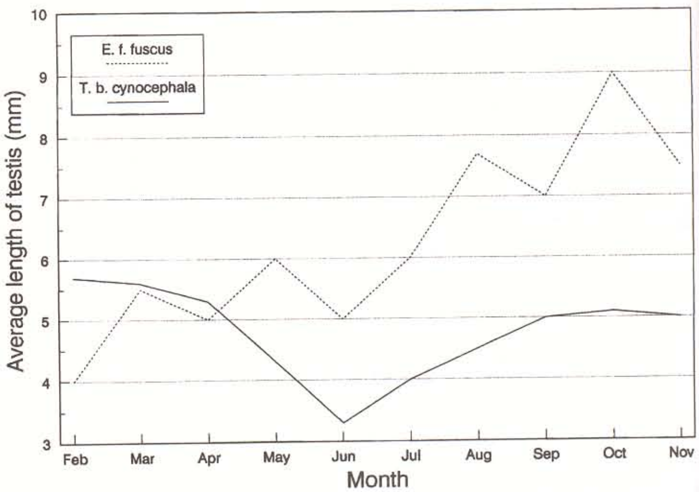

Fig. 2.—Variation in average length of testis of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* at Auburn University, Lee Co., Alabama, in 1990.

1937) and Louisiana (Pagels and Jones, 1974) revealed that copulation occurs in March. Based upon our measurements of length of testis, breeding occurs in eastern Alabama in February or March.

Number of embryos.—Average number of offspring per year for *E. fuscus* in eastern North America is two (Barbour and Davis, 1969; Christian, 1956; Kunz, 1974a). In Alabama, all pregnant *E. f. fuscus* had embryos in both uterine horns in May. The average crown-rump length of embryos was 21.0 mm (n = 7); no embryos were found in other months. With embryos this large in May, the *E. f. fuscus* we studied in Alabama must have been pregnant in April. Generally, *E. f. fuscus* from the southern part of its range are pregnant in April and parturition occurs in May (Cockrum, 1955). The first lactating *E. f. fuscus* that we observed with a young-of-the-year was on 6 June, along with many pregnant females, and this young-of-the-year weighed 8.5 g. Due to large mass of the young bat and because mass of females decreased from May to June, we assumed that parturition began in late May. Our findings regarding time of gestation and parturition coincide with previous reports (Barbour and Davis, 1969; Brimley, 1923; Gates, 1937; Harper, 1929; Kunz, 1974a).

Females of *T. b. cynocephala* give birth to one precocial young each year (Sherman, 1937). Similar to previous reports on this taxon (Sherman, 1937; Wilkins, 1989), all pregnant *T. b. cynocephala* that we examined in Alabama had embryos only in the right uterine horn; embryos were present in April (average = 6.0 mm in crown-rump length, n = 1), May (average = 18.0 mm, n = 12), and June (average = 31.0 mm, n = 8). Average crown-rump length of embryos that we observed in June (31.0 mm) was greater than lengths (25-30 mm) reported previously (Barbour and Davis, 1969; Pagels and Jones, 1974; Sherman, 1937; Wilkins, 1989). Sherman (1937) and La Val (1973) found that parturition in populations of *T. b. cynocephala* in Florida and Louisiana, respectively, usually took place in early June. In Louisiana, Pagels and Jones (1974) observed vaginal plugs and La Val (1973) found embryos in this taxon as early as March; these observations support Sherman's (1937) conclusion that the gestation period is 11-12 weeks. In our study, mass of females of *T. b. cynocephala* decreased sharply from June to July, indicating this was when parturition occurred in eastern Alabama (Fig. 1a). No evidence of twins or triplets, which previously have been reported for *T. b. cynocephala* in Alabama (Di Salvo et al., 1969), was observed.

Sex ratio.—Females represented ≥50% of the population of *E. f. fuscus* every month, but males always were present. Greatest percentages of females (83.3%) were in July and September. The sex ratio we observed in Alabama differs substantially from sex ratios observed in maternity colonies in Kentucky; only a few males were present in those colonies in late May and early June. From late June through August, number of males increased, approaching the same frequency as females in the populations (Barbour and Davis, 1969; Davis et al., 1968). Differences between colonies in Kentucky and the one we studied in Alabama may be related to geographic variation in climatic and habitat variables, or more likely, to our colony serving as both a hibernaculum and maternity colony. Males never composed the majority of the population, but they always were present in frequencies of 16.7-50.0% of the population. In Kansas (Phillips, 1966), Minnesota (Goehring, 1972; Rysgaard, 1942), Pennsylvania (Mohr, 1942, 1945), and Canada (Hitchcock, 1965), males of *E. fuscus* often were more numerous than females in hibernacula, but during winter months in eastern Alabama, there were more females in the colony.

Percentage of females in the population of *T. b. cynocephala* (Fig. 3) was lowest in March (8.3%) and greatest in May (100%). Sherman (1937) reported similar observations in Florida. In our study, males of *T. b. cynocephala* composed the majority of the population in February, March, August, September, and November, the genders were equally represented in April and October,

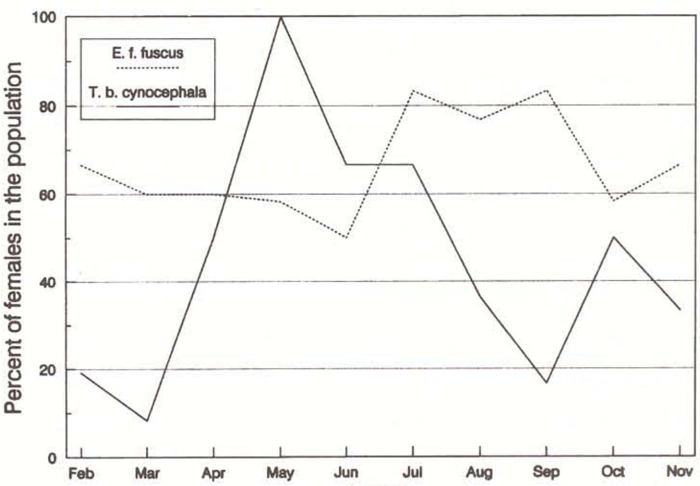

Fig. 3.—Variation in percentage of females in the population of *Eptesicus f. fuscus* and *Tadarida brasiliensis cynocephala* at Auburn University, Lee Co., Alabama, in 1990.

and females outnumbered males in May, June, and July (Fig. 3). Our observation of a sex ratio of 0.50:1.00 in July differs from the ratio of 1.00:0.81 reported for males and females in July in Louisiana (Pagels and Jones, 1974), and our observations of males being more frequent in the population during several months differs from the dominance of females in all samples examined in Louisiana by La Val (1973). At our study site, percentage of females was greatest in May (100%), indicating that males were roosting at other sites at this time.

Interspecific comparisons.—Average mass (13.6 g), length of body (71.2 mm), and length of testis (6.5 mm) of males of *E. f. fuscus* were significantly greater than in *T. b. cynocephala,* which averaged 12.5 g ($P = 0.001$; *d.f.* = 1,102; *F*-ratio = 11.2), 66.8 mm ($P < 0.001$; *d.f.* = 1,103; *F*-ratio = 54.2), and 5.1 mm ($P < 0.001$; *d.f.* = 1,90; *F*-ratio = 20.8), respectively. Average mass (17.1 g) and length of body (74.8 mm) of nonpregnant females of *E. f. fuscus* were significantly greater than in *T. b. cynocephala,* which averaged 12.1 g ($P < 0.001$; *d.f.* = 1,94; *F*-ratio = 79.4) and 64.9 mm ($P < 0.001$; *d.f.* = 1,95; *F*-ratio = 203.4), respectively.

Percentage of females in the colony varied between species (Fig. 3). Average percentage of females (66.4%; range = 50.0-83.3) in the population of *E. f. fuscus* was significantly larger than the average (44.7%; range = 8.3-100) for *T. b. brasiliensis* ($P = 0.04$; *d.f.* = 1,18; *F*-ratio = 5.1).

Parturition occurred slightly earlier in *E. f. fuscus* than in *T. b. cynocephala,* but both species had their young in late May-early June. *E. f. fuscus* had two young and *T. b. cynocephala* had one young.

While quantifying incidence of ectoparasites within our study population, Durden et al. (1992) observed that most mites recovered from *E. fuscus* were *Chiroptonyssus robustipes,* a mite that typically lives in association with *T. brasiliensis.* In contrast, only two specimens of *Steatonyssus occidentalis,* a specific ectoparasite of *E. fuscus,* were recovered from *T. brasiliensis.* Thus, from the perspective of cross-infestations of ectoparasites, *E. fuscus* appears to be at greater risk from sharing roosts with *T. brasiliensis* (Durden et al., 1992). Conversely, Hilton (1993) and Hilton and Best (1999) found endoparasites of the two species to differ significantly; trematodes predominated in *E. fuscus* and nematodes in *T. brasiliensis.*

Although we found many similarities between our results and those of other studies, we also found some differences in variation in body size and reproductive biology. Because these differences may be due to geographic or annual variation in climatic or other habitat variables, it was not possible to ascertain any patterns that indicated interspecific interactions were responsible for the observed differences. Because these bats differ in diet, parasites, body size, reproductive biology, and sex ratio, their effects upon each other at this common roost site appear insignificant.

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