

EFFECTS OF CAPTIVITY ON THERMOREGULATION AND METABOLISM IN *ARTIBEUS JAMAICENSIS* (CHIROPTERA: PHYLLOSTOMATIDAE)

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Abstract—1. In the Jamaican fig-eating bat, *Artibeus jamaicensis*, oxygen consumption (OC in cm^3/g per hr) and deep body temperature (T_b in $^{\circ}\text{C}$) are significantly related to ambient temperature (T_a in $^{\circ}\text{C}$) and length of time in captivity, but not to the direction (low to high or high to low) of T_a change.

2. OC and T_b levels as functions of T_a rapidly change from those characteristic of a non-homeothermic endotherm on the day of capture to values characteristic of a homeothermic endotherm within 3–6 days in captivity.

3. Jamaican fig-eating bats examined within 12 hr of capture were physiologically distinct from individuals of this species kept briefly (3 days) in captivity.

4. Bats tested within 12 hr of capture at T_a s of 30 and 25 $^{\circ}\text{C}$ required 1/3 and 2/3 less metabolic energy, respectively, than bats maintained briefly in captivity.

INTRODUCTION

For many neotropical bats the relationship of thermoregulation and metabolism as functions of ambient temperature remains unclear [compare McNab (1969) with Studier & Wilson (1970)]. McNab (1969) found most neotropical species he tested, including *Artibeus jamaicensis*, to be homeothermic (constant deep body temperature) endotherms. In contrast, Studier & Wilson (1970) found many neotropical species, including *A. jamaicensis* and other species studied by McNab (1969), to be highly variable in thermoregulatory capabilities, with most species showing patterns characteristic of non-homeothermic endotherms. Although these different patterns may result from genetic differences between populations of the species tested, they may reflect different methodological approaches by the investigators. Studier & Wilson (1970) usually tested their bats with 12 hr after capture, but McNab (1969) maintained his frugivorous bats in the laboratory for periods of up to 2 weeks before testing them. Furthermore, McNab (1969) apparently initially exposed his bats to a constant low ambient temperature (T_a) followed by higher T_a s, whereas Studier & Wilson (1970) started with a high T_a followed by lower T_a s. In an attempt to explain these opposing results, oxygen consumption (OC) and deep body temperature (T_b) as functions of T_a , time in captivity, and the directions of T_a change, were determined in *Artibeus jamaicensis*.

MATERIALS AND METHODS

All bats were mist-netted at night on Barro Colorado Island, Panama Canal Zone; four males and one female *A. jamaicensis* on 4 July 1977 at Lutz Creek, and three males and two females on 5 July 1977 at marker 11 on Barbour Trail. These bats were returned to the laboratory,

caged (each group of five in hardware cloth cages of 25 × 23 × 38 cm) and provided with water and food (bananas and figs) which were readily taken. Cages were covered to allow limited lighting throughout the entire period of confinement. The morning after capture (time in captivity about 12 hr), at approximately 0800 hr, bats were weighed and placed in metabolism chambers. Methods for determination of OC and T_b were essentially identical to those described by Studier & O'Farrell (1972) except that a Beckman Fieldlab (Polarographic) Oxygen Analyzer was used and air flowing through the entire system was not dried but was kept at ambient relative humidity. Bats captured on 4 July were exposed to an initial T_a of 30 $^{\circ}\text{C}$ on 5, 8 and 11 July and were allowed to equilibrate within the system until T_b and OC stabilized (at least 1.5 hr), at which time T_b , OC and chamber temperature were recorded and T_a was lowered to 25 $^{\circ}\text{C}$. Bats were allowed to equilibrate to the new T_a , and T_b , OC and chamber temperatures again were recorded. On 8 and 11 July, T_a was further lowered to 20 $^{\circ}\text{C}$ and readings were taken a third time. The bats caught on 4 July thus comprised the high to low group. Bats caught the night of 5 July represented the low to high group, and were tested on 6, 9 and 12 July as previously described, except that on 6 July bats were first exposed to 25 $^{\circ}\text{C}$, allowed to equilibrate, and readings were taken. Ambient temperature was raised to 30 $^{\circ}\text{C}$ for a second set of readings. On 9 and 12 July, these bats were first exposed to a T_a of 20 $^{\circ}\text{C}$, followed by later exposure to 25 $^{\circ}\text{C}$, and finally to 30 $^{\circ}\text{C}$. The time of initial testing for each group represented about 12 hr of captivity, and is hereafter referred to as day 0; the second and third testing of each group thus was done on days 3 and 6. After the final day of testing, all bats were released at their original capture sites.

Although one female from the low to high group died of unknown causes in captivity, all captive bats ate readily and exhibited no appreciable weight change. Mean weights on days 0, 3 and 6 were 48.7, 48.1 and 49.0 g, respectively. Originally we intended to examine two groups of five bats each at T_a s of 30, 25 and 20 $^{\circ}\text{C}$; however, on day 0 the T_b s of several individuals in the high to low group dropped markedly at 25 $^{\circ}\text{C}$ and we decided that exposure to a T_a

of 20 C might result in the death of some bats and would obviously prevent further testing on days 3 and 6. To obtain equal cell sizes for the ANOVA, the data set for one of the five bats in the high to low group was randomly selected and discarded. A multiple factor ANOVA (Sokal & Rohlf, 1969) was performed on data from two groups of four bats each with direction of T_a change (low to high and high to low), day of testing (days 0, 3 and 6), and T_a (25 and 30 C) as independent variables, and OC and T_b as dependent variables. Statistical significance was set at $P < 0.025$.

RESULTS AND DISCUSSION

Results of the ANOVA are condensed in Table 1. Both T_a and time in captivity significantly affect OC and T_b , whereas the direction of T_a change does not. Additionally, OC is significantly related to the interaction of T_a and days in captivity. This significant interaction means that regressions of OC on T_a change (increase) with days of captivity, i.e. regression slopes (conductance) are significantly affected by length of captivity. Most noteworthy is that both OC and T_b increase significantly with days of captivity, thus the bats exhibit metabolic patterns characteristic of a non-homeothermic endotherm at day 0, but those of a homeothermic endotherm by day 3. This phenomenon may be readily visualized by inspection of Figs 1 and 2. This "captivity effect" probably accounts for the dichotomy between our previous data (Studier & Wilson, 1970) and those of McNab (1969) for *A. jamaicensis*. The divergent data on other neotropical frugivorous bats in these two studies may also be explained by a "captivity effect" as would the similarities in the data on neotropical insectivores like *Pteronotus*. McNab (1969) tested *Pteronotus* soon after capture, after discovering that these bats would not feed in captivity, and obtained thermoregulatory data comparable to ours (Studier & Wilson, 1970). The length of time in captivity may also explain the conflicting thermoregulatory and metabolic data reported by Stones & Wiebers (1967) and Studier & O'Farrell (1972) for *Myotis lucifugus*. The former authors studied captive bats and found them to be homeothermic endotherms, whereas the latter authors

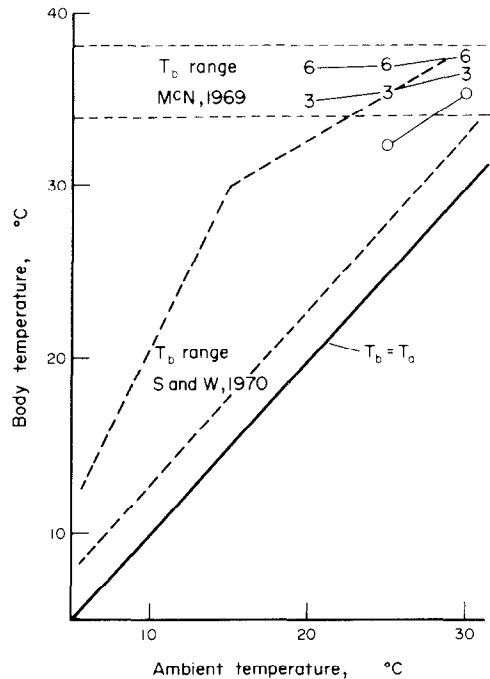


Fig. 1. The relationship of body temperature to ambient temperature in *Artibeus jamaicensis*. Dotted lines represent the ranges of previously reported data for this species by McNab (1969) and dashed lines the ranges from Studier & Wilson (1970). Mean body temperatures are shown for bats tested after 0, 3 and 6 days in captivity.

studied freshly caught individuals and found them to be highly variable in respect to thermoregulatory performance and metabolism. The "captivity effect" may well also resolve other conflicting data on thermoregulatory activities and metabolism in other small mammals. A massive literature is devoted to thermoregulation in *Peromyscus leucopus* (see Gaertner *et al.*, 1973; Hill, 1977) where conflicting data may be the result of time in captivity before testing. That season, reproductive condition, habitat selection and grouping may significantly affect metabolic and thermo-

Table 1. ANOVA of relationships of oxygen consumption and deep body temperature to ambient temperature (T_a s of 25 and 30 C), direction of T_a change, days in captivity (0, 3 and 6), and interactions in captive *Artibeus jamaicensis*

SOURCE	OXYGEN CONSUMPTION		BODY TEMPERATURE (°C)	
	F	MS	F	MS
Temperature (25/30)	1	3.8534	24.610*	69.693†
Direction of T_a	1	0.3852	2.096	1.2969
Day (0/3/6)	2	3.7174	27.271*	64.7759
$T_a \times D$	2	0.2693	7.112	1.9408
$T_a \times D \times C$	2	0.1122	0.089	0.0902
$T_a \times D \times C \times D$	2	0.7910	6.138	6.1830
$T_a \times D \times C \times D \times C$	2	0.1829	1.889	1.1911
Error	80	0.1363		0.2711

* Significant at $P < 0.0005$.
 # Significant at $P < 0.0025$.
 † Significant at $P < 0.025$.

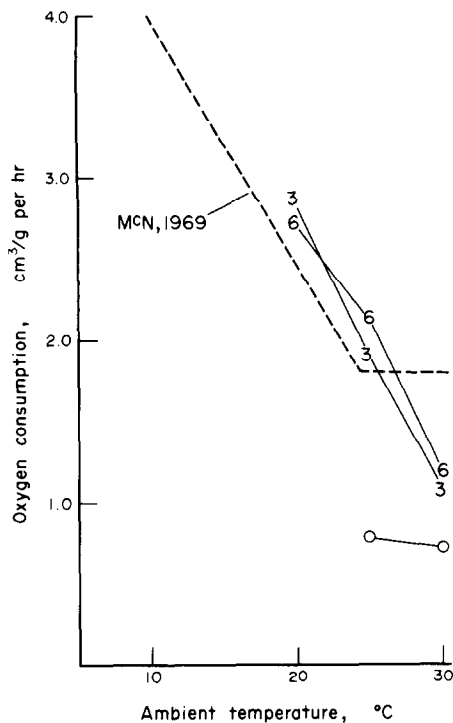


Fig. 2. The relationship of oxygen consumption to ambient temperature in *Artibeus jamaicensis*. Dashed line represents mean oxygen consumption found by McNab (1969). Mean oxygen consumption of bats tested after 0, 3 and 6 days in captivity are shown.

regulatory performances in bats is acknowledged (see Studier & O'Farrell, 1972). Time spent in captivity also should be recognized as a critical variable because bats tested immediately after capture are physiologically distinct from those tested after a short period of captivity.

Although the "captivity effect" describes the previously discussed divergent data on thermoregulation and metabolism in bats, it does not show which data set represents the natural thermoregulatory and metabolic activity of bats. Pertinent to this question are data reported by Studier & O'Farrell (1972) for *M. lucifugus* and *M. thysanodes*. They found that the *T_b*s of these bats in their natural roosting sites were highly variable and similar to the data they presented for freshly caught, lab tested individuals. It would appear then that data on bats tested soon after capture reflect the natural thermoregulatory performance of the species, whereas data on captive bats reflect the greatest homeothermic capabilities of the species.

Although no attempt was made to determine which components of the "captivity effect" are responsible, either singly or in combination, for the changeover in thermoregulatory performance, several probabilities exist. It is unlikely that the increased homeothermic response in this study results from thermal acclimation. No attempt was made to hold captive bats at constant *T_a*, rather *T_a* for captive bats fluctuated in slightly muted fashion with natural environmental *T_a*. Furthermore, the "captivity effect" would not seem to be a general stress response since stress would probably be greatest during the initial hours in captivity and we thus would expect bats to be most

accurately homeothermic on day 0 testing. The "captivity effect" may result from the individual or combined actions of reduced activity while caged or the continual presence of excess food, allowing the bats to eat at any time of day.

We theorize that in its natural environment, *A. jamaicensis* is a homeothermic endotherm during periods of feeding and flight activity, but loosens *T_b* control (becoming a non-homeothermic endotherm) during roosting (non-feeding, non-flying) periods. The slight reduction in *T_b* at such times would conserve large amounts of energy. In this situation a non-homeothermic *A. jamaicensis* conserves 38.7 and 67.4% of the energy required of homeothermic individuals at *T_a*s of 30 and 25°C, respectively. This would certainly amount to a major energy cost reduction over a half-day roosting period. We assume that the slight *T_b* reduction in *A. jamaicensis* (*T_b* of 35.2°C at *T_a* of 30°C and *T_b* of 32.5°C at *T_a* of 25°C) would not reduce the responsiveness of individuals to environmental stimuli during roosting nor would it preclude flight initiation in this species.

The "captivity effect" described herein is the opposite of what one might expect. Animals that are good homeotherms may lose their ability to thermoregulate in captivity because of stress or poor nutritional state. Here we show that *A. jamaicensis* is a heterotherm when first captured, and quickly becomes homeothermic in captivity.

It is possible that thermoregulation is dependent on nutritional state in these animals. In the wild, *A. jamaicensis* feeds on fruit which varies seasonally in abundance from scarce to plentiful; individual bats may undergo a natural period of diel torpor, whereas animals kept with *ad lib* food may never go torpid as long as the food supply is constant and plentiful. It would be interesting to see if imposing food stress on captive animals reverses the trend towards homeothermy shown here. Future studies directed towards the relationship between food availability, nutritional state, and thermoregulation in tropical bats might help explain why these animals show such variation in thermoregulatory response.

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