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RESEARCH NOTE

COMPARATIVE LOCOMOTOR ECOLOGY OF GIBBONS AND MACAQUES: DOES BRACHIATION MINIMIZE TRAVEL COSTS?

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ABSTRACT

Agile gibbons (*Hylobates agilis*) rightfully deserve their name as they traveled at three times the rate (1.09 vs. 0.31 m/s) of long-tailed macaques (*Macaca fascicularis*). Although both species generally traveled the same distance during each complete locomotion bout (7.0 vs. 6.0 m), the gibbons tended to deviate less from a straight path (1.17:1 vs 1.46:1) than the macaques. Using various published equations to calculate transport costs per unit distance, given the above observations, we demonstrate that, when the total distance travelled is considered, brachiating gibbons are twenty percent more energy efficient than the quadrupedal macaques and almost forty percent more efficient over the straight line distance between two points.

Keywords: gibbons, macaques, locomotor ecology, travel costs, West Kalimantan

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INTRODUCTION

Gibbons (*Hylobates spp.*) are monogamous, territorial brachiating apes and are widely distributed across Southeast Asia. Nearly everywhere they are found, one or two of the several species of macaque (*Macaca spp.*), all of which are polygamous, non-territorial quadrupedal monkeys, also live sympatrically with the gibbons (Roonwal and Mohnot, 1977). Both gibbons and macaques are omnivorous, feeding mainly on fruit (McKinnon and McKinnon, 1978; Rodman, 1978; Gittins, 1982; van Schaik and van Noordwick, 1986) but also on insects, leaves, and flowers. Their diets certainly overlap, e.g. when both species encounter a large fruit patch simultaneously, such as a *Ficus sp.* (Moraceae) hemiepiphyte, the macaques actively exclude the gibbons (pers. obs.). While direct competition for resources is rather infrequent, the two species do demonstrate a preference for ripe fruit, when it is available. In a larger context, both species, because they are living sympatrically, have roughly the same set of resources available to them, and therefore, face roughly the same foraging problems, but they obviously solve these problems in very different ways, most notably in their social systems and primary modes of locomotion.

Despite any food preferences they might have, the difference in their actual diets may be more pronounced than what is generally stated in the literature, with gibbons being ripe fruit specialists, while macaques subsist more on unripe fruit and insects.

Because these aspects of foraging behavior cannot be studied simultaneously, we chose to compare the locomotor strategy of the agile gibbon (*Hylobates agilis*) and the long-tailed macaque (*Macaca fascicularis*) and to examine the implications these differences might have for their coexistence and in their foraging behavior.

Comparative studies of suitable sympatric species are a powerful method to examine differences in behavioral and evolutionary ecology because this matched situation controls for the background ecological conditions not under study and which vary between locations and times.

Gibbons and macaques are well-suited for a comparative study of locomotor behavior and its possible effects on foraging efficiency. They are both medium sized primates (Grand, 1984) and their diets are roughly similar (McKinnon and McKinnon, 1978; Rodman, 1978; Gittins, 1982; van Schaik and van Noordwick, 1986). The comparison also addresses the divergence between Old World apes and monkeys and the theory that suspensory behavior minimized travel costs for apes over quadrupedal monkeys and allowed them to be more selective in their choice of travel paths and to travel more rapidly (Temerin and Cant, 1983). In a previous paper (Cannon and Leighton, 1994), we demonstrated that gibbons are more selective in their use of canopy structure and that macaques are constrained to the most continuous layer of the canopy because they do not habitually cross the wide gaps present between most tree crowns (>1.0 m). The ability of gibbons to cross wider gaps allows them to travel disproportionately in the emergent layer where the mean length of continuous structure is greater than in the main canopy (>11 vs. <9 m). So, gibbons are more selective in their use of canopy structure but does this allow them to minimize their travel costs relative to the macaque?

To answer this question, we tested whether agile gibbons travel at a higher rate and more directly than macaques and then used estimates of rate and directness, along energy costs of travel for each species. Travel occurs within a rich context of objectives, with animals simultaneously foraging for insects, moving from Point A to Point B, keeping track of other members of the group, etc., therefore an attempt was made to limit this test to "directed" travel. Ultimately, all animals must move from Point A to Point B, whether this distance is between fruit resources or simply between tree crowns, and it is this more fine-grained approach to travel, i.e. movement between two nearby points (often less than ten meters), which we will use to focus on "directed" travel.

METHODS

This research was conducted at the Cabang Panti Research Station in the Gunung Palung National Park, West Kalimantan, Indonesia (see site description in Cannon and Leighton, 1994). A single pair of adult gibbons and a single troop of long-tailed macaques, consisting of one adult male and two adult females, were chosen for this study. A juvenile female still traveled with the gibbon pair, while a number of juveniles of both sexes were

present in the macaque group, but observations were not taken from these individuals. The gibbons' territory of roughly 25 hectares was completely within the much larger home range of the macaques. Boundaries of home territories were personally estimated after several months of morning follows and from information provided by other researchers (e.g. Mitani, 1990). Travel observations were collected during early morning follows from February to June 1988. The unit of observation was a complete bout of directed travel. A bout began when an individual started moving from a resting posture until it resumed a resting posture again and stopped traveling. Bouts were rejected if any behavior other than travel was observed; the individual stopped to forage for insects, even visually; interacted with another individual; or pursued another activity except resting at the endpoint of the observation. This criterion would limit the data collected to bouts of "directed" travel, or bouts during which the individual's objective appeared to be moving from Point A to Point B. Of course, this criterion is not perfect, but provides a standard for collection.

An additional three criteria had to be met before an observation was accepted as "directed" travel: 1) the individual must be observed and targeted before sampling began; 2) an entire sequence of travel must be observed, or rather, the individual must be under observation from resting posture to resting posture; and 3) the end of the sequence must be observed. The first criteria would avoid the over representation of eye catching and unusual behavior. The second criteria ensured that even brief but perhaps critical behavior is observed. Finally, the last criteria ensured that we only sampled complete bouts of travel. Duration of travel was measured in seconds using a stopwatch, while distance was estimated using the mean body length of each species as a measuring stick, the distance traveled being counted in body lengths as the animal progressed and then multiplied by 0.5 meters. The direct distance traveled was estimated by pacing the distance on the ground beneath the travel route of the observed individual.

A great deal of work exists on the allometric relationships between body size and rate of travel for terrestrial, aquatic and flying animals but little has been done to explore the effects of arboreality on this relationship, possibly because of the great difficulty in simulating an arboreal environment in the laboratory, but the energetics of gibbon and macaque locomotion, using the rates and directness measures above, can be estimated by manipulating available equations. For a running terrestrial animal, a strong allometric relationship has been demonstrated by Peters (1983) as:

$${}_wR_{\text{run}} = 4.24 W^{-0.25} + V 11.3 W^{-0.28}$$

where W is the weight of the animal, V is the rate of travel, and ${}_wR_{\text{run}}$ is the energy expenditure per unit time. It is obvious from this equation that energy expenditures go up directly with higher rates of travel but diminish with increasing body size. This base equation will be used to represent a traveling macaque.

Parsons and Taylor (1977) studied the relationship between energy costs, body size and velocity for brachiation in spider monkeys (*Ateles geoffroyi*) and found that the energy costs increased with increased rate of travel more rapidly than expected for other animals walking and running. Although spider monkeys, usually only classified as "semi-brachiators" (Hallgrímsson and Swartz, 1995), may not be an adequate model for gibbons, highly specialized brachiators, I will use these findings for lack of any better. Heglund

(1985) compiled a list of energy consumption and rate of travel for a number of primates. Representative slopes for this study are the spider monkey ($0.37V\text{mlO}_2(\text{mkg})^{-1}$) and the stump-tailed macaque (*Macaca arctoides*: $0.25V\text{mlO}_2(\text{mkg})^{-1}$), where V is rate of travel. To obtain the equation for the energetic costs of a brachiating animal, the ratio of the two slopes given above, i.e. 1.48:1 brachiation:running, will be placed into the previous equation for a running terrestrial animal.

$$wR_{\text{brachiate}} = 4.24 W^{-0.25} + V 16.7 W^{-0.28}$$

This equation will represent a brachiating gibbon.

RESULTS AND DISCUSSION

A total of 72 "directed" bouts of travel were observed for the macaques during which they traveled 617 m in 1,883 seconds, while 34 bouts were observed for the gibbons, covering 262.5 m in 208 sec. The macaques traveled more than four times longer in duration (22 vs. 5 sec, $p < .0001$, Mann-Whitney U) than the gibbons and yet only traveled a meter farther in distance (7.0 vs. 6.0 m; n.s.; Table 1). Both species traveled at characteristic rates (Fig. 1; $p < .05$ for both regressions); gibbons traveled at three times the rate of macaques (1.09 vs. 0.31 m/s). When the straight line distance is compared, the macaques actually moved a meter less than the gibbons (4.5 vs. 5.5 m, n.s.) during each bout. This deviation from a straight path of travel means that for every straight meter of

Table 1. Travel bout characteristics of sympatric long-tailed macaques (*Macaca fascicularis*) and agile gibbons (*Hylobates agilis*) in the Gunung Palung National Park, Indonesia. All estimators are medians and sample sizes are enclosed in parenthesis. Interspecific comparisons were made using a Mann-Whitney U test and significant results are marked with an asterisk ($p < 0.0001$)

	<i>Macaca fascicularis</i>	<i>Hylobates agilis</i>
Bout Duration (sec)	22 (72)	5 (36) *
Actual Distance (m)	7.0 (74)	6.0 (37)
Direct Distance (m)	4.5 (74)	5.5 (37)
Rate of Travel (m/s)	0.32 (72)	1.16 (36) *

distance measured on the ground, the macaques actually moved 1.46m, while the gibbons moved only 1.17m (Fig. 2).

Combining the energetics equations for each species and the results obtained from the behavioral observations, a transformation comparing the energetic efficiency of the two species, given by Peters (1983), can be obtained:

$$R_{\text{b,r}} = (4.24(5.6\text{kg})^{-0.25}/(1.16\text{m/s}) + 16.7(5.6\text{kg})^{-0.28}) / (4.24(5.0\text{kg})^{-0.25}/(0.32\text{ m/s}) + 11.3(5.0\text{kg})^{-0.28})$$

where 5.6 kg is the mean body weight of a gibbon (Jungers, 1984) and 5.0 kg of a macaque (Gingerich et al., 1982). The result of this transformation is 0.79:1 energy cost per unit distance of brachiation to running. Therefore the gibbons were twenty percent more efficient than the macaque in travel cost per unit distance. If the difference in straight line

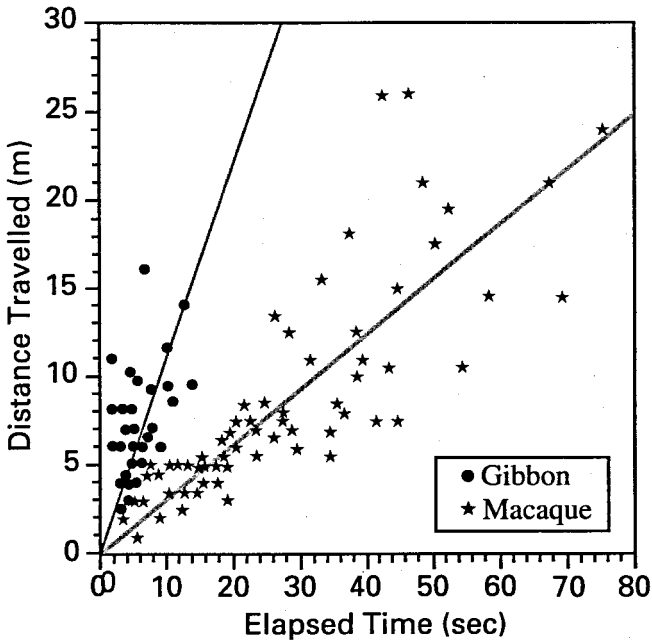


Figure 1. Rate of travel during directed travel for agile gibbons (*Hylobates agilis*), ($y=1.09x$, $r^2=0.27$, $p<0.05$); and long-tailed macaques (*Macaca fascicularis*) ($y=0.31x$, $r^2=0.66$, $p<0.05$).

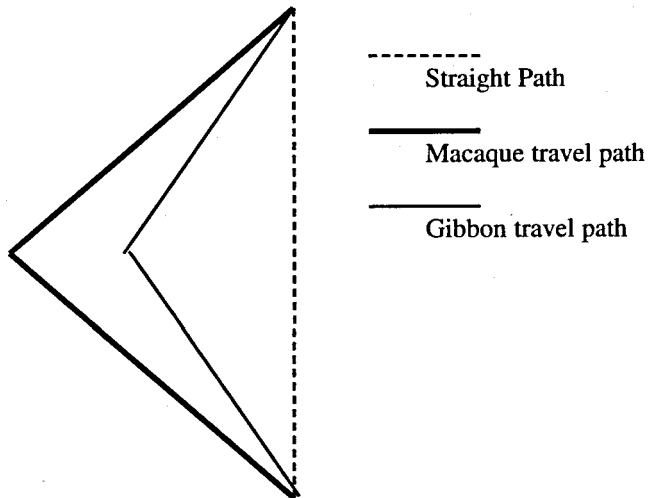


Figure 2. The deviation from a direct path observed during travel by agile gibbons (*Hylobates agilis*), and long-tailed macaques (*Macaca fascicularis*) at the Cabang Panti Research Station in Gunung Palung National Park, West Kalimantan, Indonesia.

distance is also included (Fig. 2), the ratio of travel costs becomes 0.63:1, advantage gibbons. The gibbons, because of their greater energy efficiency, can travel further on a given fruit yield and because of their high rate of travel, will actually spend much less time traveling than the macaques. Also, because gibbons live in small family units of two to four adult individuals (Mitani, 1990) and often forage individually (pers. obs.), they can better subsist on small, widely distributed patches of ripe fruit and are better able to defend them against other gibbons and primates. Therefore, gibbons can act more as "ripe fruit" specialists (MacKinnon and MacKinnon, 1978; Raemakers and Chivers, 1980) than macaques.

Of course, this behavior must be looked at within the context of many other behaviors which influence the relative cost of travel efficiency. The large polygamous social groups which macaques form may be limiting their ability to exploit small ephemeral fruit patches and to defend a known territory and therefore they would gain little by being able to travel quickly and directly. Their meandering and cautious way of moving through the canopy may improve their ability to catch insects. Even the strict criteria used in observing travel behavior in this study will not eliminate the possibility that the macaques were constantly foraging for insects and thus not interesting in traveling in a straight line. Nonetheless, considering the actual distance each species traveled, the gibbons are still twenty percent more efficient per unit distance than the macaques. The evidence from this paper does not conflict with the theory that the suspensory locomotion adopted by apes allowed them to travel more rapidly and more directly through the canopy than monkeys and thus minimized their travel costs. For the gibbons, a rapid rate of locomotion, combined with small group size, may allow them to maintain territories and defend small patches of fruit, while macaques, traveling in larger groups, must find sufficiently large patches and constantly forage for insects.

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