ECONOMY OF HAREM MAINTENANCE IN THE GREATER SPEAR-NOSED BAT, *PHYLLOSTOMUS HASTATUS*

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To investigate constraints on males associated with maintenance of harems, we used a time-energy approach to explore the relationship between temporal occupancy of roosts and nightly foraging activity in male and female greater spear-nosed bats, *Phyllostomus hastatus*. Harem males and females differed significantly in frequency and duration of nightly foraging bouts. Harem males spent less time away from their roost at night and departed and returned more frequently than did other members of the harem. Adult females and one subadult male foraged mostly during the first 2–3 h after sunset. Total time spent foraging by harem males, adult females, and a subadult male, averaged 98, 152, and 115 min per night, respectively. On average, harem males engaged in 7.2 randomly spaced foraging bouts per night, compared with 2.1 bouts for harem females and 2.0 bouts for a subadult male. Field metabolic rate, expressed on a mass-specific basis (ml CO$_2$ g$^{-1}$ h$^{-1}$), averaged 3.4 ± 0.69 SD for harem males, 3.0 ± 0.85 for adult females, 1.9 ± 0.08 for a subadult male. These values varied predictably but did not differ significantly. Similarly, daily energetic expenditure, expressed on a whole-animal basis (kJ/day), averaged 168.6 ± 32.5 for harem males and 124.9 ± 38.9 for adult females but did not differ significantly. Because harem males allocate less time to nightly foraging activity compared with adult females, males should have more time and energy available for vigilance at the roost and/or the defense of females.

Key words: *Phyllostomus hastatus*, Phyllostomidae, daily energetic expenditure, doubly-labeled water, harems, time budgets, Trinidad

Studies on the energetics of reproduction in free-ranging mammals have mostly focused on physiological costs associated with pregnancy (Kurta and Kunz, 1987; Kurta et al., 1989, 1990; Ofstedal, 1986) and lactation (Costa et al., 1986; Kenagy et al., 1990; Kurta et al., 1989, 1990; Racey and Speakman, 1987; Stern et al., 1997). In part, this reflects observations that pregnancy and lactation are the most energetically expensive periods in an animal’s life (Gittleman and Thompson, 1988; Kurta and Kunz, 1987). Few studies have examined time and energetic costs associated with other aspects of reproduction, including male-male competition or guarding of potential mates (Gittleman and Thompson, 1988).

In polygynous species, mating strategies of males usually involve some form of competition among males or defense of territories of potential mates (Clutton-Brock, 1989). An important consequence of the amount of time and energy allocated to those activities is that competing males may have less time available for foraging, which ultimately could reduce their fitness. In lek-forming species such as the Uganda kob (*Kobus kob*), males that engage in territorial displays do not leave their territories for long periods without risk of losing them to competing males (Clutton-Brock, 1989).
Thus, foraging sites of territorial males become highly overgrazed, and these individuals are unable to acquire adequate amounts of high-quality food. These males often "burn out" in days or weeks, leave the lek, and subsequently are replaced. By contrast, successful male sage grouse (Centrocercus urophasianus) expend more energy displaying on their lek and spend more time away from feeding areas than unsuccessful males, but they seem to experience lower losses of body mass (Gibson and Bradbury, 1985). From these and similar studies, there is still no clear consensus with respect to the severity of costs associated with male-male competition.

Among Chiroptera, activities associated with maintenance of a harem by a male include defense of foraging areas or roosts (Balasingh et al., 1995; Bradbury and Vehrencamp, 1976; Fleming, 1988; Gerrell and Lundberg, 1985; Kunz et al., 1983; Lundberg and Gerrell, 1986; Morrison and Morrison, 1981; Williams, 1986) and/or the defense of female groups (McCracken and Bradbury, 1981). Defense of foraging areas by a harem male of the white-lined bat (Saccopteryx bilineata) involves use of vocalizations and active pursuit of conspecific males (Bradbury and Vehrencamp, 1976, 1977). Defense of a roost by harem males of the Jamaican fruit bat (Artibeus jamaicensis) and short-nosed fruit bat (Cynopterus sphinx) involves nightly surveillance flights in the vicinity of harem roosts (Balasingh et al., 1995; Morrison and Morrison, 1981). From those observations, one would expect trade-offs in the amount of energy invested by males in maintaining a harem and benefits derived from increased mating success.

The greater spear-nosed bat (Phyllostomus hastatus) forms harems, and a single male is known to defend females or their roosts from intrusions by other males (McCracken and Bradbury, 1981). This bat is widely distributed in the Neotropics (Hall, 1981; Koopman, 1982); in Trinidad, it commonly roosts in caves and manmade structures and forms highly structured social groups of 10–100 individuals (Bradbury, 1977; McCracken and Bradbury, 1981). A harem usually consists of several adult females (with or without young), a single harem male, and sometimes one or more subadult males. Females form year-round stable roosting groups, and harem males appear to gain preferential reproductive access to these individuals (McCracken and Bradbury, 1977, 1981). Bachelor groups consisting of adult and subadult males may occupy other areas within the same cave.

A single annual mating period in P. hastatus extends from November through January (James, 1977; McCracken and Bradbury, 1981), and females usually give birth to a single pup in April or May. Females from the same harem group forage in the same or overlapping areas, whereas females from other groups forage in different areas (McCracken and Bradbury, 1981; Wilkinson and Boughman, 1998). However, nightly foraging behavior of harem males differs from adult females in being located closer to the harem roost (McCracken and Bradbury, 1981). In this study, we employed a time-energy approach to explore relationships between temporal occupancy of roosts and foraging activity of male and adult female greater spear-nosed bats. We tested the hypothesis that competition among males leads to differences in allocation of time and energy to foraging and roost occupancy by male and female members of the harem. We predicted that males should invest less time and energy in foraging activities than females and thus more time and energy should be available for defense of the harem or roost.

MATERIALS AND METHODS

Study site.—Our study was conducted at Guanapo Cave, a small limestone cavern in Trinidad, West Indies, located in the Northern Range, ca. 10 km ENE of Arima. Bats in this cave have been the subject of several previous investigations, including those on homing be-
havior (Williams et al., 1966; Williams and Williams, 1967, 1970), reproduction (James, 1977), milk composition (Stern et al., 1998), postnatal growth (Stern and Kunz, 1998), flight (Stern et al., 1997), social behavior (McCracken and Bradbury, 1977, 1981), and communication (Boughman, 1997; Wilkinson and Boughman, 1998). At least 20 relatively discrete harems of P. hastatus and several less-structured groups of non-harem (bachelor) males roost in this cave. Small colonies of Carollia perspicillata, Natalus tumidirostris, and Pteronotus parnaillii also are present at this site.

Climate of Trinidad is wet-tropical (Beard, 1946). Annual precipitation varies from 175 cm in the west and south to 240 cm in the north. The rainy season usually begins in May and lasts through December. In the Northern Range, the highest rainfall occurs during July and August, averaging ca. 25 cm in each month. The lowest rainfall occurs from January through April, averaging <10 cm each month. Lowest monthly maximum and minimum temperatures have been recorded in January and February, averaging 30°C and 20°C, respectively. We conducted our study from early to mid-January (1985–1987) because observations of mating activity have been made during this period, and thus the defense of roosts or females by harem males should be greatest at this time.

Field protocol.—Before entering Guanapo Cave, we covered the entrance with a net of nylon mesh to prevent bats from escaping during our efforts to capture them (Kunz and Kurta, 1988). Harems were captured using a plastic and wire-mesh bucket trap (McCracken and Bradbury, 1981). Some marked individuals were captured by hand. After sex, age, and reproductive status of bats were determined, they were banded, measured for length of forearm with dial calipers (±0.1 mm), and weighed (±0.01 g) using a portable electronic balance. On one occasion we used a spring scale (±0.2 g) to weigh individuals because of failure of the electronic balance. Bats were individually marked on the forearm with numbered, butt-end (bird) bands made from stainless steel. Greatest length of testis for males was measured (±0.1 mm) with dial calipers.

Harem males were distinguished by their prominent roosting position in the harem, their relatively large body mass, and well-developed testes. Subadult males that were members of a harem group were distinguished from harem males by their smaller body mass and smaller testes. Bachelor males (adults and subadults) typically roosted together, but separate from harem groups. Males in bachelor groups were judged to be reproductively mature if their testes were well-developed and their body masses were comparable to those of harem males. We captured all members of four harems and one group of bachelor males. All members of the bachelor group abandoned the cave after they were measured, weighed, and released. Bats that were sampled for the purpose of estimating field metabolic rate (FMR) were captured by hand to minimize disturbance to harems. External ambient (\( \bar{X} = 26°C \pm 2 SD \)) and air temperatures in Guanapo Cave (\( \bar{X} = 28°C \pm 0.2 \)) were recorded with maximum-minimum thermometers.

Time-activity budgets.—We attached small (<2 g) radio-transmitters (Holohil Systems, Ltd., Carp, Ontario, Canada) to selected individuals and recorded amount of time that they were absent from the cave at night. After first trimming a small patch of hair from the mid-dorsal region, radio-transmitters were attached to 20 different individuals using surgical adhesive. On a given night, four to five bats from a single harem were monitored. Most radio-transmitters remained attached for 1–2 weeks, but some fell off or were removed by the bats when they were absent from the cave. Mass of each radio-transmitter was <2.5% of an individual's body mass, and thus we assumed that these devices did not adversely affect behavior of bats or their energetic expenditure (Gessaman and Nagy, 1988a). An omnidirectional antenna was placed inside the cave to detect signals from the radiotagged animals. Each signal was monitored manually at 5-min intervals using a LA-12 receiver (AVM Instruments, Livermore, CA) positioned outside the opening of the cave and connected to the antenna with coaxial cable.

Nightly time-budgets were monitored from 30 min before to 30 min after sunset. Although the amount of time that bats spent away from the cave reflected a combination of time spent commuting, foraging, and resting, we referred to those absences as foraging bouts. Judging from observations of feeding behavior of P. hastatus and other phyllostomids (Fleming, 1988), we suspect that when females were absent from their harem roost at night, they spent most of
this time searching (in flight), consuming food, and intermittently resting in feeding roosts.

Twelve bats fitted with radiotransmitters were labeled with isotopes to measure simultaneously time-activity budgets and FMR. Individuals from the red harem (designated by the color of bands used) were fitted with radiotransmitters on 7 January 1987, and their foraging activity was monitored on the nights of 7–8, 13–14 and 14–15 January. Individuals from the yellow harem were radiotagged and monitored on the nights of 13–14 and 14–15 January. We present time-budget data for nine radiotagged bats that consistently remained faithful to Guanapo Cave. Four subadult males captured with other members of harems and six mature males captured as part of a bachelor group abandoned the study site after being injected with isotopes.

Field metabolic rate.—Doubly-labeled water (H218O) was used to measure FMR, after calculating the differential turnover of injected isotopes of hydrogen (H) and oxygen (18O) in the pool of body water of selected individuals. Isotopes of hydrogen are lost from the body as H2O, and isotopes of oxygen are lost both as H2O and as respiratory CO2. The difference in rates of turnover of these two isotopes was used to calculate production of CO2 (Nagy, 1980). The theory, assumptions and practical aspects of using this technique are discussed in Kunz and Nagy (1988), Lishon and McClintock (1966), and Nagy (1980, 1983).

Bats were injected intraperitoneally with 210 μl of sterile solution consisting of 32 μCi/ml enrichment of tritiated water (H2) and a 99.8 atom % enrichment of 18O in water. After allowing 60 min for isotopic equilibration with body fluids, ca. 60 μl blood were drawn from the antecubital vein of one wing (Kunz and Nagy, 1988). Samples of blood were also taken from unlabeled animals to measure background activity of isotopes. Geletin powder or firm pressure from the index finger and thumb was applied to the punctured vein to stop bleeding when necessary. All bats were released into the cave after processing. Isotopically labeled bats were recaptured 24–48 h later, and a second sample of blood was taken. Samples of blood were collected in capillary tubes, temporarily sealed with plastic caps, and cooled using gel coolants or refrigeration, until the tubes could be flame-sealed in the laboratory (usually ≤24 h). Samples of blood were refrigerated until they were vacuum distilled, and the resulting water was analyzed for isotopic activity (Nagy, 1983). Activity of tritium in the distillate was measured with a liquid scintillation counter, and 18O was measured by proton activation (Wood et al., 1975).

Time required for isotopic equilibration in the pool of body water was established by injecting six adult females with 210 μl of tritiated water (32 μCi/ml) and withdrawing 40 μl of blood every 15 min for 90 min. Activity of tritium was measured with a liquid scintillation counter. In these experiments, equilibration of tritium was complete within 45–60 min. Six other adult females were captured and injected with doubly labeled water to validate use of isotopes for estimating volume of body water. In this experiment, samples of blood were taken and analyzed for activity of 18O. Those bats were then euthanised, frozen, and analyzed in the laboratory for total body water by drying the carcass. Total body water (48.0 ± 3.4 g), as estimated from the dilution of 18O in the pool of body water, was not significantly different from estimates derived from desiccation (46.7 ± 3.0 g) using a paired t-test (t = 1.72, n = 6, P = 0.11), although estimates based on isotopic dilution averaged 2.8 % higher than those from desiccation.

Conversion factors.—To estimate daily energetic expenditure (DEE), we converted production of CO2 into equivalent units of energy based on composition of an assumed diet. For this study, we assumed that P. hastatus consumed 50% fruit and nectar, and 50% insects (metabolizable dry mass), and that individual bats obtained all their water from food (preformed and metabolic) to meet their daily requirements. We also assumed that when bats ate fruit, they ingested most of the pulp and juice (Morrison, 1980). We used values of 85% water, 1.4% protein (estimated by 4.7 N rather than 6.25 N to exclude ca. 25% nonproteinaceous nitrogenous compounds in fruit—Milton and Dantzig, 1981), 0.6% fat, and 7.6% usable carbohydrate (Hladik et al., 1971) for fruit known to be eaten by P. hastatus (Boughman, 1997; Gardner, 1977; Greenhall, 1965; James, 1977). We assumed that rates of assimilation for protein, fat, and carbohydrate were 86.5%, 81%, and 81%, respectively (Karasov, 1982).

We used conversion factors for protein, fat, and carbohydrate from Table 3 in Gessaman and Nagy (1988b:509) to derive equivalent metabolic rates and amount of metabolic water produced.
per gram of diet. Rates of exchange for CO₂ were converted to equivalent rates of heat production (23.2 kJ/l CO₂) and production of metabolic water (0.65 ml/l CO₂) for a mixed diet of insects and fruit (Nagy, 1983, as modified by Gessaman and Nagy, 1988b).

Statistical analyses were performed with SAS version 6.07 (SAS Institute, Inc., 1988). Results are presented as means ± one standard deviation.

RESULTS

Nightly foraging activity was recorded for individuals of *P. hastatus* from two different harems. Foraging activities of the harem male, a single subadult (yearling) male, and two adult females from the red harem were monitored on 3 nights, and foraging activities of the harem male and four adult females from the yellow harem were monitored on 2 nights (Fig. 1). To avoid possible bias associated with pseudoreplication due to repeated measurements on the same individuals, differences in nighty activity patterns reflecting harem membership, harem status (harem male, harem female, or nonreproductive male), and date were examined using a three-way, repeated-measures analysis of variance. The one subadult male from the red harem was excluded from this analysis. Because of differences in numbers of replicates between the two harems, test statistics were calculated using Type IV sums of squares (SAS Institute, Inc., 1988).

Total time that individual *P. hastatus* spent foraging was independent of status in a harem (*F* = 3.16, *d.f.* = 1, 4, *P* = 0.15), membership in a harem (*F* = 0.94, *d.f.* = 1, 4, *P* = 0.39), and date (*F* = 0.97, *d.f.* = 2, 5, *P* = 0.44). No interaction effects were significant (*P* > 0.05, Fig. 2). The harem male (R15) from the red harem foraged for 93.3 ± 32.1 min over 3 nights of observation compared with 145.8 ± 26.7 min by the two adult females from this harem (Figs. 1 and 2). The harem male (Y52) from the yellow harem foraged for 105.0 ± 21.2 min over the 2 nights of observation compared with 156.2 ± 45.1 min by the four adult females. The subadult male (R15) from the red harem foraged for 115.0 ± 10 min over 2 nights (Figs. 1 and 2).

The number of foraging bouts per night that harem members engaged in was significantly influenced by status in the harem (*F* = 24.41, *d.f.* = 1, 4, *P* < 0.01), but was independent of harem membership (*F* = 0.89, *d.f.* = 1, 4, *P* = 0.40) and date (*F* = 2.35, *d.f.* = 2, 5, *P* = 0.19). No interaction effects were significant (*P* > 0.05, Fig. 2). Harem males left the cave more frequently than adult females. The harem male from the red harem engaged in 6.0 ± 2.6 bouts/night compared with 1.5 ± 0.5 bouts/night by the two adult females in this harem. Similarly, the harem male from the yellow harem engaged in 9.0 ± 1.4 foraging bouts/night compared with 2.6 ± 1.9 bouts/night by the four adult females from this harem. The one subadult male from the red harem engaged in 2.0 ± 1.0 bouts/night (Fig. 1).

Mean duration of foraging bouts was significantly influenced by status in the harem (*F* = 9.08, *d.f.* = 1, 4, *P* < 0.05) but independent of harem membership (*F* = 0.26, *d.f.* = 1, 4, *P* = 0.63) and date (*F* = 1.39, *d.f.* = 2, 5, *P* = 0.33). No interaction effects were significant (*P* > 0.05, Fig. 2). The duration of each foraging bout was significantly less for harem males than for adult females. Average duration of foraging bouts for the harem male from the red harem was 16.0 ± 1.5 min compared with 110.0 ± 49.4 min for the two adult females. Similarly, the average duration of foraging bouts for the harem male from the yellow harem was 12.0 ± 4.2 min compared with 90.5 ± 59.0 min for the four adult females.

Harem males were active throughout the night, but the activity of females was concentrated mostly in the early part of the night (Fig. 1). To evaluate if foraging bouts of harem males were distributed randomly throughout the night, we arbitrarily divided the night into 30-min periods, scored if a bat was absent from the cave during each period, and used a non-parametric runs test (Zar, 1984). In all cases, temporal distri-
Fig. 1.—Nightly foraging activity of harem males, adult females, and a subadult male from two *P. hastatus* harems (A, red harem and B, yellow harem) during the mating season. Activity was monitored telemetrically at 5-min intervals from 30 min before sunset to 30 min after sunrise. Absence of a signal from a radiotagged bat (indicated by upward deflections) indicates time absent from the cave (i.e., foraging bouts).

The distribution of nightly foraging bouts for harem males did not differ from random (two-tailed test, $Z = -1.56$ to 0.50, $P > 0.11$). When examined across nights and harems, adult females engaged in one long foraging bout on 8 of 14 nights, and on all nights, most females were absent from the cave for nearly 3 h.

Data on body mass, FMR, and DEE were obtained from bats in three harems; the red harem on 4 nights, the yellow harem on 2 nights, and the pink harem on 1 night (Table 1). Group members typically included one harem male, several adult females, and sometimes a subadult male. Because composition of the group and number of sampling nights varied among harems, we could not use a repeated-measures design.
Fig. 2.—Comparison of A) total time spent foraging by *P. hastatus*, averaged across nights, B) mean number of foraging bouts per night, and C) mean duration of foraging bouts recorded for harem members (harem males, females and a subadult male) in early January. Error bars represent one standard deviation; levels of probability are based on a one-way analysis of variance.

for this analysis. Thus, as needed, we calculated means of body mass, FMR, and DEE for each individual and then tested for differences based on harem status using a one-way analysis of variance. That analysis provided a conservative test for differences in harem status, although it could not be used to distinguish between different harems or dates of capture.

Body mass differed significantly based on an individual's status in a harem ($F = 8.67, d.f. = 3, 16, P < 0.005$, Fig. 3). Body mass of harem males averaged $87.1 \pm 4.4$ g ($n = 3$) and was greater than adult females ($74.4 \pm 4.2$ g, $n = 15$) and the subadult male ($74.5$ g, $n = 1$, Duncan's Multiple Range test, $P < 0.05$). Mean body mass of bachelor males ($83.8 \pm 5.3$ g, $n = 11$) was not different from that of harem males (Duncan's Multiple Range test, $P < 0.05$). We injected six members of one bachelor group in an effort to assess FMR and DEE, although none of the bats were recaptured.

There were no significant differences in FMR or DEE among harem members (Fig. 3). When expressed on a mass-specific basis (ml CO$_2$ g$^{-1}$ h$^{-1}$), FMR was $3.4 \pm 0.69$ ($n = 3$) for harem males, $3.1 \pm 0.85$ ($n = 15$) for adult females, and $1.9 \pm 0.08$ for a subadult male, respectively ($F = 1.08, d.f. = 3, 16, P = 0.39$). When calculated on a whole-animal basis and expressed as DEE (kJ/day), there was no difference among groups ($F = 1.35, d.f. = 3, 16, P = 0.29$), and was $159.7 \pm 28.6$ for harem males, $132.2 \pm 39.5$ for adult females, and $79.7$ for a subadult male, respectively.

**Discussion**

Harem males spent significantly less time away from their roost at night than females and departed from and returned to the cave throughout the night more often than females. Harem males made several short foraging bouts spaced randomly throughout the night—a behavior consistent with activity of males in other species of bats known to form harems (Balasingh et al., 1995; Bhat and Kunz, 1995; Fleming, 1988; Morrison and Morrison, 1981). Although our estimates of FMR and DEE did not differ significantly among harem members, those
Table 1.—Body mass, water flux, and field energetics of individual harem members of Phyllotomus hastatus during the mating period in early January.

<table>
<thead>
<tr>
<th>Harem</th>
<th>Capture date</th>
<th>Band number</th>
<th>Status</th>
<th>Body mass (g)</th>
<th>H₂O in (μl/day)</th>
<th>H₂O out (μl/day)</th>
<th>FMR ml CO₂ g⁻¹ h⁻¹</th>
<th>DEE (kJ/day)</th>
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<tbody>
<tr>
<td>Pink</td>
<td>14 Jan 85</td>
<td>P55</td>
<td>Harem female</td>
<td>75.5</td>
<td>397</td>
<td>401</td>
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<td>P64</td>
<td>Harem male</td>
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<td>P69</td>
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<td>655</td>
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<td>Red</td>
<td>7 Jan 87</td>
<td>R1</td>
<td>Harem female</td>
<td>81.5</td>
<td>485.8</td>
<td>502.1</td>
<td>2.88</td>
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<td></td>
<td>7 Jan 87</td>
<td>R3</td>
<td>Harem female</td>
<td>72.3</td>
<td>652.9</td>
<td>675.5</td>
<td>3.97</td>
<td>163.2</td>
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<td>7 Jan 87</td>
<td>R5</td>
<td>Harem female</td>
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<td>307.1</td>
<td>331.5</td>
<td>2.72</td>
<td>123.5</td>
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<td>7 Jan 87</td>
<td>R6</td>
<td>Harem female</td>
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<td>5.53</td>
<td>253.9</td>
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<td>7 Jan 87</td>
<td>R9</td>
<td>Subadult male</td>
<td>75.5</td>
<td>162.5</td>
<td>180.4</td>
<td>1.87</td>
<td>76.5</td>
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<td>R11</td>
<td>Harem female</td>
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<td>Harem female</td>
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<td>1.98</td>
<td>82.9</td>
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<tr>
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<td>R13</td>
<td>Harem female</td>
<td>67.9</td>
<td>458.3</td>
<td>475.9</td>
<td>2.88</td>
<td>111.1</td>
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<td></td>
<td>13 Jan 87</td>
<td>R16</td>
<td>Harem male</td>
<td>88.0</td>
<td>618.3</td>
<td>610.4</td>
<td>3.99</td>
<td>199.7</td>
</tr>
<tr>
<td></td>
<td>14 Jan 87</td>
<td>R16</td>
<td>Harem male</td>
<td>87.8</td>
<td>666.9</td>
<td>678.5</td>
<td>4.19</td>
<td>209.2</td>
</tr>
<tr>
<td>Yellow</td>
<td>13 Jan 87</td>
<td>Y51</td>
<td>Harem female</td>
<td>77.0</td>
<td>420.9</td>
<td>454.6</td>
<td>2.97</td>
<td>130.2</td>
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<td>Harem female</td>
<td>79.5</td>
<td>341.0</td>
<td>373.5</td>
<td>2.52</td>
<td>114.1</td>
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<tr>
<td></td>
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<td>Y54</td>
<td>Harem female</td>
<td>69.8</td>
<td>253.7</td>
<td>285.5</td>
<td>2.34</td>
<td>92.8</td>
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<tr>
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<td>Y56</td>
<td>Harem female</td>
<td>73.3</td>
<td>370.0</td>
<td>401.6</td>
<td>2.37</td>
<td>98.2</td>
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<td>Y51</td>
<td>Harem female</td>
<td>72.8</td>
<td>153.5</td>
<td>194.8</td>
<td>1.27</td>
<td>52.4</td>
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<tr>
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<td>Harem male</td>
<td>91.3</td>
<td>691.0</td>
<td>687.7</td>
<td>2.44</td>
<td>126.8</td>
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<td></td>
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<td>Y53</td>
<td>Harem female</td>
<td>76.5</td>
<td>409.3</td>
<td>427.3</td>
<td>2.83</td>
<td>123.3</td>
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<tr>
<td></td>
<td>14 Jan 87</td>
<td>Y54</td>
<td>Harem female</td>
<td>67.8</td>
<td>490.0</td>
<td>496.0</td>
<td>2.93</td>
<td>112.9</td>
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<tr>
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<td>Harem female</td>
<td>71.8</td>
<td>530.0</td>
<td>524.2</td>
<td>2.63</td>
<td>107.4</td>
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</table>

Values did vary predictably with the highest values observed for harem males and adult females and the lowest for a subadult male. Harem males were absent from the cave for an average of 98 min each night, whereas adult females were absent for an average of 152 min. The longer period of time that females were absent from the cave compared with males presumably reflects differences in time allocated to foraging activity. That adult females forage at greater distances from harem roosts than males (McCracken and Bradbury, 1981) suggests that it is energetically more profitable for females to remain near sources of food rather than return periodically to their roost from distant foraging sites. Similar foraging patterns observed for adult females and subadult males suggest that subadult males are not subject to the same constraints in time and energy as are harem males.

The significant difference in time spent foraging by harem males and females (Fig. 1) and the lack of a significant difference in field metabolic rates (Fig. 2) suggest that harem males maximize amount of time spent in their roost at night, which makes it possible for them to allocate more time and energy to defense of roosts or females. Relatively short and unpredictable (random) patterns of nightly foraging bouts exhibited by harem males (Figs. 1 and 2) should...
males. Because attempts at copulation are sometimes made by non-harem males (McCracken and Bradbury, 1981), we would expect these attempts most often when harem males are absent from their roosts. Reduced foraging time for males, relative to females, is consistent with the hypothesis that males make a trade-off between successful harem maintenance on one hand and time spent foraging on the other (Balasingh et al., 1995). Random departures and returns by the harem male at night should reduce the ability of other males to predict an opportune time for surreptitious matings in the roost. It should not matter if the harem male is absent from the roost at night when females are present, or that the male is present when females are absent, as long as the male’s absence cannot be predicted by a potential competitor. Spending large amounts of time in the roost appears to be an important behavior for successful defense of harem roosts in other species. Our observations of short random foraging bouts by harem males of P. hastatus are consistent with observations that harem males of A. jamaicensis, Carolia perspicillata, and Cynopterus sphinx also feed mostly in the vicinity of their harem roosts (Balasingh et al., 1995; Fleming, 1988; Morrison and Morrison, 1981).

Because female P. hastatus give birth over 3–4 weeks and length of gestation is similar for all females (A. A. Stern, pers. comm.), harem males should assess receptivity of individual females in their harems on a regular basis during the mating period. By feeding near their roost, foraging for short periods, and departing and returning randomly to their roost, harem males should be able to meet their daily energetic requirements and at the same time maintain high levels of vigilance needed to assess receptivity of females and defend them from male competitors.

It remains to be determined which males have the highest probability of gaining access to a group of females after a harem male dies or is dispossessed. Because ten-
ure by the harem male in *P. hastatus* appears to persist for several years and harem males tend to be older than bachelor males (Kunz et al., 1983; McCracken and Bradbury, 1981), the oldest bachelor males probably have the best prospects for access to harem females, especially if they sometimes share a roost (McCracken and Bradbury, 1981). In *A. jamaiensis*, age and size appear to be important criteria for successful maintenance of a harem with the oldest and largest males having the largest harems (Kunz et al., 1983).

Presence of one or more subadult males in a harem should pose little or no immediate paternity threat to a harem male. Membership in a harem group, however, may allow a subadult male to become familiar with female members of the harem and subsequently assume the dominant position if the harem male dies or is ousted by a competitor. Moreover, if a subadult male from one harem assumes a position in another harem and maintains nightly time budgets similar to adult females, this familiarity may make it possible for the male to better assess receptivity of females. Similar behavior was reported in the gelada baboon (*Theropithecus gelada*) in which subordinate “follower” males established social bonds with groups of females (Dunbar, 1988). Although some young males were displaced harem-holders, others apparently benefited by assuming the status of the harem male or established an independent harem following the fissioning of the original group.

Further research is needed to establish if the intensity required to maintain a harem remains the same throughout the year and if vigilance and defense of females or roosts are highest during the mating season. If tenure of harems is a function of male vigilance at the harem site and the probability of a male losing his position is constant, one would expect patterns of nightly foraging and vigilance at the roost (or the harem) to be the same throughout the year. However, if intensity of competition for female groups increases as females become sexually receptive, vigilance by harem males should increase during the mating period. If this hypothesis is correct, we would expect harem males to engage in shorter but more frequent foraging bouts during the mating period compared with the non-mating season.

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