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Body weight, diet and home range area in primates

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Primates show a strong positive relationship between body weight and home range area. Dietary habits also influence home range area. Folivorous primates occupy smaller home range areas for their body weight than do frugivores and omnivores. Primates generally require smaller home range area per individual than solitary terrestrial mammals, but primates living in social groups have much larger total home range than individual solitary mammals. This trend may necessitate higher expenditures of energy in food-gathering or modifications in movement patterns.

NUMEROUS studies during the past decade have shed light on relationships between various aspects of primate ecology[1–5], but as yet there has been no quantitative summary of data on home range area of primates that takes into account the effects on spatial needs of both body size and diet. A strong positive relationship exists between body weight and home range area in lizards[6], birds[7,8] and solitary mammals[9], while McNab[9] showed for mammals and Schoener[8] for birds that feeding habits also have a predictable effect on the home range area of many species. Clutton-Brock[10] pointed out that rather small differences in feeding ecology may affect markedly the ranging patterns of primates. Here we analyse data on the body weight, diet and home range area of 36 primate species, and demonstrate a relationship among these variables.

The home range data in this paper are taken from diverse sources and are undoubtedly not perfectly comparable (Table 1). Most body weights were obtained by averaging adult male and adult female body weights, and thus do not take into account interspecies differences in socionomic sex ratio or the fact that many group members may be subadult. Average weights in general are probably overestimated, particularly in the case of large terrestrial omnivores like the baboon (*Papio*), in which sexual dimorphism is marked. For most species, however, sufficient data are not available, either on group composition or weight variation with age and sex, to permit calculation of more accurate average weights. In addition, rather large (for example, twofold) errors in estimating body weight will cause a shift in log weight of $< 10\%$ of the entire range of data. We believe that errors introduced by differences in techniques of home-range estimation and those resulting from inaccuracies in calculating weight are not sufficient to be critical to our general conclusions.

Diet was determined from the sources of home-range information whenever possible, supplemented by material summarised by Jolly[3] and Kay[11]. We classify as folivores those species that seem to depend on foliage, mature or immature, as their staple diet. Frugivores are primarily fruit eaters, taking only a small amount of foliage and little or no animal protein. Species eating roughly equal proportions of both foliage and fruit and little or no animal protein are classified as generalist primary consumers, and those which seem to actively seek out and probably to depend on animal protein in the diet are classified as omnivores. Obviously there are degrees of folivory' frugivory and omnivory and no category should be regarded as definitive; they are our best estimate of the dietary preferences of individual species. Terrestriality and arboreality, too, are points on a continuum, and assignments should not be regarded as absolute. Generally, unless a species is known to consistently travel or forage on the ground each day, we considered it arboreal.

Regressions of $\log_{10}$(home range) on $\log_{10}$(body weight) were fitted by the method of least squares. Significance of the regressions was determined by calculating Student's t-statistic for the deviation from zero of the slopes. Our criterion for significance is the 0.05 level of probability. Spearman rank correlation coefficients ρ for the untransformed data served as an additional confirmation of correlation between variables. The tests were in agreement in all cases.

Individual home range allocation

Figure 1 shows home range area divided by the number of individuals per group (HR_i) as a function of body weight. The species are listed in Table 1. There is a strong positive relationship between body weight and home range area in primates ($r^2 = 0.44$; $t = 5.14$, $P < 0.005$). The slope of the regression line is 0.79, compared with 0.63 found by McNab[9] for temperate-zone solitary terrestrial mammals. The figure also shows each species placed in one of the four dietary categories. The more folivorous primates show a strong tendency toward a smaller HR_i than the frugivorous and omnivorous species. Eight of twelve terrestrial primates have a larger HR_i than might be expected for their weight, whereas arboreal primates show a wider scatter both above and below the regression line.

McNab divided mammals on the basis of food habits into 'hunters' (discrete particle feeders, for example, gramnivores, frugivores, insectivores, carnivores) and 'croppers' (browsers and grazers). Frugivorous and omnivorous primates resemble McNab's hunters in feeding habits, whereas the folivores are more like his croppers. Figure 2 shows primates grouped as hunters (frugivores and omnivores) or croppers (folivores), compared with relationships predicted by McNab for hunters and croppers. Generalist primary consumers are not considered in this comparison because they are not readily assigned to either category, and because the small sample size and weight range involved severely limits the value of any statistical treatment. The trend in this group seems, however, to resemble that among croppers more than hunters.

Both of the subgroups considered show stronger relationships between body weight and HR_i than do primates in general (for primate hunters, $r^2 = 0.66$, for croppers $r^2 = 0.49$). The slope of the primate hunter line, 0.83, is close to that calculated for hunters by McNab, although the expected values are only about half those predicted by McNab. The slope of the line for primate croppers is 1.06, steeper than that of McNab's cropper line or the primate hunter line but not significantly different from either. Analysis of covariance of log HR_i with feeding category and body weight for primate hunters and croppers using a randomised groups design[12], shows that adjusted group means are significantly different ($F = 69.1$, $P < 0.01$), with croppers having substantially smaller home ranges. Primate

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croppers also tend to occupy smaller HR_i than do solitary, non-primate croppers up to $\sim 2\times10^4$ g.

Values of HR_i should give some idea of the relative amount of space required to provide adequate resources for individuals of a species. What factors determine HR_i? Clearly body size is very important; once this has been accounted for other influences become more apparent. Folivory is associated with allocation of relatively small areas per individual in arboreal primates. Most of these animals are at least partially croppers in the sense of McNab[9], and are likely to have concentrated resources available. Also, the height of the tree canopy may have an especially marked effect on the size of the home range of leaf eaters. This third dimension adds to the density of resources per unit area and to the actual distance travelled in space per unit area[13–15]. In addition, McNab has recently suggested (personal communication) that rates of metabolism of arboreal folivorous mammals may be below those expected for mammals in general, so conceivably the energy requirements of many folivorous primates are relatively low. All of these explanations, however, entail difficulties, some of which are discussed below.

Frugivores tend to have larger HR_i than folivores. Typical tropical forests are highly heterogeneous in species composition[16–18]. Fruiting trees are often widely dispersed in time and space. Thus most frugivores depend on clumped, unstable food sources, a resource pattern which has been associated with a relatively large home range area[10]. Also, there is some reason to suspect that frugivory is correlated with high rates of metabolism[19].

Among generalist primary consumers HR_i may vary with the proportion of fruit and leaves eaten. For example, in Guanacaste, Costa Rica, where it feeds $\sim$70% of the time on foliage, *Alouatta palliata* has a small HR_i (K. Glander, personal communication) when compared with the same species on Barro Colorado Island where it spends approximately equal amounts of time feeding on foliage and fruit (K. M., personal

Table 1 Species, home range, and source of data

Species	Weight* (g)	HR_i (ha)	HR_t (ha)	Class†	Reference	Remarks
Prosimians						
Galago demidovii	60	0.80	0.80	AO	41	♀♀ only
Lemur catta	2,300	0.29	5.7	TP	42	
L. catta	2,300	0.44	7.4	TP	21	
L. fulvus rufus	2,370	0.10	0.88	AL	21	
Lepilemur mustelinus	650	0.24	0.24	AL	43	
Microcebus murinus	60	0.20	0.20	AO	44	♀♀ only
Propithecus verreauxi	3,800	1.8	9.0	AL	45	
P. verreauxi	3,800	0.48	2.4	AL	42	
Ceboidea						
Alouatta palliata	6,875	0.76	9.9	AP	K. Glander, personal communication	70% folivorous
A. palliata	6,875	2.8	45	AP	K. Milton, personal observation	50% folivorous
A. seniculus	7,250	0.38	3.2	AP	46	
Ateles belzebuth	5,800	14	320	AF	47	
Callicebus moloch	600	0.15	0.44	AO	48	
Cebus capucinus	3,100	6.1	86	AO	39	
Saimiri oerstedii	840	0.74	17	AO	49	
Saguinus geoffroyi	550	2.4	8	AO	50	HR_t estimated from maximum linear range
Cercopithecoidea						
Cercocebus albigena	7,900	1.2	21	AF	51	
C. albigena	7,900	9.0	140	AF	52	
Cercopithecus aethiops	3,800	1.4	40	TO	53	
C. mitis	6,000	2.8	70	AO	R. Rudran, personal communication	Weight estimated by H. Schlichte, personal communication
C. talapoin	1,130	4.0	400	AO	3	
Colobus badius	8,000	2.5	100	AL	10	
C. guereza	8,000	2.7	20	AL	10	
C. guereza	8,000	1.8	14	AL	54	
Erythrocebus patas	9,260	170	5,200	TO	55	
Macaca mulatta	7,300	7.9	200	TO	56	
M. radiata	5,140	8.9	520	TO	57	
M. sinica	5,130	3.0	38	TF	15	
Nasalis larvatus	15,100	6.5	130	AL	58	
Papio anubis	21,400	10	470	TO	59	Gallery forest
P. anubis	21,400	60	2,300	TO	1	Savanna
P. cynocephalus	15,100	62	2,500	TO	31	
P. ursinus	20,600	24	1,100	TO	1	
Presbytis cristatus	6,300	0.63	20	AL	60	
P. entellus	17,200	12	630	TL	34	Kankori site
P. entellus	17,200	34	640	TL	34	Orcha site
P. entellus	17,200	0.87	19	TL	61	Dwhar site
P. entellus	17,200	0.56	14	TL	15	Polonnaruwa, Ceylon, site
P. johnii	8,170	18	160	AL	62	
P. senex	5,980	3.0	12	AL	15	
Hominoidea						
Hylobates lar	5,540	11	45	AF	63	
H. lar	5,540	34	100	AF	20	
Gorilla gorilla gorilla	145,000	150	3,300	TL	64	
Pan troglodytes	40,700	23	1,100	TF	35	
Pongo pygmaeus	36,500	65	65	AP	65	♀♀ only
Symphalangus syndactylus	10,500	10	42	AP	66	

* Body weights taken from Kay[11], Napier and Napier[40], or from same source as home range data.

† Indicates habitat and feeding class: A, arboreal; T, terrestrial; L, folivore; F, frugivore; P, generalist primary consumer; O, cmnivore.

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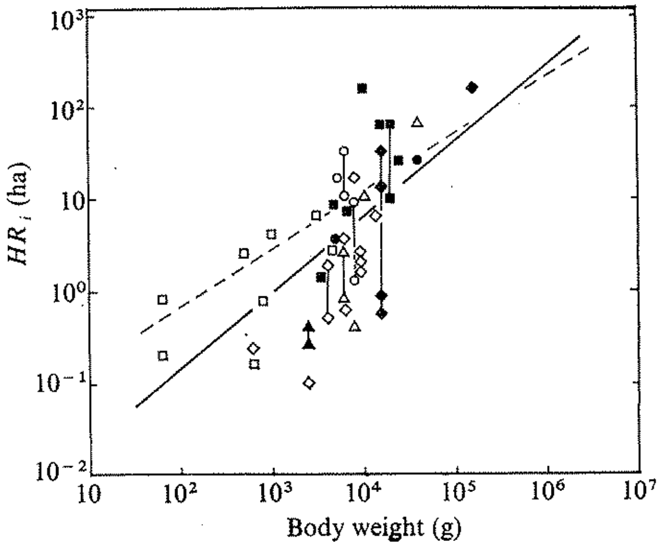

Fig. 1 Home range per individual as a function of body weight. Vertical lines connecting similar symbols indicate data from different studies of the same species. Values for the log of the mean home range for the species were substituted for these points in all calculations here and in Figs 2 and 3. Heavy solid line is least squares regression of $\log_{10}HR_i$ on $\log_{10}$(body weight) for primates ($\log HR_i = 0.79 \log BW - 2.32$). Dashed line is regression calculated by McNab[9] for solitary, temperate zone mammals. Open symbols designate arboreal species, solid symbols terrestrial species. ◇◆, Folivores; ○●, frugivores; △▲, generalist primary consumers; □■, omnivores.

Arboreal omnivores generally occupy a large HR_i for their body weight, as large, in fact, as terrestrial omnivores. This suggests that arboreality *per se* does not reduce the area required to provide adequate nutritional resources for omnivores. Arboreal omnivores probably depend more heavily on insects in the diet than the larger, terrestrial omnivores, and may, therefore, occupy a slightly higher trophic level than their terrestrial counterparts. Nevertheless, solitary arboreal squirrels, which are also discrete particle feeders (but are certainly primarily herbivorous), have HR_i comparable to the primate HR_i of this group[22,23].

Terrestrial primates as a group tend to have an HR_i somewhat larger than expected for their body weight. Some of these species live in arid regions that probably have lower densities of resources per given area[2]. The patas monkey (*Erythrocebus patas*) is an extreme case and it has a very large HR_i. Home range data are not available for two other arid country species, the hamadryas baboon (*Papio hamadryas*) and the gelada (*Theropithecus gelada*), but information on daily range indicates that they also cover very large home range areas[3]. Except for these arid land forms, it is not clear that terrestriality in itself is correlated with large HR_i. Terrestrial folivores do have larger HR_i values than arboreal folivores, but the differences may arise simply from their larger size.

Primate hunters and croppers generally have lower values of HR_i than predicted for temperate zone solitary mammals of corresponding feeding habits. The small individual home ranges may reflect: (1), the fact that some hunters may sometimes graze or browse; (2), the high productivity of many tropical areas compared to mesic temperate zone habitats; (3), the additional resource space provided by the depth of the forest canopy; or (4), the greater efficiency of utilisation of area as a result of being social. All of these factors may contribute in particular cases. Certainly some frugivores, and very probably some terrestrial omnivores, eat enough leaves or grass to make a substantial impact on their resource area requirements. The year-round high productivity of many tropical regions may be important, but much of this productivity may be unavailable as animal food[16,24–26]. The idea that the greater vertical extent of the resource space for arboreal species should reduce the HR_i required is attractive *a priori*, but it is not clear why this should apply to folivores only. Some of the possible effects of sociality are discussed below.

We have not tried to take into account the effect on home range area of overlap between conspecific groups, although one might expect that HR_i as well as total home range would be larger in species with greater overlap. The little data available suggest this may be true, since most species with non-overlapping ranges (for example, *Callicebus moloch*, *Symphalangus syndactylus*, *Colobus guereza*, *Propithecus verreauxi*), occupy home range areas smaller than or equal to the predicted values.

Total home range

Figure 3 shows total group home range (HR_t) as a function of body weight. The slope of the regression is significant ($r^2 = 0.56$; $t = 6.54$, $P < 0.005$). Much of the deviation from the regression in Fig. 3 may be due to variation in group size, since there is a strong correlation between group size and HR_t ($\rho = 0.67$; $P < 0.0001$) irrespective of body weight.

Broad patterns of variation in total group home range are generally similar to those noted for HR_i. Both folivores and generalist primary consumers tend to have smaller HR_t than frugivores and omnivores. To a greater extent than HR_i, HR_t of terrestrial species tends to be higher than expected.

Perhaps the most interesting aspect of Fig. 3 is that HR_t for many group-living primates is far larger than the home range of solitary animals of similar body weight, although solitary

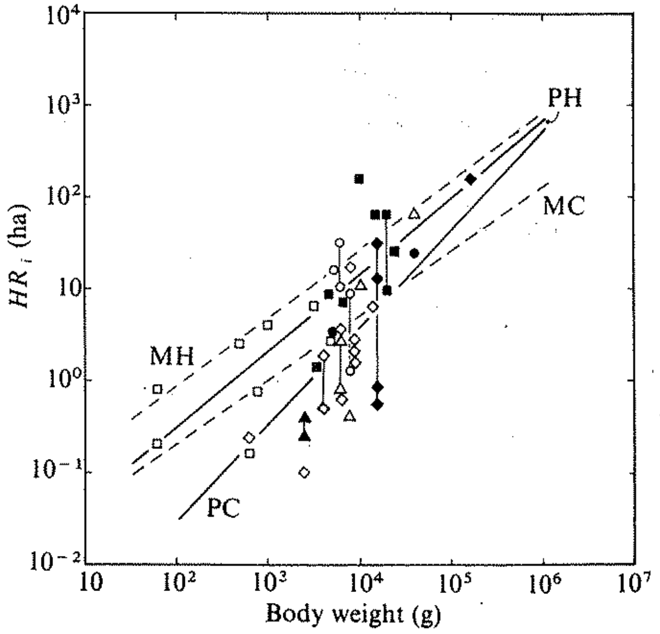

Fig. 2 Influence of diet on HR_i. Heavy solid lines are regressions of $\log_{10}HR_i$ on $\log_{10}$(body weight) for frugivores and omnivores (primate hunters, PH; $\log HR_i = 0.83 \log BW - 2.17$) and folivores (primate croppers, PC; $\log HR_i = 1.06 \log BW - 3.66$) separately. Generalist primary consumers are excluded from the calculations. Dashed lines are regressions calculated by McNab[9] for solitary, temperate zone hunters and croppers (MH, hunters; MC, croppers). Species symbols as in Fig. 1.

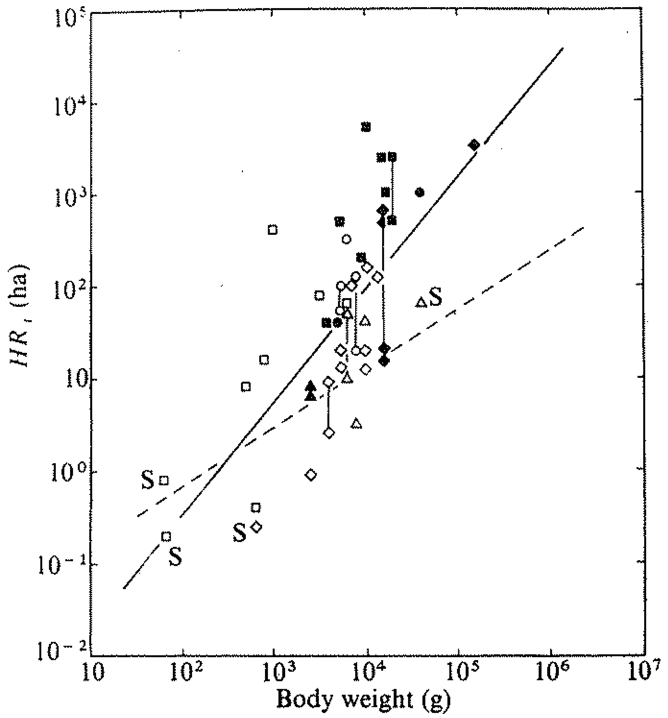

Fig. 3 Total home range per group as a function of body weight. Symbols as in Fig. 1. S indicates solitary foragers. Regression equation for primates is $\log HR_t = 1.23 \log \mathrm{BW} - 2.86$.

primates occupy home ranges similar to those of other mammals. If, within a given time interval, the primate group covers the same proportion of its home range using the same movement patterns as a solitary mammal, the individual primate may have to expend much more energy in travel than solitary mammals of similar size. How can social primates afford or avoid the higher cost of obtaining their resources? We can suggest three possibilities which are not mutually exclusive and the second and third may be related. First, it is possible that locomotion is a negligible portion of the energy budget. This seems unlikely in view of what is known of the metabolic cost of locomotion[27]. Second, it may be that foraging as a group increases food-finding efficiency enough to compensate for increased travel costs. Undoubtedly energy required for foraging is reduced by a shared pool of traditional knowledge about resource timing and location and travel routes[28–30]. Third, and probably most important, the pattern of movement within the home range may differ consistently between social and solitary animals. For example, a group may traverse a large area over a broad front while each individual moves over a fairly straight course[31,32]. A solitary animal would have to zig-zag back and forth many times to cover the same area. A social animal can feed on smaller food patches in its path and cue other group members to the location of rich patches if the latter are encountered. Some species of iguanid lizards use conspecific cuing for locating rich food resources, and this is probably a time-saving method of food location[33]. A similar model might apply within a group of primates, on a short time scale. As long as there is intraspecific tolerance of feeding at the same patch, straight line movement with cuing on other group members would be an efficient strategy, particularly if food is often clumped in fairly rich patches.

Many social animals seem to move directly between known resource patches rather than depending on chance encounters. Solitary foragers also do this (G. G. Montgomery, personal communication), but perhaps, as suggested above, group knowledge encourages such behaviour by increasing the probability that resource patches will be accurately recognised and remembered. In addition, social animals may utilise only a small portion of their home range within a given time span, covering the entire area only in the course of weeks or even months. Certainly many group-living primates show such behaviour (for example, *Alouatta palliata* (K. M., personal observation); *Presbytis entellus*[34]; *Pan troglodytes*[35]; *Papio cynocephalus*[31]). Data on daily movements within their home range are scanty for solitary mammals. Red foxes generally cover most of their range each night[36], while raccoons[37], rabbits[38], and anteaters (*Tamandua* (G. G. Montgomery, personal communication)) do so in a few days to a week. Certain social primates traverse much of their home range in a single day, at least occasionally, but except for species which defend relatively small territories, this behaviour is usually interspersed with relatively long periods in a small area (for example, *Cebus capucinus*[39]).

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