

## Defended versus undefended home range size of carnivores, ungulates and primates

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**Summary.** We tested the hypothesis that undefended home ranges are larger than defended home ranges using data collected from the literature for three groups of mammals. A matched-pairs analysis of populations within species or species within genera showed that undefended home ranges were larger than defended home ranges for carnivores and male ungulates, but not for primates. Primates may have been an exception because they violated a key assumption of the hypothesis, that defence costs increase with the size of the defended area. Undefended home ranges were 5.4 and 15.2 times larger than defended home ranges for carnivores and male ungulates, respectively. Whether or not a home range is defended is an important source of variation that should be included in future studies of home range size.

### Introduction

The area that an animal occupies must be large enough to provide an adequate supply of resources. This presumably explains why home range size increases with either body size or metabolic requirements of the residents of the home range in a wide variety of taxa (mammals, McNab 1963; Clutton-Brock and Harvey 1977; Harestad and Bunnell 1979; Gittleman and Harvey 1982; birds, Armstrong 1965; Schoener 1968; lizards, Turner et al. 1969; fish, Grant and Kramer 1990). After body size or metabolic requirements, diet has been recognized in virtually all studies as the most important factor influencing home range size. Carnivorous animals typically have larger home ranges than omnivores or herbivores of a similar size (Schoener 1968; Harestad and Bunnell 1979; Gittleman and Harvey 1982; Mace et al. 1983).

The influence of defence behaviour on home range size has been largely ignored, despite good theoretical

reasons to believe that the amount of space required by an animal will depend on how that space is used. Models of optimal territory size assume that the costs of defence increase as territory area increases (e.g. Hixon 1980; Schoener 1983, 1987) because residents of large territories spend more energy patrolling, encounter and expel more intruders, and travel farther to expel each intruder, than residents of small territories. Hence, all else being equal, a cost-of-defence argument predicts that undefended home ranges will be larger than defended home ranges.

An undefended home range can be used by other individuals. An animal can reduce the number of resource competitors on its range by defence (e.g. Cheney 1987), and hence increase the yield of resource per unit area per individual (e.g. Gill and Wolf 1975; Stamps 1984; Stamps and Eason 1989). Thus, a defended range can potentially be smaller than an undefended range and yet provide the same amount of resource per individual. Although others have proposed that undefended home ranges are larger than territories (e.g. Alcock 1975; Wilson 1975; Mitani and Rodman 1979; Mace et al. 1983), we are not aware of any general test of the hypothesis.

The first goal of our study, therefore, was to test the hypothesis that undefended home ranges are larger than defended home ranges. We used literature data for carnivores, male ungulates and primates because these groups of mammals have been well studied and exhibit remarkable intraspecific variation in whether or not they defend their home range (see Table 2.4 of Lott 1991). To test the hypothesis, we used a matched-pairs analysis of populations within species or species within genera because of its statistical power and its ability to control for phylogenetic effects (see Pagel and Harvey 1988: 431–432). The second goal of our study was to determine the importance of defence behaviour, whether or not a home range is defended, as a predictor of home range size.

## Methods

**Definitions.** A home range is usually defined as the area used by an individual (in solitary species) or group during its normal day-to-day activities (e.g. Gittleman and Harvey 1982). Home range size can be calculated in a variety of ways. However, most authors in our study used a version of the minimum polygon technique (Schoener 1981) in which the smallest polygon that includes either all or 95% of the observations is taken as the home range. A defended home range (territory) was defined as an area occupied more or less exclusively by means of overt expulsion of intruders (see Wilson 1975). However, non-overlap of home ranges was not taken as sufficient evidence of defence.

There was not sufficient information to score the population or species for defence in many studies, particularly carnivores. Many animals occupying non-overlapping home ranges advertise their presence by scent-marking or vocalizing. Without some observations of active expulsion of conspecifics we scored these cases as undefined and excluded them from the analysis. "No defence" was defined as overlapping home ranges with no evidence of defence and some evidence of tolerance towards intruders.

**Paired analysis.** Defence of a home range is a property of the individual or group occupying a range but is often defined at the population level in the literature. We searched the literature for species (or genera) in which some populations (or species) defended their range and some did not. We began our literature search by referring to general reviews: Lott (1984, 1991) for mammals in general; Sandell (1989) for carnivores; Geist and Walther (1974), Leuthold (1977), Owen-Smith (1977), and Gosling (1986) for ungulates; and Cheney (1987) for primates. We contrasted individuals or groups in populations that defended their range with those from spatially distinct populations where there was no defence. We did not compare individuals of different age or sex classes because our goal was to compare the home range size of similar individuals that differed in their defence behaviour, presumably because of different environmental conditions. If there was no intraspecific variability in defence behaviour, we compared species within genera.

Ungulates were a special case because we compared the size of defended versus undefended home ranges of males only during the reproductive season. To make the comparison as meaningful as possible, we included only "all-purpose" (type A of Wilson 1975) territories which provided space for courtship, mating, and food for the male and the female (while on the territory). Hence, lek territories were excluded from the analysis. The size of the social group was defined as one if the male wandered alone to encounter females or if it defended a territory through which females wandered. If males followed a single harem or defended a territory around a harem, then the group size was the number of females and offspring plus one.

Some of the carnivores and many male ungulates did not occupy their measured home range all year long. Because tenure on a home range could influence home range size, we included it as a covariate in some analyses (see below). We did not record tenure for primates because virtually all occupied permanent home ranges.

We followed the taxonomy of Leuthold (1977) for ungulates and included the orders Proboscidea, Perissodactyla and Artiodactyla. We followed the taxonomy of Cheney (1987) and Smuts et al. (1987) for primates and Gittleman (1989) for carnivores.

For each pair of defended and undefended ranges (i.e. populations within species or species within genera), we collected or calculated the following data from the literature.

1. Home range size (km<sup>2</sup>). We used the mean home range size reported in original studies. If several populations were studied, we used the mean of the population means. For intrageneric comparisons, we calculated the mean of species means.
2. Body mass (kg). Average male and female mass for each species were taken from general sources whenever possible. Following

Clutton-Brock and Harvey (1977), the mass of juveniles was assumed to be half the adult mass.

3. Size of the social group. The mean number of animals that normally associated together and occupied the same range was taken from original studies.

4. Group composition. The number of adult males, adult females and juveniles in a group was recorded from original studies. Means for populations or species were calculated if needed. If group composition was unknown, we assumed an adult male:adult female:juvenile ratio of 1:1:2, following Clutton-Brock and Harvey (1977).

5. Group mass (kg). The total mass of the group that occupied the home range was calculated using body mass, group size and group composition data.

6. Tenure (months). The duration for which a measured home range was used. This varied from 0.9 for some breeding home ranges of male ungulates to 12 for permanently occupied home ranges.

7. Diet. Diet was quantified for carnivores as the percentage of flesh in the diet for carnivores, taken from Gittleman and Harvey (1982), and for primates as the percentages of leaves in the diet, taken from original sources.

8. Index of defendability (*D*). We calculated Mitani and Rodman's (1979) index of mobility for primates because it was related to whether or not a home range was defended in their study. *D* was calculated as:

$$D = d/(4A/\pi)^{0.5}$$

where *d* = day range length in km and *A* = home range size in km<sup>2</sup>.

**Descriptive analyses.** We used the largest data set available for each group to determine the importance of defence behaviour as a predictor of home range size in relation to other important factors like group mass and diet. We assumed that whether or not a home range is defended is a behavioural decision influenced by ecological factors rather than phylogeny. Our assumption is supported by a nested analysis of variance which showed that most of the variation in defence behaviour (see Appendix) occurred at the population within species level (carnivores – 94%; ungulates – 68%; primates – 82%). Hence we did not use a formal comparative analysis (see Harvey and Pagel 1991). However, because diet and body mass are both potentially influenced by phylogeny, we used a nested analysis of variance to identify the appropriate taxonomic level for analysis.

We used at most two data points per genus for carnivores and primates, one each for defended and undefended home ranges, because much of the variance in home range size, group mass and diet was at the genus level or below (carnivores – 55, 42 and 46%, respectively; primates – 46, 13 and 73%, respectively). We used one data point per species for ungulates because 50 and 34% of the variance in home range size and group mass occurred at the species level or below. We randomly deleted one observation for those species of ungulates that both defended and did not defend their home range. We used model I regression to relate home range size to group mass because we were primarily interested in controlling for the effects of mass rather than in estimating the slope of the relationship (see Harvey and Pagel 1991, p. 181).

## Results

### *Carnivores*

We found 11 species (or genera) in which some populations (or species) defended their home range and some did not (Appendix). Undefended home ranges were larger than defended home ranges in 10 of 11 cases

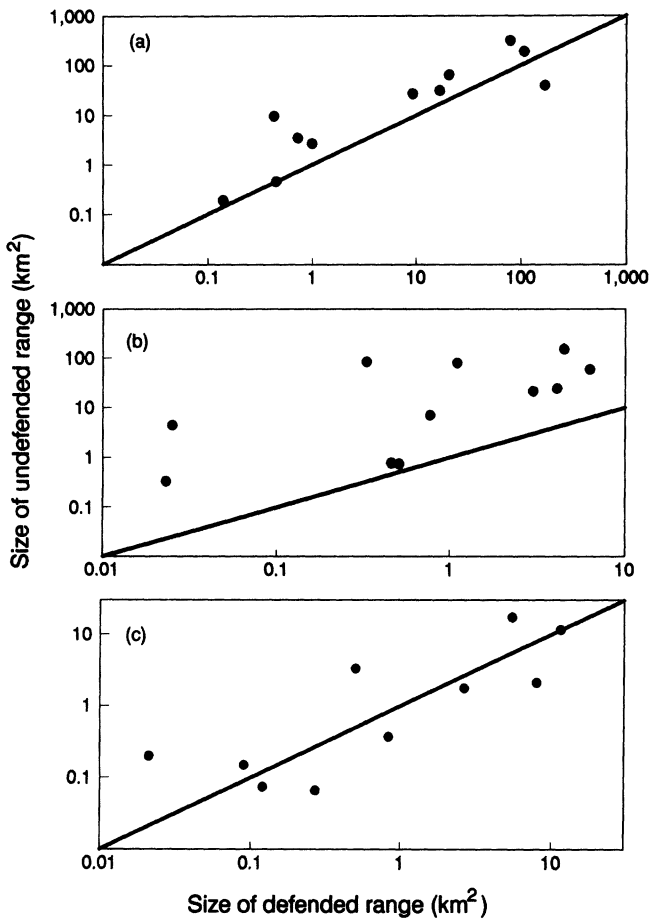


Fig. 1 a–c. Paired analysis of the size of undefended and defended home ranges of populations within species or species within genera of a carnivores, b male ungulates, and c primates. The 1:1 line is shown in each

(Fig. 1 a; paired  $t=2.51$ ,  $P=0.031$ ). This difference occurred despite the fact that group mass on undefended home ranges was less than group mass on defended ranges (paired  $t=3.05$ ,  $P=0.012$ ). There was no difference in tenure ( $P=0.34$ ) between home ranges that were defended or not.

To control statistically for the effect of group mass, we calculated the residuals from a regression of home range size vs. group mass (Fig. 2). Now the paired analysis was even stronger; on average, undefended ranges were 4.5 times larger than defended ranges (paired  $t=5.19$ ,  $P=0.0004$ ).

To quantify the importance of defence behaviour as a predictor of home range size, we included it in a multiple regression along with group mass and diet (the percentage of flesh in the diet). We included data for 27 species (Appendix) which represented 22 data points when analyzed at the generic level. Home range size increased with group mass (Fig. 3) and the percentage of flesh in the diet, and undefended home ranges were 5.4 times larger than defended ranges (Fig. 3). Group mass was the best predictor of home range size, followed by defence behaviour and diet (Table 1).

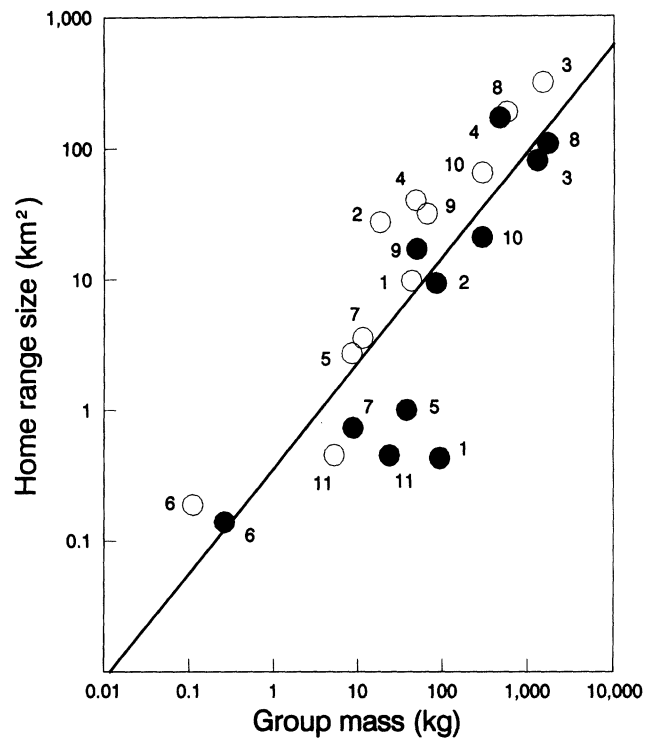


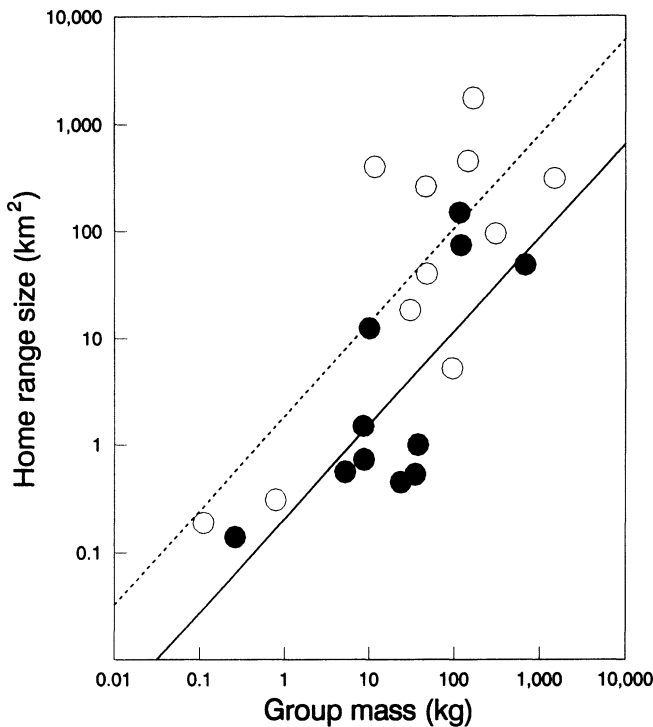
Fig. 2. Defended (solid circles) and undefended (open circles) home range size of carnivores from Fig. 1 a in relation to group mass. A paired analysis of the residuals from the least-squares regression ( $\log_{10} Y = 0.808 \log_{10} X - 0.443$ ,  $r^2 = 0.696$ ) showed that undefended home ranges are larger than defended home ranges ( $t=5.19$ ,  $P=0.0004$ ). The numbers refer to the following taxa: 1 = *Canis aureus*, 2 = *C. latrans*, 3 = *Crocuta crocuta*, 4 = *Hyaena brunnea*, 5 = *Meles meles*, 6 = *Mustela erminea/nivalis*, 7 = *Otocyon megalotis*, 8 = *Pathera leo*, 9 = *P. pardus/onca*, 10 = *P. tigris*, 11 = *Vulpes vulpes*

#### Male ungulates

We found 11 species (or genera) in which males of some populations (or species) defended their home range during the breeding season whereas in others they did not (Appendix). Undefended home ranges were, on average, 15.6 times larger than defended ranges (Fig. 1 b; paired  $t=5.32$ ,  $P=0.0003$ ). This difference could not be attributed to differences in group mass ( $P=0.85$ ) or how long males occupied their range ( $P=0.12$ ; defended mean = 9.2 months, undefended mean = 7.2 months).

To quantify the importance of defence behaviour as a predictor of home range size, we included it in a multiple regression along with group mass. We could not find an objective measure of diet for ungulates, so diet was not included in the analysis. We found data for 55 species (Appendix). Home range size increased with group mass and undefended ranges were 15.2 times larger than defended home ranges (Fig. 4). The most surprising result was that defence behaviour was a better predictor of home range size than group mass (Table 1 b).

It was also apparent from Fig. 4 that group mass was smaller on defended (mean = 121 kg) than on undefended (mean = 788 kg) home ranges ( $t=3.37$ ,  $P=0.0008$ ). Differences in body mass ( $t=3.37$ ,  $P<0.0014$ )



**Fig. 3.** Analysis of covariance of home range size of carnivore genera in relation to group mass and whether or not the range is defended (*solid circles and solid line*:  $\log_{10}Y=0.877 \log_{10}X-0.687$ ) or not (*open circles and broken line*:  $\log_{10}Y=0.877 \log_{10}X+0.271$ )

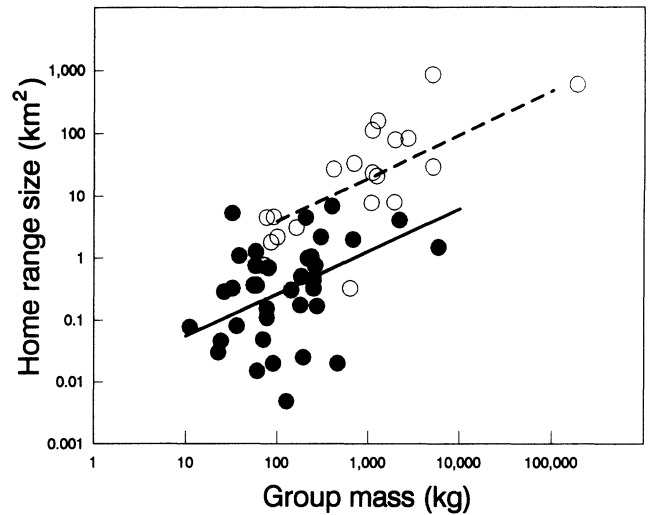
**Table 1.** Group mass, diet and defence behaviour (whether a home range is defended or not) as predictor variables of home range size

Independent variable	<i>F</i> and <i>P</i> values <sup>1</sup>	Explained variation (%) <sup>2</sup>
(a) Carnivores ( <i>n</i> = 19)		
Group mass (kg)	55.7, <i>P</i> < 0.0001	66.6
Defence behaviour	8.0, <i>P</i> = 0.021	9.6
Flesh in diet (%)	4.9, <i>P</i> = 0.043	5.9
(b) Male ungulates ( <i>n</i> = 55)		
Defence behaviour	25.4, <i>P</i> < 0.0001	49.9
Group mass (kg)	22.4, <i>P</i> < 0.0001	15.1
(c) Primates ( <i>n</i> = 29)		
Group mass (kg)	83.0, <i>P</i> < 0.0001	57.0
Leaves in diet (%)	22.1, <i>P</i> < 0.0001	19.6
Defence behaviour	0.85, <i>P</i> = 0.37	0.8

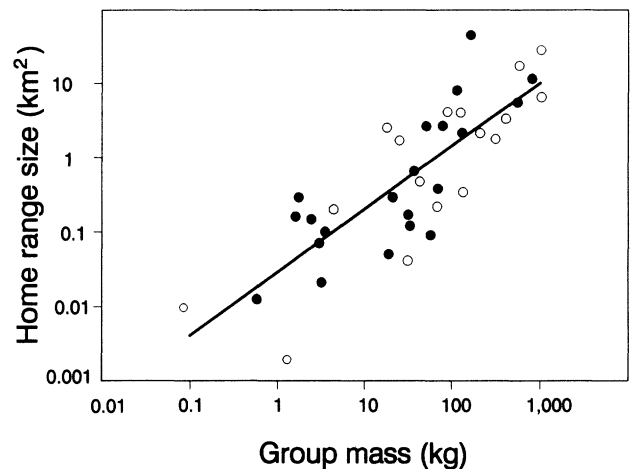
<sup>1</sup> Partial *F*-values when the independent variable was entered last into the regression model

<sup>2</sup> The independent variables were entered into the multiple regression in the order listed

rather than differences in group size ( $t=1.89$ ,  $P=0.071$ ) accounted for this result. Though unexpected, this result quantitatively confirms Jarman's (1974, see also Owen-Smith 1988) qualitative observation that smaller antelopes defend food resources whereas larger antelopes do not. This relationship may be related to diet because



**Fig. 4.** Analysis of covariance of home range size of male ungulates in relation to group mass and whether the range is defended (*solid circles and solid line*:  $\log_{10}Y=0.692 \log_{10}X-1.966$ ) or not (*open circles and broken line*:  $\log_{10}Y=0.692 \log_{10}X-0.783$ )



**Fig. 5.** Analysis of covariance of home range size of primate genera plotted against mass of the group inhabiting the range. There was no significant difference in the slopes ( $P=0.98$ ) or intercepts ( $P=0.70$ ) for defended (*solid circles*) or undefended (*open circles*) home ranges, so a Model I regression for the complete data set is shown ( $\log_{10}Y=0.85 \log_{10}X-1.55$ ,  $r^2=0.67$ ,  $n=38$ ,  $P<0.0001$ ,  $SE(b)=0.182$ )

small species feed selectively on discrete food items, whereas large species feed unselectively on dispersed food (Jarman 1974).

#### Primates

We found 10 species (or genera) in which some populations (or species) defended their home range and some did not (Appendix). Defended and undefended home ranges did not differ significantly in size (Fig. 1c; paired  $t=0.33$ ,  $P=0.75$ ).

To confirm this finding in a larger data set, we found home range size data for 72 cases (Appendix) which

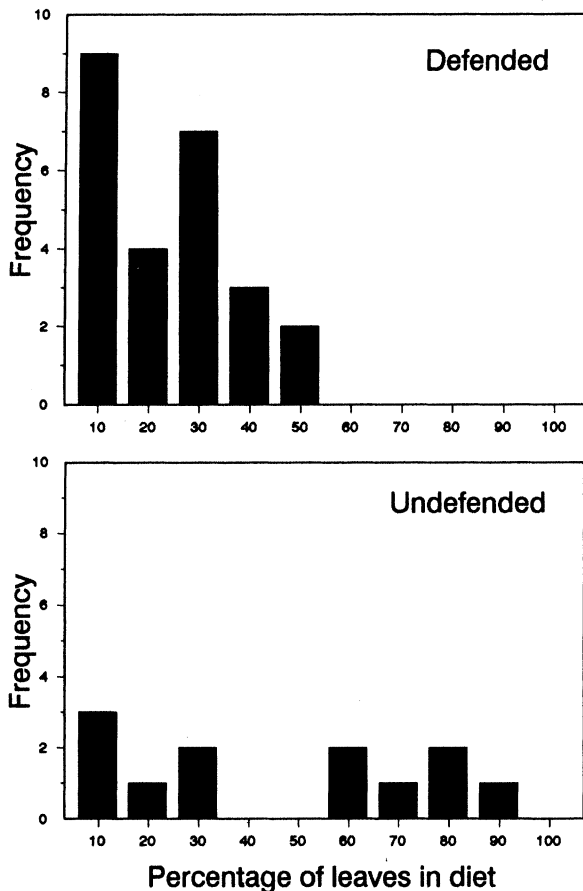


Fig. 6. The percentage of leaves in the diet in relation to defence of a home range in 29 genera of primates

represented 38 data points when combined at the genus level. Home range size increased with group mass ( $F=68.41$ ,  $df=1, 35$ ,  $P<0.0001$ , ANCOVA), but there was no difference in the slopes ( $P=0.98$ ) or intercepts ( $P=0.70$ ) between troops that defended or did not defend their home range (Fig. 5). The data for primates, therefore, were not consistent with the hypothesis that undefended ranges are larger than defended ranges, suggesting that factors other than space alone were important in influencing the decision of whether or not to defend the home range.

Diet and mobility potentially influence home range size and defence in primates. Folivores have smaller home ranges than frugivores or insectivores (Clutton-Brock and Harvey 1977). The same trend occurred in our data set; the correlation between the percentage of leaves in the diet (arcsine, square-root transformed) and home range size was negative, after controlling for the effect of group mass (partial  $r=-0.676$ ,  $n=29$ ,  $P<0.0001$ ). If diet influences the decision of whether or not to defend only via its influence on home range size, then primates that defend their range will have a higher percentage of leaves in their diet than those that do not defend. In fact, our data showed the opposite trend: leaves made up a lower percentage of the diet of those that defended (mean=16.7,  $n=17$ ) than those that did not defend (mean=40.3,  $n=12$ ) their home range

(Fig. 6;  $t=2.47$ ,  $P=0.020$ ). This same trend occurred in the paired analysis; leaves composed 28.6% of the diet of primates that defended their range and 44.9% of the diet of primates that did not defend their range (paired  $t=2.77$ ,  $n=6$ ,  $P=0.0395$ ).

Mitani and Rodman (1979) suggested that the decision to defend a range was influenced primarily by mobility of the troop. They quantified mobility using an index ( $D$ , see methods), and demonstrated a positive association between mobility and defence. In our data set, species that defended (mean=2.10,  $n=26$ ) their range had higher values of  $D$  than those that did not defend (mean=1.29,  $n=19$ , Mann-Whitney test,  $P=0.054$ ), but the difference was less than in Mitani and Rodman's (1979) study. Values of  $D$  did not differ significantly in the paired analysis (defended=1.55, undefended=1.35, paired  $t=0.47$ ,  $n=6$ ,  $P=0.66$ ).

In a multiple regression analysis, group mass was the best predictor of home range size, followed by diet (Table 1c). Mobility (day range length) was not included in this analysis because of missing data. However, when included in a multiple regression with group mass, diet and defence behaviour, mobility was the least important predictor, explaining only 1.2% of the variation in home range size ( $n=20$ ,  $P=0.38$ ).

## Discussion

The paired analysis of carnivores and male ungulates provides the first general support for the hypothesis that undefended home ranges are larger than defended home ranges. The carnivore data in particular suggested that defended home ranges occur in areas of high resource abundance, because defended home ranges were not only smaller but supported a larger group of individuals than were found on undefended home ranges.

The paired analysis of primate data did not support the hypothesis or Cheney's (1987) conclusion, from a qualitative analysis, that undefended home ranges are larger than defended home ranges. A key assumption of the hypothesis, that defence costs increase with home range size, may have been violated for primates because of the effects of diet on mobility. Primates that feed primarily on fruit and insects are mobile (Mitani and Rodman 1979) and have large home ranges, presumably because the distribution of their food is patchy in space and time (Clutton-Brock and Harvey 1977). Hence, there may be little additional cost for such mobile primates to monitor and defend boundaries, as suggested by Mitani and Rodman (1979). Even though folivores have small home ranges, their lack of mobility (Mitani and Rodman 1979) apparently makes the extra costs of defence prohibitive. In addition to its effect via mobility, diet may also have a direct influence on the decision to defend the home range. Leaves may not be a very depressible food resource (*sensu* Charnov et al. 1976; Isbell 1991), so the benefits of excluding competitors may be lower for folivores than for frugivores or insectivores. Further testing with other groups of mammals and other animals in general will be required to

determine whether primates prove to be an isolated exception to a general finding.

Our results may have implications for testing resource defence theory in the wild. The economic defendability of a resource is thought to be influenced by the spatial and temporal distribution of those resources (Brown 1964; Emlen and Oring 1977; Warner 1980). Unfortunately, resource distribution is notoriously difficult to measure, so there have been few quantitative tests of resource defence theory in the field. We suggest that home range size can be used as a surrogate measure for resource distribution, because an animal's response to the distribution of resources in its environment will be reflected by its movements (Mitani and Rodman 1979; Waser and Wiley 1979). For example, an economically defensible resource should be dense, spatially clumped, spatially predictable and temporally dispersed (Warner 1980; Grant in press). These same conditions should allow an animal to restrict its movements to a small home range. Because home range size is easier to measure than resource distribution, it may be a useful predictor of whether or not an animal will defend its range in the wild. This is not a trivial prediction because home range size is often easier to measure than defence behaviour, particularly in nocturnal animals or animals with large home ranges.

Our descriptive analysis has implications for allometric studies of home range size in general. undefended home ranges were 5.4 and 15.2 times larger than defended home ranges in carnivores and male ungulates, respectively. Defence behaviour was the best predictor of home range size in male ungulates and was a better predictor of home range size than diet in carnivores. This is an important source of variation that has been largely ignored in studies of home range size to date. Defence behaviour should be included as a variable in future studies of home range size, in addition to other important variables like body size, metabolic requirements and diet.

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**Appendix.** Species and data used in the analyses for (a) carnivores, (b) male ungulates and (c) primates. Type: D = defended, U = undefended; HRS = home range size (km<sup>2</sup>); GS = group size; GM =

group mass (kg); Diet = proportion of flesh in diet for carnivores and proportion of leaves in diet for primates; DRL = day range length (m).

Species	Type	HRS	GS	GM	Diet	DRL	Sources <sup>a</sup>
<b>(a) Carnivores</b>							
<i>Herpestes auro-punctatus</i>	U	0.31	1	0.78	0.15	–	57
<i>Helogale parvula</i>	D	0.56	10.4	5.2	0.09	–	142, 150
<i>Panthera leo</i>	D	108	14.4	1690	1.00	–	36, 155, 158
<i>Panthera leo</i>	U	189	5.2	565	1.00	–	37
<i>Panthera pardus</i>	D	16.9	2	49	0.97	–	9
<i>Panthera onca</i>	U	31.5	1	65	0.97	–	156
<i>Panthera tigris</i>	D	20.7	3	288	0.98	–	164
<i>Panthera tigris</i>	U	65	3	288	0.98	–	154
<i>Felis concolor</i>	U	263	1	46	1.00	–	161

Species	Type	HRS	GS	GM	Diet	DRL	Sources <sup>a</sup>
<i>Acinonyx jubatus</i>	D	150	2.5	116	1.00	–	14, 15
<i>Crocota crocuta</i>	D	80	32.5	1268	1.00	–	68, 92
<i>Crocota crocuta</i>	U	315	38	1482	1.00	–	48, 173
<i>Hyaena brunnea</i>	D	170	13	463	0.65	–	133
<i>Hyaena brunnea</i>	U	40	1	48	0.65	–	132
<i>Proteles cristatus</i>	D	1.5	1	8.5	0.06	–	95
<i>Ailuropoda melanoleuca</i>	U	5.2	1	95	0.00	–	157
<i>Ursus americanus</i>	U	69.6	1	100	0.05	–	3, 51, 107, 182
<i>Ursus arctos</i>	U	844	1	189	0.05	–	162
<i>Alopex lagopus</i>	D	12.5	3	10	–	–	69
<i>Canis aureus</i>	D	0.43	13	92.6	0.58	–	109, 122
<i>Canis aureus</i>	U	9.7	6	42.8	0.58	–	98
<i>Canis latrans</i>	D	9.3	7	83.5	0.93	–	7
<i>Canis latrans</i>	U	27.2	1.5	18	0.93	–	7, 26
<i>Canis lupus</i>	D	280	11	273	1.00	–	137
<i>Canis mesomelas</i>	D	5.3	5.5	30	–	–	44, 122
<i>Lycan pictus</i>	U	1750	9.8	167	1.00	–	47
<i>Otocyon megalotis</i>	D	0.73	4.9	8.7	0.14	–	96
<i>Otocyon megalotis</i>	U	3.53	6	11.3	0.14	–	111
<i>Vulpes vulpes</i>	D	0.45	4.4	23.6	0.64	–	69
<i>Vulpes vulpes</i>	U	0.45	1	5.2	0.64	–	64
<i>Enhydra lutris</i>	D	0.53	1	35	–	–	13, 52, 108
<i>Meles meles</i>	D	1.0	4	37.6	0.22	–	93
<i>Meles meles</i>	U	2.7	1	8.4	0.22	–	94
<i>Gulo gulo</i>	U	405	1	11.6	–	–	71
<i>Mustela erminea</i>	D	0.14	1	0.26	0.95	–	38, 39
<i>Mustela nivalis</i>	U	0.19	1	0.11	0.95	–	86
<b>(b) Male Ungulates</b>							
<i>Loxodonta africana</i>	U	864	1	5000	–	–	105
<i>Ceratotherium simum</i>	D	1.5	2	5900	–	–	134
<i>Diceros bicornis</i>	D	4.1	2	2200	–	–	104
<i>Diceros bicornis</i>	U	24.2	1	1100	–	–	55, 80, 124
<i>Equus asinus</i>	D	0.77	1	260	–	–	180
<i>Equus asinus</i>	U	6.95	1	260	–	–	90, 180
<i>Equus caballus</i>	D	3.0	11	3500	–	–	153
<i>Equus caballus</i>	U	21.4	4	1225	–	–	8, 43
<i>Equus grevyi</i>	D	6.3	1	430	–	–	54, 91
<i>Equus quagga</i>	U	160	7	1263	–	–	89
<i>Equus zebra</i>	U	7.8	5	1080	–	–	78a, 91
<i>Phacochoerus aethiopicus</i>	U	1.8	1	85	–	–	104
<i>Tayassu tajacu</i>	D	1.0	10	216	–	–	160
<i>Lama vicugna</i>	D	1.7	7	275	–	–	49
<i>Alces alces</i>	U	27.6	1	411	–	–	6, 138
<i>Axis axis</i>	U	4.5	1	76	–	–	154
<i>Cervus canadensis</i>	D	2.2	8	301	–	–	159
<i>Cervus elaphus</i>	D	0.023	1	122	–	–	16
<i>Cervus elaphus</i>	U	0.33	7	632	–	–	21
<i>Cervus nippon</i>	D	0.048	1	70	–	–	120
<i>Dama dama</i>	D	0.015	1	60	–	–	22, 97, 136
<i>Capreolus capreolus</i>	D	0.29	1	26	–	–	141
<i>Odocoileus hemionus</i>	D	0.46	1	72	–	–	118
<i>Odocoileus hemionus</i>	U	0.77	1	72	–	–	28
<i>Odocoileus virginianus</i>	U	4.6	1	91	–	–	117, 127
<i>Giraffa camelopardalis</i>	U	113	1	1100	–	–	46, 104
<i>Antilocapra americana</i>	D	1.27	1	58	–	–	11, 87
<i>Bos gaurus</i>	U	30	10	5076	–	–	154
<i>Syncerus caffer</i>	U	601	310	186000	–	–	121
<i>Tragelaphus angasi</i>	U	3.1	1.5	162	–	–	4, 171
<i>Tragelaphus imberbis</i>	U	2.2	1	100	–	–	103
<i>Tragelaphus scriptus</i>	D	0.025	3	193	–	–	174
<i>Tragelaphus strepsiceros</i>	U	8.0	9.7	1930	–	–	135
<i>Taurotragus oryx</i>	U	34	1	690	–	–	59
<i>Cephalophus monticola</i>	D	0.03	3	22.5	–	–	33
<i>Redunca arundinum</i>	D	0.51	3	183	–	–	81
<i>Redunca arundinum</i>	U	0.74	1	78	–	–	72
<i>Redunca redunca</i>	D	0.45	6	250	–	–	67b
<i>Kobus ellipsiprymnus</i>	D	1.05	1	236	–	–	62, 85, 165, 166, 179
<i>Kobus kob</i>	D	0.02	1	90	–	–	101

Species	Type	HRS	GS	GM	Diet	DRL	Sources <sup>a</sup>
<i>Kobus leche</i>	D	0.0049	1	127	–	–	100, 146
<i>Kobus vardonii</i>	D	0.11	1	77	–	–	32, 152
<i>Hippotragus equinus</i>	U	84	10	2700	–	–	79
<i>Hippotragus niger</i>	D	0.33	1	250	–	–	60
<i>Oryx gazella</i>	D	4.5	1	205	–	–	59
<i>Oryx gazella</i>	U	151	8	1640	–	–	59, 178
<i>Connochaetes gnou</i>	D	0.18	1	180	–	–	42, 145
<i>Connochaetes taurinus</i>	D	0.02	1	462	–	–	40, 42
<i>Alcelaphus buselaphus</i>	D	0.31	1	142	–	–	58
<i>Damaliscus dorcas</i>	D	0.155	1	77	–	–	29
<i>Damaliscus lunatus</i>	D	2.0	5	680	–	–	78b, 123
<i>Damaliscus korrigum</i>	U	80.0	15	1950	–	–	76
<i>Aepyceros melampus</i>	D	0.37	1	59	–	–	74, 102, 125, 126
<i>Antidorcas marsupialis</i>	D	0.33	1	32	–	–	30, 114
<i>Antilope cervicapra</i>	D	1.1	1	38	–	–	154
<i>Gazella granti</i>	D	0.71	1	80	–	–	41, 175, 176
<i>Gazella thomsoni</i>	D	0.046	1	24	–	–	41, 177
<i>Litocranius walleri</i>	D	5.3	1	32	–	–	104
<i>Oreotragus oreotragus</i>	D	0.081	2	36	–	–	34
<i>Madoqua kirki</i>	D	0.077	2	11	–	–	67a
<i>Ourebia ourebia</i>	D	0.37	2.5	55	–	–	131, 166
<i>Pelea capreolus</i>	D	0.77	3	58	–	–	131
(c) Primates							
<i>Microcebus murinus</i>	U	0.010	1	0.08	0.47	–	144
<i>Indri indri</i>	D	0.17	4	31.5	0.35	500	19, 139, 140
<i>Propithecus verreauxi</i>	D	0.05	7	19	0.27	500	19, 119, 140, 143
<i>Lemur catta</i>	D	0.12	16	32.7	0.25	–	12, 19, 70, 77, 170
<i>Lemur catta</i>	U	0.074	18	46.5	0.44	950	12, 19, 70, 77, 170
<i>Lemur fulvus</i>	U	0.009	9.5	95.5	0.89	138	19, 170
<i>Lepilemur mustelinus</i>	U	0.002	2	1.28	0.51	–	70, 140, 143, 144
<i>Galago alleni</i>	D	0.26	6	1.1	0.00	–	10
<i>Galago crassicaudatus</i>	D	0.085	6	6	0.62	–	10
<i>Galago demidovii</i>	D	1.3	10	4.7	0.10	–	10
<i>Galago garnetti</i>	D	0.15	3	0.58	0.00	–	10
<i>Galago senegalensis</i>	D	0.12	6	1.0	0.48	–	10
<i>Galago zanzibanicus</i>	D	0.023	6	0.66	0.00	–	10
<i>Perodicticus potto</i>	D	0.16	2	1.6	0.21	–	10
<i>Tarsius bancanus</i>	D	0.015	2	0.25	0.00	–	10
<i>Tarsius spectrum</i>	D	0.01	6	0.9	0.00	–	10
<i>Saguinus fuscicollis</i>	D	0.3	6.5	1.75	0.00	1220	19, 56, 172
<i>Saguinus imperator</i>	D	0.3	3.6	1.1	0.00	1420	19, 56, 172
<i>Saguinus labiatus</i>	D	0.32	4.2	1.3	–	–	56
<i>Saguinus oedipus</i>	D	0.25	6	1.7	–	1708	56, 128
<i>Alouatta palliata</i>	U	0.22	12	64	0.54	387	20, 25, 119
<i>Alouatta pigra</i>	U	1.25	5.5	25.3	–	250	25
<i>Alouatta seniculus</i>	U	0.16	7.2	39	0.53	547	19, 25
<i>Ateles belzebuth</i>	D	3.24	14.5	65	0.12	2250	19, 88, 148
<i>Ateles geoffroyi</i>	U	1.39	42	120	0.21	–	17, 23, 27, 148
<i>Ateles paniscus</i>	D	2.06	20	92	0.12	2380	110, 148, 151
<i>Lagothrix lagothricha</i>	U	4.0	33	126	–	–	148
<i>Cebus albifrons</i>	U	1.5	15	29	0.10	1800	19, 148
<i>Cebus apella</i>	U	0.8	10	20	0.02	2070	19, 148, 172
<i>Cebus capucinus</i>	D	0.65	15	37	0.15	–	148
<i>Cebus olivaceus</i>	U	2.75	20	36.7	0.05	2100	19, 148
<i>Saimiri sciureus</i>	U	2.5	35	18	0.00	–	19, 148, 172
<i>Aotus trivirgatus</i>	D	0.1	4.5	3.5	0.10	710	148
<i>Callicebus moloch</i>	D	0.021	3.1	3.2	–	570	19, 113, 147, 149
<i>Callicebus torquatus</i>	U	0.20	4	4.4	0.13	820	19, 149
<i>Chiropotes albinasus</i>	D	3.0	25	59.2	0.10	2250	149
<i>Chiropotes satanas</i>	D	2.25	19	42.6	0.01	2500	149
<i>Cercocebus albigena</i>	U	4.1	15.4	89	0.05	–	19, 119, 149
<i>Pithecia pithecia</i>	D	0.07	2.7	3	0.00	–	149
<i>Cercopithecus aethiops</i>	D	0.83	23	64	0.35	1446	19, 50, 65, 66, 83, 84, 116, 167
<i>Cercopithecus aethiops</i>	U	0.37	50	120	0.51	1670	18, 83, 84, 115
<i>Cercopithecus ascanius</i>	D	0.31	30	80	0.13	1495	19, 24
<i>Cercopithecus campbelli</i>	D	0.03	10.5	56.7	–	–	24

Species	Type	HRS	GS	GM	Diet	DRL	Sources <sup>a</sup>
<i>Cercopithecus cephus</i>	D	0.36	11.5	30.2	0.06	1637	24
<i>Cercopithecus mitis</i>	D	0.37	26	115	0.23	1217	19, 24
<i>Cercopithecus neglectus</i>	U	0.066	4	16.4	0.09	530	24, 53
<i>Erythrocebus patas</i>	D	45.3	28	164	–	3290	19, 24
<i>Macaca fuscata</i>	U	1.42	37	286	–	–	19, 116
<i>Macaca mulatta</i>	D	8.0	33	114	–	1428	19, 106
<i>Macaca radiata</i>	U	2.79	32	134	–	790	19, 116, 163, 169
<i>Papio anubis</i>	U	12.9	68	566	0.59	5200	1, 19, 20, 31, 63, 116
<i>Papio ursinus</i>	U	14.7	50	643	0.90	5533	19, 61
<i>Papio ursinus</i>	D	5.5	60	557	0.90	–	5, 19, 31, 116
<i>Papio cynocephalus</i>	U	24.1	41	535	0.80	5900	2, 19, 116
<i>Colobus badius</i>	U	0.53	34	208	0.74	557	19, 148, 168
<i>Colobus guereza</i>	U	0.15	12	59.5	0.77	535	19, 35, 112, 130
<i>Colobus guereza</i>	D	0.09	8	57	0.60	481	19, 130, 168
<i>Presbytis entellus</i>	D	0.50	22	170	–	360	19, 73, 168
<i>Presbytis entellus</i>	U	3.3	43	411	0.90	–	19, 73, 75, 119
<i>Presbytis johnii</i>	D	1.62	9	90	0.78	–	19, 168
<i>Hylobates agilis</i>	D	0.29	4.4	18	0.39	1217	19, 99
<i>Hylobates hoolock</i>	D	0.22	3.2	16	0.32	–	99
<i>Hylobates klossii</i>	D	0.065	3.8	17.4	0.02	1514	19, 99
<i>Hylobates lar</i>	D	0.49	3.4	16.5	0.31	1545	19, 99
<i>Hylobates muelleri</i>	D	0.36	3.4	15.4	0.32	833	19
<i>Hylobates pileatus</i>	D	0.36	3.7	16.8	0.13	833	19, 99
<i>Hylobates syndactylus</i>	D	0.34	4	37.5	0.44	854	19, 99
<i>Gorilla gorilla</i>	U	6.5	11	1041	0.86	328	19, 45
<i>Pan paniscus</i>	U	45	63	1285	–	–	19, 82
<i>Pan troglodytes</i>	D	11.5	28	810	0.37	–	19, 129
<i>Pan troglodytes</i>	U	11.5	28	766	0.28	–	19, 119, 181

<sup>a</sup> 1 = Aldrich-Blake et al. (1971), 2 = Altmann and Altmann (1970), 3 = Amstrup and Beecham (1976), 4 = Anderson (1980), 5 = Anderson (1981), 6 = van Ballenberghe and Peeke (1971), 7 = Bekoff and Wells (1986), 8 = Berger (1977), 9 = Bertram (1982), 10 = Breader (1987), 11 = Bromley (1969), 12 = Budnitz and Dainis (1975), 13 = Calkins and Lent (1975), 14 = Caro and Collins (1986), 15 = Caro and Collins (1987); 16 = Carranza et al. (1990), 17 = Chapman (1988), 18 = Chapman and Fedigan (1984), 19 = Cheney (1987), 20 = Clutton-Brock (1977), 21 = Clutton-Brock et al. (1982), 22 = Clutton-Brock et al. (1988), 23 = Coelho et al. (1976), 24 = Cords (1987), 25 = Crockett and Eisenberg (1987), 26 = Danner and Smith (1980), 27 = Dare (1974), 28 = Dasmann and Taber (1956), 29 = David (1973), 30 = David (1978), 31 = DeVore and Hall (1965), 32 = DeVos (1965), 33 = Dubost (1980), 34 = Dunbar and Dunbar (1974a), 35 = Dunbar and Dunbar (1974b), 36 = Elliott and McTaggart Cowan (1978), 37 = Eloff (1973), 38 = Erlinge (1977), 39 = Erlinge and Sandell (1986), 40 = Estes (1966), 41 = Estes (1967), 42 = Estes (1969), 43 = Feist and McCullough (1976), 44 = Ferguson et al. (1983), 45 = Fossey and Harcourt (1977), 46 = Foster and Dagg (1972), 47 = Frame et al. (1979), 48 = Frank (1986), 49 = Franklin (1974), 50 = Galat and Galat-Luong (1976), 51 = Garshelis and Pelton (1981), 52 = Garshelis et al. (1984), 53 = Gauthier-Hion and Gauthier (1978), 54 = Ginsberg (1989), 55 = Goddard (1967), 56 = Goldizen (1987), 57 = Gorman (1979), 58 = Gosling (1974), 59 = Gosling (1986), 60 = Grobler (1974), 61 = Hamilton et al. (1976), 62 = Hanks et al. (1969), 63 = Harding (1976), 64 = Harris (1980), 65 = Harrison (1983a), 66 = Harrison (1983b), 67a = Hendrichs (1975a), 67b = Hendrichs (1975b), 68 = Henschel and Skinner (1991), 69 = Hersteinsson and Macdonald (1982), 70 = Hladik (1979), 71 = Hornocker and Hash (1981), 72 = Howard (1986), 73 = Hrdy (1977), 74 = Jarman (1979), 75 = Jay (1965) 76 = Jewell (1972), 77 = Jolly (1972), 78a = Joubert E (1972), 78b = Joubert S (1972), 79 = Joubert (1974), 80 = Joubert and Eloff (1971), 81 = Jungius (1971), 82 = Kano (1982), 83 = Kavanagh (1978), 84 = Kavanagh (1981), 85 = Kiley-Worthington (1965), 86 = King (1975), 87 = Kitchen (1974), 88 = Klein and Klein (1975), 89 = Klingel (1969), 90 = Klingel (1972), 91 = Klingel (1974), 92 = Kruuk

(1972), 93 = Kruuk (1978), 94 = Kruuk and Parish (1987) 95 = Kruuk and Sands (1972), 96 = Lamprecht (1979), 97 = Langbein and Thirgood (1989), 98 = van Lawick-Goodall and van Lawick-Goodall (1970), 99 = Leighton (1987), 100 = Lent (1969), 101 = Leuthold (1966), 102 = Leuthold (1970), 103 = Leuthold (1974), 104 = Leuthold (1977), 105 = Leuthold and Sale (1973), 106 = Lindburg (1977), 107 = Lindzey and Meslow (1977), 108 = Loughlin (1980), 109 = Macdonald (1979), 110 = MacFarland Symington (1988), 111 = Malcolm (1986), 112 = Marler (1972), 113 = Mason (1968), 114 = Mason (1976), 115 = McGuire (1974), 116 = Melnick and Pearl (1987), 117 = Michael (1965), 118 = Miller (1974), 119 = Mitani and Rodman (1979), 120 = Miura (1984), 121 = Mloszewski (1983), 122 = Moehlman (1986), 123 = Monfort-Braham (1975), 124 = Mukinya (1973), 125 = Murray (1982a), 126 = Murray (1982b), 127 = Nelson and Mech (1981), 128 = Neyman (1978), 129 = Nishida (1979), 130 = Oates (1977), 131 = Oliver et al. 1978, 132 = Owens and Owens (1978), 133 = Owens and Owens (1979), 134 = Owen-Smith (1972), 135 = Owen-Smith (1984), 136 = Pember-ton and Balmford (1987), 137 = Peterson (1977), 138 = Phillips et al. (1973), 139 = Pollock (1977), 140 = Pollock (1979), 141 = Prior (1968), 142 = Rasa (1987), 143 = Richard (1977), 144 = Richard (1987), 145 = Von Richter (1972), 146 = Robbell and Child (1975), 147 = Robinson (1981), 148 = Robinson and Janson (1987), 149 = Robinson et al. (1987), 150 = Rood (1983), 151 = van Roosmalen (1980), 152 = Rosser (1990), 153 = Rubenstein (1981), 154 = Schaller (1967), 155 = Schaller (1972), 156 = Schaller and Cranshaw (1980), 157 = Schaller et al. (1989), 158 = Schenkel (1966), 159 = Schmidt and Gilbert (1978), 160 = Schweinsburg (1971), 161 = Seidensticker et al. (1973), 162 = Servheen (1983), 163 = Simonds (1965), 164 = Smith et al. (1987), 165 = Spinage (1969), 166 = Spinage (1982), 167 = Struhsaker (1967), 168 = Struhsaker and Leland (1987), 169 = Sugiyama (1971), 170 = Sussman (1977), 171 = Tello and Van Gelder (1976), 172 = Terborgh (1983), 173 = Tilson and Henschel (1986), 174 = Verheyen (1955), 175 = Walther (1965), 176 = Walther (1972a), 177 = Walther (1972b), 178 = Walther (1978), 179 = Wirtz (1982), 180 = Woodward (1979), 181 = Wrangham (1977), 182 = Young and Ruff (1982)