



Ontogeny of Ranging in Wild Chimpanzees

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We examined the relationship between juvenile age and distance traveled per day, or day range, in Kanyawara chimpanzees. Because the energy cost of locomotion is greater for small-bodied animals, we predict that day range is constrained by body size, i.e., younger individuals tend to have shorter day ranges. To test this hypothesis, we measured day range for 200 day-ranges of groups in which we recorded the age of the youngest juvenile present. As predicted, day range correlated positively with age for juveniles. Comparisons of day range vs. estimated stature support the hypothesis that the increase in day range with age was a consequence of body size. To assess other sources of variation in day range, we also measured the effects of group size and the presence of a carried infant. While day range correlated significantly with group size, the presence of a carried infant had no effect on adult female day range. Our results suggest the size of a juvenile may constrain ranging for mothers and their offspring.

KEY WORDS: chimpanzees; day range; maternal investment; ontogeny; primate locomotion.

INTRODUCTION

As large-bodied, ripe-fruit specialists, chimpanzees (*Pan troglodytes*) depend on widely dispersed food patches. Combined with other demands such as territorial defense, their dietary specialization results in long day ranges—distance traveled per day— i.e., means of 2–5 km (Gombe, Wrangham, 1977; Taï, Herbinger *et al.*, 2001; Kibale, Pontzer and Wrangham, 2004). Terrestrial travel accounts for 10–15% of total daily

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energy expenditure, equal to the estimated combined cost of feeding, climbing, socializing, and resting (Pontzer and Wrangham, 2004; Leonard and Robertson, 1997). Travel costs appear sufficiently high to influence the intensity of scramble competition and fission–fusion grouping pattern (Janson and Goldsmith, 1995; Wrangham, 2000), but for chimpanzees researchers previously have examined the effects of such costs only for adults.

We consider the ontogeny of ranging costs among chimpanzees by examining the impact of body size on day range. Because juveniles are smaller than adults and the energy mass-specific energy cost of locomotion tends to be inversely proportional to body size (Taylor *et al.*, 1970, 1982), we expect juveniles to use more mass-specific energy per km than adults. Therefore, if the energy budget of juveniles is constrained in the same way as it appears to be for adults, we expect juveniles to keep the total cost of locomotion low by maintaining shorter day-ranges than those of adults. To test this hypothesis, we assume that age closely predicts juvenile size. Accordingly, we examined the relationship between juvenile age and day range in wild chimpanzees.

Interspecific studies of numerous mammalian groups including primates have demonstrated that small animals expend significantly more energy per kg of body mass than large animals do during walking and running (Taylor *et al.*, 1982). Ontogenetic studies of locomotor performance in several species showed that juveniles have higher mass-specific energy costs of travel than those of adults, perhaps because of inefficient gait or increased basal metabolic rate (humans: DeJaeger *et al.*, 2001; Frost *et al.*, 2002; rabbits: Carrier, 1994; chickens: Muir *et al.*, 1996; guinea pigs: Trillmich *et al.*, 2003), and Steudel-Numbers (2003) proposed that juvenile chimpanzees are similarly inefficient. Inefficiency in food handling and processing relative to that of adults, and later patch arrival times resulting from slower travel speeds, likely magnify the additional energy cost of travel. Because of their smaller body size and long developmental periods, juvenile primates are also inherently more vulnerable to changes in net energy intake than adults are (Janson and van Schaik, 1993). Indeed, juvenile mortality in wild chimpanzees is roughly twice that of captive juveniles, while mortality rates are similar in adults (Hill *et al.*, 2001). Further, studies have shown that suboptimal foraging efficiency during the juvenile period decreases lifetime reproductive fitness in other primates (baboons: Altmann, 1991). Thus, juveniles may use shorter day ranges to minimize the daily energy cost of terrestrial travel (Fig. 1).

Previous work on the ontogeny of locomotor behavior in chimpanzees focused primarily on the types of locomotor behavior they used (Doran, 1992; 1997). Via comparisons of chimpanzees with bonobos (*Pan pygmaeus*) and mountain gorillas (*Gorilla gorilla berengei*), Doran (1992, 1997)

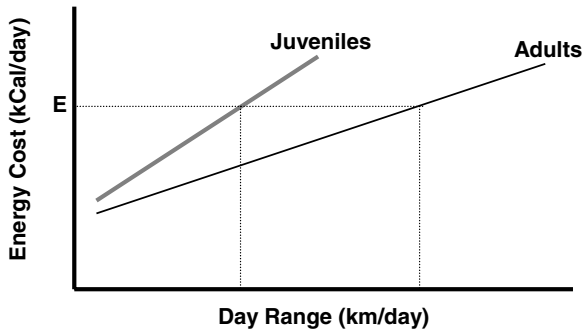


Fig. 1. Proposed effect of body size on preferred day range. Daily energy costs increase with day range. Juveniles, because of higher relative energy costs of travel (energy/body mass/distance), experience a greater increase in cost with day range than adults. Therefore, for any acceptable level of energy cost (E), juveniles will use shorter day ranges.

found that body size correlated with locomotor behavior across species. Chimpanzees, bonobos, and gorillas of similar body size used similar locomotor budgets, with young, small individuals climbing more and knuckle-walking less than adults did. Similarly, in a comparison of the relative demands of terrestrial travel and vertical climbing in chimpanzees, Pontzer and Wrangham (2004) found juveniles used shorter day ranges than those of adult males but on average, climbed more per day, than adults did. While Doran (1997) cautioned against interpreting locomotor behavior as simply a function of size, the results suggest size body has an important effect on locomotor behavior, and perhaps day range, in chimpanzees.

We tested the effect of juvenile age on day range using data from the Kanyawara chimpanzee community in Kibale National Park, Uganda. We hypothesize that day range is limited in juveniles as a consequence of smaller body size, and test the prediction that day range increases with age for juveniles. We then examine whether increases in day range track increases in body size for juveniles and young adults.

In investigating the effect of juvenile age, it is necessary to control for other factors that may affect day range, e.g., group size, because larger groups need to visit more food patches to meet energy demands (Clutton-Brock and Harvey, 1977; Janson and Goldsmith, 1995). Also, because juvenile chimpanzees travel with their mothers until ≥ 10 yr of age (Goodall, 1986), locomotor constraints on mothers may also affect juvenile day range. Studies examining the effect of infant carrying on ranging in adult female chimpanzees suggest carrying decreases travel speed (Williams *et al.*, 2002; Wrangham, 2000), which may in turn decrease day

range. We investigated the effect of foraging group size and the presence of a carried infant on day range to control for these variables.

MATERIALS AND METHODS

Study Site

We obtained ranging data from wild, habituated chimpanzees in the Kanyawara chimpanzee community in Kibale National Park, Uganda, from field observations. The Kanyawara area ($0^{\circ}30' - 0^{\circ}41'N$ and $30^{\circ}19' - 30^{\circ}30'E$) is a mid-altitude (1500 m) tropical rain forest, with a canopy height ranging from 20 to 30 m (Chapman and Wrangham, 1993), and 150 m of topographical relief typical. The community consisted of *ca.* 50 individuals.

Day Range

We measured day range—the distance traveled in a day—from 200 records of parties we observed continually throughout the day, *i.e.*, from leaving night nests to entering night nests. Data come from a 5-yr period (January 1998–December 2002). We included follows in the analysis only if ≥ 1 individual was present for the entire day, such that each follow represents a complete nest-to-nest follow for ≥ 1 individuals. We included all nest-to-nest follows recorded during the study period in the analysis except 1) observations of ill or injured individuals and 2) observations that occurred in poorly mapped areas and were therefore potentially biased or inaccurate ($n < 15$ unused follows). Party composition data, which we recorded at 15-min intervals, enabled us to measure the maximum, minimum, and modal party size for each follow. We defined maximum and minimum party size as the largest and smallest number of individuals listed as present for any 15-min interval, respectively. We defined modal party size as the party size present for the largest number of 15-min observations per day.

We measured day range via an ArcView 3.1 GIS map file of the Kanyawara area (Pontzer and Wrangham, 2004). Field assistants created maps of day journeys that recorded the position of the party every 15 min using a trail map of the area. We drew the maps into the GIS file as a polyline theme with a mouse-driven cursor, taking care to recreate the field maps accurately. We then calculated the length of the lines in ArcView 3.1 via the [shape]:returnlength function. To test intraobserver reliability, we mapped a sample of 10 follows twice on separate occasions. Path lengths

calculated on these 2 occasions were highly correlated ($r^2 = 0.94$, slope = 0.99, $n = 10$), and were not significantly different ($p = 0.60$, paired 2-tailed t -test).

Classes and Body Size

We defined classes as follows: infants, 0–2.9 yr old; juveniles, nonclinging offspring 3.0–9.9 yrs old; subadults, individuals 10–14.9 yr old; adults, individuals 15 yrs and older. We knew birth dates for all juveniles in our study to within 2 mo from field observations.

We define the start of the juvenile period as 3 yr based on observational data from Kanyawara and other sites (Gombe: Goodall, 1986; Tai: Doran, 1992; Mahale: Hiraiwa-Hasegawa, 1990), which suggest chimpanzee juveniles travel independently, i.e., with the mother but not carried, by 36 mo. Previous studies of the locomotor behavior of chimpanzee juveniles in the wild (Doran, 1992; Hiraiwa-Hasegawa, 1990, p. 263) showed juvenile chimpanzees travel independently of the mother for 50% of long-distance travel bouts by 3 yr of age. Because adult females may carry juveniles for much longer, we also performed analyses with 3–3.9 yr-olds removed to ensure results were not simply due to this problematic age group.

We mark the end of the juvenile period at 9.9 yr, as growth studies of both captive (Hamada and Udono, 2005) and wild (Pusey *et al.*, 2005) chimpanzees show growth rate slows markedly at *ca.* 10 yr of age, though body size, particularly body mass, increases slowly for some years afterward (Pusey *et al.*, 2005). We use stature as a measure of body size rather than body mass because it is less variable over time (Hamada and Udono, 2002; Pusey, 1990; Pusey *et al.*, 2005), has a more similar trajectory between males and females (Hamada and Udono, 2002), and may provide a more accurate measure of maturation in locomotor anatomy.

We used data for body size in Hamada and Udono (2002), which combined longitudinal ($n = 12$ individuals) and cross-sectional ($n = 105$) growth data to determine growth trajectories for chimpanzees. Though other researchers have measured body mass in wild populations (Pusey, 1990; Pusey *et al.*, 2005), we had the advantage of providing measurements of stature that include limb length, an important measure of locomotor performance (Alexander, 1984; Hildebrand, 1985; Kram and Taylor, 1990; Pontzer, 2005). We converted sex-specific lowess curves of growth trajectories of stature, presented graphically in Hamada and Udono (2002, p. 271), into percentage of adult stature (stature/adult stature) trajectories

and averaged for males and females. We then estimated percentage of adult stature at each age for juveniles and subadults for comparison with day range data collected for this study.

Data Analysis

We entered day range data and party composition data into Excel (Microsoft Co. Ltd.) for basic analyses and SPSS 6.1 (SPSS Co. Ltd.) for regression and partial correlation statistics. For comparisons between classes, we extracted ranging data for each individual present for the entire follow, i.e., the individuals for which the group follow also represents a focal individual follow from night-nest to night-nest. We considered individuals present for the entire follow only if they were present during unnesting and nesting, and not out of sight of field observers for more than 45 continuous min (3 15-min observations). We calculated mean day range and party sizes for each individual, and pooled the mean values for comparisons between classes. In this way, class means are not biased by well-habituated individuals for which we recorded more follows. For adult females that were present both with and without carried infants during the period studied, we calculated mean day range and party sizes separately for each state to allow within-subjects comparison of ranging behavior.

In using group follows rather than individual focal follows, it was critical that we address 3 biases inherent in the data set. First, parties that moved faster or were more silent were more likely to be lost before the end of the day. Thus day range data in our study, as in others, is to some degree right-censored, and the calculated mean day range may be less than the true mean. Second, because observers in the field preferentially followed parties rather than lone individuals. Our data set does not represent a true random sample of day ranges but instead is biased toward larger parties. As a result, 1) measures of party size may be skewed upward from the true mean, 2) mean day range may be overestimated, especially for mothers, as large parties travel further per day than small parties, and 3) mothers that travel solitarily or in small parties may be underrepresented. Third, day ranges for multiple individuals in the same full-day follow are not statistically independent data points. Therefore, in testing the relationship between individual characteristics, such as age, and day range or party size, it was necessary to eliminate redundancy within the data set to avoid pseudoreplication, i.e., 1 group follow appearing as separate data points. Where applicable, we describe methods for limiting the data set for each of the statistical tests. We then discuss limitations of our analyses.

RESULTS

Day Range

The following are mean day ranges \pm SE, with median, sample size, for each class: adult males, 2.4 km/d \pm 0.04 (2.3, $n = 11$ individuals); adult females without cling infants, 2 \pm 0.16 (1.7, $n = 11$); adult females with clinging infants, 1.9 \pm 0.13 (1.6, $n = 11$); subadult males, 2.4 \pm 0.13 (2.2, $n = 3$); subadult females, 2.4 \pm 0.06 (2.2, $n = 3$); juveniles, 2 \pm 0.12 (1.6, $n = 15$) (Table I). They are the means of the means for all individuals in a class. In comparisons between each class, adult males and subadults of both sexes each used significantly greater mean day ranges than adult females, with and without clinging infants and juveniles ($p < 0.05$, 1-tailed Student's t -test using means for individuals). There is no significant difference in mean day range within the 2 groups: day range for males is not significantly different from that of subadults, either male or female ($p > 0.05$, 1-tailed Student's t -test using means for individuals), and day range for adult females without clinging infants is not significantly greater than that for adult females without infants or for juveniles ($p > 0.05$, 1-tailed Student's t -test using means for individuals).

Effect of Juvenile Age and Body Size

Juvenile day range correlates significantly with age. Of the 200 group follows in our data set, 123 included full-day follows for ≥ 1 juveniles. To avoid the problem of nonindependence, i.e., 1 group follow being

Table I. Mean day range for Kanyawara chimpanzees

Class	Day range (km/d)			
	Mean	SE	n	fws
Males	2.4	0.04	11	662
Females–no infant	1.9	0.15	11	107
Females–with infant	1.9	0.09	11	165
Subadult males	2.4	0.06	3	85
Subadult females	2.4	0.13	3	58
Juveniles	2.0	0.12	15	239
Total	2.1		54	1318

Note. SE = standard error; n = number of individuals; fws. = number of extracted follows. We used number of individuals to calculate standard error. Classes and group size measures are defined in text.

represented by data points for multiple individuals, we limited our sample for the analysis to include only the youngest juvenile in each follow, thus allowing us to treat them as statistically independent full-day follows. Day range correlates significantly and positively with juvenile age ($r = 0.30$, $p < 0.01$, $n = 123$). As day range also correlates significantly with maximum party size for the sample ($r = 0.33$, $p < 0.01$, $n = 123$), we also tested the relationship between juvenile age and day range using partial correlation controlling for maximum party size. Controlling for maximum party size strengthened the age-day range correlation slightly ($r = 0.36$, $p < 0.01$, $df = 120$). To further avoid the problem of pseudoreplication, we calculated mean day range calculated for each yr of age in the set of 123 follows, and treated mean day range at each age as an independent data point in a rank order correlation. We combined day ranges for the 8–9.9-yr-olds to maintain samples of $n > 10$ for each age group. The correlation between mean day range and age is significant ($r = 0.99$, $p < 0.05$, $n = 6$, Spearman) (Fig. 2). This relationship remains significant when we remove juveniles 3–3.9 yr-olds from the analysis ($r = 0.99$, $p < 0.05$, $n = 5$, Spearman).

When we converted age to percentage of adult stature, mean day range correlated significantly with estimated stature ($r = 0.93$, $p < 0.01$, $n = 7$, LSR). It was not possible to quantitatively separate the effects of age and

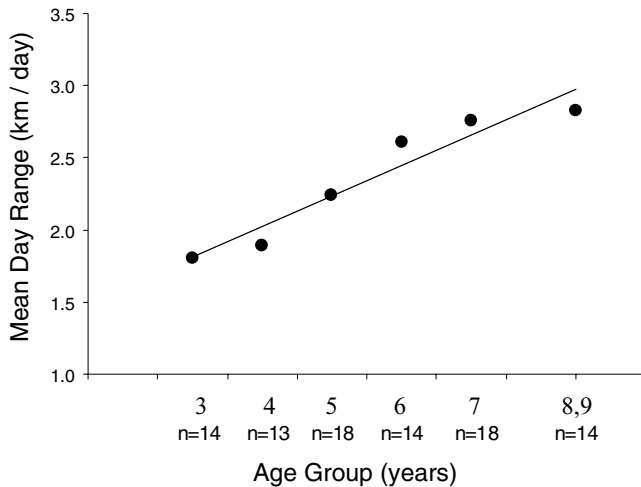


Fig. 2. Mean day range (km/d) vs. age (yrs) for Kanyawara juveniles. Number of follows for each age is given in parentheses. Age groups are given as: 3: 3.0–3.9 yrs old; 4: 4.0–4.9; 5: 5.0–5.9; 6: 6.0–6.9; 7: 7.0–7.9; 8,9: 8.0–9.9. Sample sizes are given below each age group. Line indicates LSR. Spearman rank correlation: $r = 0.99$, $p < 0.05$, $n = 6$.

body size for the data set because we based estimates of size solely on age. However, while day range is highly correlated with age for juveniles (age 3–9.9 yrs) (Fig. 2), day range is independent of age in a combined sample ($n = 272$ follows) of subadults and young (≤ 20 yrs old) adult males. Indeed, plotting both stature and mean day range against age, it appears that increasing day range plateaus at *ca.* 10 yr of age, i.e., when individuals reach adult stature (Fig. 5). Thus the increase in day range through ontogeny appears to track increases in body size as well or better than increases in age.

Effects of Party Size and Infants

As expected, day range correlates positively with party size (Fig. 3), though there is considerable variance around the least squares regression. Though all measures of party size—minimum, maximum, and modal—correlates significantly with day range ($p < 0.01$), maximum party size is the best predictor ($r = 0.31, p < 0.01, n = 200$ group follows). Least squares regression suggests an increase in maximum party size of 10 individuals increases day range by an average of 0.6 km (Fig. 3), *ca.* 25–30% of mean day range.

Comparisons of day range revealed no difference between adult females with and without a carried infant. A 1-tailed Student’s *t*-test of mean day ranges assuming unequal variance showed no significant difference between them ($p = 0.49$). Further, within-subjects comparisons for females

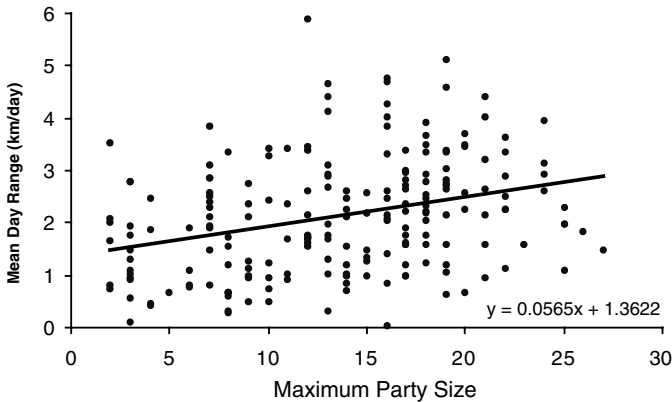


Fig. 3. Day range (km/d) vs. maximum party size. Line indicates LSR (equation in figure). $r = 0.31, n = 200$ group follows, $p < 0.01$.

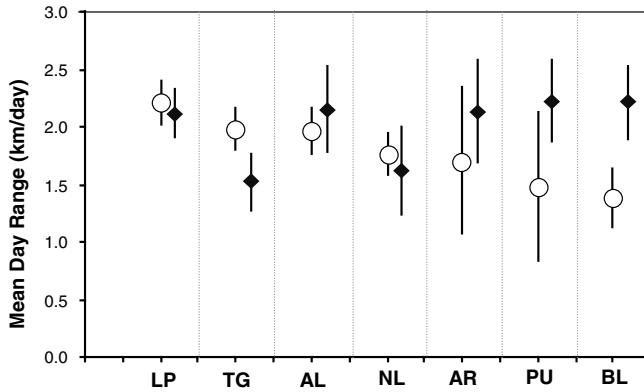


Fig. 4. Within-subjects comparison of mean day range (km/d) for 7 females without clinging infants (open circles) vs. with clinging infants (black diamonds). All females for whom data were collected in both conditions are included. Initials (x-axis) specify individuals.

with and without clinging infants, i.e., comparisons of the same individual in both conditions, showed no difference in mean day range ($p = 0.38$, Student's paired-sample, 1-tailed t -test, $n = 7$ individuals) (Fig. 4). This was true both for first-time mothers ($p = 0.24$, Student's 1-tailed paired-samples t -test, $n = 3$ individuals) as well as parous females. Thus, no effect of the presence of a clinging infant is apparent.

DISCUSSION

The use of group follows presents certain problems in analysis. Most notably, it biased our data toward larger groups. Indeed, our estimate of modal party size based on this set of group follows (13.8) is significantly larger than the 5–6 individuals reported earlier for Kanyawara by Chapman *et al.* (1993) and Wrangham *et al.* (1994). In contrast, mean day ranges for Kanyawara chimpanzees are lower than those at most other sites [Gombe: males: 4.6 km, females 3.2 (Wrangham, 1977); Tai (north): males, 3.7; females, 3.6 (Herbinger *et al.*, 2001); Mahale (combined seasons): 4.8 (Matsumoto-Oda, 2002); Pontzer and Wrangham, 2004]. Further, inter-class differences are similar to those reported elsewhere (*ibid.*), suggesting that the use of group follows, though not ideal, has not significantly affected our measures of day range or the comparisons we draw between classes. By comparing means for individuals rather than extracted follows, and therefore greatly reducing the degrees of freedom in our analyses, we

have presumably minimized the problems of nonindependence inherent in the use of group follows.

Though the correlation between maximum party size and day range is highly statistically significant, the variance about the least squares regression line is considerable (Fig. 3). This degree of variance is similar to that Williams *et al.* (2002) found in an analysis of the effect of party size on day range in a much larger sample of full-day follows ($r = 0.45$, $n = 2706$, $p < 0.01$, least squares regression). Such a high degree of variance suggests that, while day range may be primarily a response to the ecological imperative of encountering and procuring sufficient food to meet energetic demands, numerous factors affect ranging decisions on any given day. The range of day range lengths in this sample (0.04–5.88 km) suggests that chimpanzees do not balance energy intake and expenditure each day, but instead do so over multiple days. Thus the mean distance traveled over several consecutive days, rather than 24 h, is likely to be the best indicator of the distance required to meet energetic demands. This underscores the need for large samples of follows in ecological analyses of day range, and may explain why even ecologically salient measures are relatively poor predictors of the distance traveled during single days.

Effect of Juvenile Age on Day Range

Day range correlated strongly with juvenile age. Further, increases in day range appear to track increases in body size, with juveniles of adult stature, i.e., 9–10 yr, using mean day ranges as long as adult males. The relationship between day range and juvenile age remained significant even when we discarded follows of juveniles 3–3.9 yr of age. The results support the hypothesis that juveniles are constrained in their ranging behavior. Further, the agreement between mean day range and estimated stature (Fig. 5) suggests juvenile ranging is limited as a consequence of smaller body size.

Though our data cannot directly address the mechanism by which juvenile age affects group day range, the apparent effect is likely an artifact of our data collection strategy and the effect of juveniles on their mother's ranging. Our data suggest mother-juvenile pairs leave parties as day range increases. Younger juveniles, and their mothers, drop out earlier, resulting in the correlation between juvenile age and group day range. In the scenario, juveniles constrain their mothers' ranging, but not that of the entire group. The mechanism by which a juvenile limits its mother's ranging warrants future investigation. One plausible hypothesis is that juvenile chimpanzees, as a consequence of smaller body size, are simply

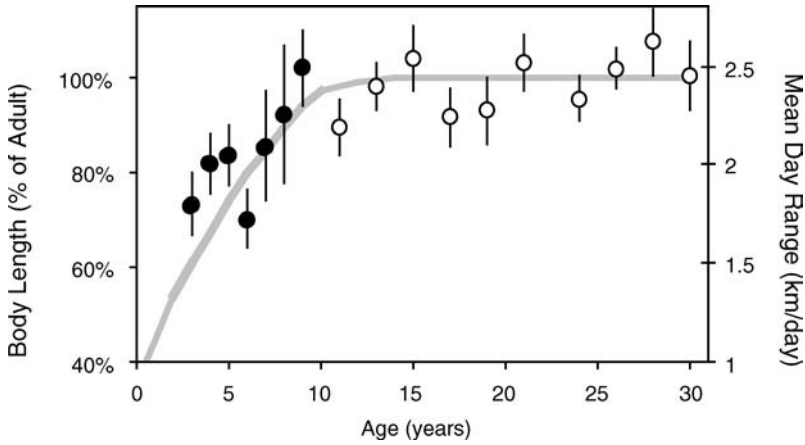


Fig. 5. Mean day range (km/d) and body length (% of adult) vs. age. Body length (gray line) is given as a percentage of adult body length, adapted from Hamada and Odonno (2002). Circles indicate mean day range for a given age. For juveniles (black circles), mean day range is calculated for each yr of age. For subadults and adult males (white circles) mean day range is calculated for every 2 yrs of age, i.e., 10.0–11.9, 12.0–13.9, etc. to maintain samples of greater than 20 follows. Error bars indicate the standard error of the mean.

unable or unwilling to travel long distances, and therefore mothers must use shorter day ranges or abandon their juveniles.

Benefits of Carrying and Costs of Cotraveling

Our analyses reveal no effect of a clinging infant on adult female day range. Comparisons of mean day range between females with and without clinging infants, including within-subjects comparisons of individuals in either condition, suggest clinging infants, despite the energetic costs they must incur through lactation and carrying, had no effect on mothers' ranging in the data considered here. Though this runs counter to Williams *et al.* (2002), this contradiction may be due to the use of distance traveled rather than travel speed as a measure of travel cost: it is possible that infant carrying lowers preferred speed (Wickler *et al.*, 1998) but not day range. In either case, the results of our study suggest one needs to factor juvenile age into analyses of adult female ranging. Females may be constrained in their ranging by young cotraveling offspring that are unable or unwilling to use long day ranges, which would in turn have social implications: because day range increases for larger groups, juveniles avoiding long day ranges may constrain their mothers' gregariousness.

Further analyses, preferably employing focal data, are necessary to address this issue.

Investigations of infant carrying have typically focused on the associated costs to maternal energy budgets (Altmann and Samuels, 1992; Ross, 2001; Williams *et al.*, 2002; Wrangham, 2000). However, results of our study and others (Altmann and Samuels, 1992; van Schaik, 1999) suggest infant carrying may provide important foraging benefits for mothers, specifically increased daily travel distance and speed. Comparisons between primate species suggest carrying is associated with increased maternal investment, including increased neonatal weight, delayed maturation, and decreased infant mortality (Ross, 2001). Carrying may enable this increased investment by improving maternal foraging efficiency, as mothers that carry can travel farther and faster than mothers with independently traveling infants, and are not constrained to return to parked or nested offspring.

Conversely, the relationship between juvenile age and day range suggests that, for species in which mothers travel with offspring for long developmental periods, young, independently traveling juveniles may play a greater role in limiting maternal foraging effort than smaller, carried infants do. Indeed, ontogenetic studies in numerous primate species (chimpanzees: Hiraïwa-Hasegawa, 1990; Doran, 1992; bonobos: Doran, 1992; gorillas: Doran, 1997; macaques: Wells and Turnquist, 2001; baboons: Altmann and Samuels, 1992) indicate that maturation in locomotor behavior tracks maturation in body size, often taking years to develop. In contrast, the precocial maturation of the locomotor anatomy in group-living ungulates may in part be a strategy for reducing the energy cost to juveniles of foraging with adults in large groups. Detailed day-range measurements for precocial species would provide a means to investigate this issue. Similarly, ranging analyses for group living aquatic species such as dolphins, for which developmental periods are long but travel costs are low (Schmidt-Nielson, 1998), would test the prediction that juveniles do not constrain mothers in absence of significant travel costs.

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