Chapter 9
Ranging Behavior and Spatial Cognition of Howler Monkeys

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Abstract Since the first long-term field study of mantled howler monkeys carried out by Clarence R. Carpenter on Barro Colorado Island about 80 years ago, howler movement patterns and range use have been studied in several species and study sites throughout Mexico, Central, and South America. Howler monkeys often use small home ranges (<30 ha) and travel short distances each day (<1,000 m) compared with other atelines. Home range size, day range length, and patterns of use of space may vary both within- and between-species in response to differences in forest structure, patterns of resource distribution and phenology, the area of habitat available, group size, and population density. Within-species variability has been shown to increase with increasing sample size. In addition, howlers present a pattern of repetitive use of a limited number of routes to travel between feeding and

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sleeping sites that has been related to a strategy aimed at reducing the distance travelled while allowing them to keep track of the phenology of important food sources. In this chapter we present the results of a comprehensive review of the literature on the ranging behavior of *Alouatta* (spp.). We used Generalized Linear Models (GLMs) to test whether home range is affected by (1a) fragment size, (1b) population density, (1c) group size, and (1d) group biomass, and whether day range is affected by (2a) fragment size, (2b) population density, (2c) group size, and the contribution of (2d) fruits and (2e) leaves to the diet. We also included species and method of estimating home range as factors in the models. We found that the size of the home range is negatively influenced by population density, and that there are differences between species (*A. palliata* uses significantly larger home ranges), and estimating methods. We also found that the length of the day range is negatively affected by population density, and the contribution of fruits and leaves to the diet, but positively affected by group size. Interspecific comparisons showed that *A. guariba clamitans* tends to travel farther daily than *A. palliata*. Cognitively, recent evidence supports the idea that howler monkeys are capable of encoding, processing, updating, and recalling a topological spatial representation of a set of landmarks (including major feeding and resting sites) as prominent beacons for navigating along commonly used routes within their home ranges.

Resumen Desde los primeros estudios a largo plazo que realizó Clarence R. Carpenter hace alrededor de 80 años en la Isla de Barro Colorado, los patrones de desplazamientos y el uso del hábitat de los monos aulladores han sido ampliamente estudiados en varias especies y sitios a lo largo de México, Centro y Suramérica. Los monos aulladores frecuentemente presentan pequeñas áreas de acción (<30 ha) y desplazamientos diarios cortos (<1.000 m) en comparación con otros atélidos. El tamaño del ámbito hogareño, longitud de los desplazamientos diarios y los patrones de uso del espacio pueden variar tanto dentro y entre las especies en respuesta a las diferencias en la estructura del bosque, los patrones de distribución de los recursos y fenología, el área del hábitat disponible, el tamaño del grupo, y la densidad de población. La variabilidad dentro de las especies se ha demostrado que aumenta con el aumento de tamaño de la muestra. Además, los aulladores presentan un patrón de uso repetitivo de un número limitado de rutas de viaje entre los sitios de alimentación y descanso, algo que se ha relacionado con una estrategia de reducción de la distancia que, al mismo tiempo, les permite monitorear la fenología de las potenciales fuentes de alimentación. En este capítulo se presentan los resultados de una revisión exhaustiva de la literatura sobre el comportamiento de desplazamiento y uso del espacio en *Alouatta* (spp.). Utilizamos modelos lineales generalizados (MLG) para someter a prueba si el ámbito hogareño se ve afectado por (1a) el tamaño del fragmento, (1b) la densidad poblacional, (1c) el tamaño del grupo, y (1d) biomasa proporcional de los grupos; y si los desplazamientos diarios se ven afectados por (2a) el tamaño del fragmento, (2b) la densidad poblacional, (2c) el tamaño del grupo, y la contribución de (2d) frutas y (2e) hojas en la dieta. También se incluyeron las especies y el método de estimación del ámbito hogareño como factores en los modelos. Se encontró que el tamaño del ámbito hogareño se ve influenciado negativamente por la densidad poblacional, y que existen diferencias entre especies (*A. palliata* utiliza ámbitos hogareños significativamente más grandes), y los métodos de estimación. También se encontró que la longitud del recorrido diario se ve afectada negativamente por la densidad poblacional y la contribución de frutas y hojas en la dieta; pero positivamente afectada por el tamaño del grupo. Comparaciones interespecíficas mostraron que *A. guariba clamitans* tiende a viajar más lejos que *A. palliata*. Cognitivamente, las evidencias recientes apoyan la idea de que los monos aulladores son capaces de codificar, procesar, actualizar y recordar la representación espacial topológica de un conjunto de puntos de referencia (incluyendo los más importantes sitios de alimentación y descanso) como elementos prominentes para navegar a lo largo de rutas comúnmente usadas dentro de su ámbito hogareño.

Keywords Day range • Habitat use • Home range • Memory • Movements

9.1 Ranging Behavior

Howler monkeys were the focus of the first systematic primate field study, carried out by Clarence Raymond Carpenter on Barro Colorado Island, Panama, between 1931 and 1932. Carpenter (1934) described the ranging behavior of mantled howler monkeys (*Alouatta palliata*) based on 22 consecutive days of observation. He argued that howler travel was characterized by the repeated use of familiar routes to navigate between feeding sites, a behavior that suggests that these monkeys may mentally represent spatial information as a route-based map in which a forager is expected to acquire, recall, and integrate a set of interconnected pathways or route segments that are linked by a set of landmarks or nodes (Bennet 1996; Urbani 2011). Despite Carpenter's limited period of observation, he identified key aspects of the ranging behavior of howler monkeys (Urbani 2011), that were confirmed by later and more extended field studies (Milton 1980; Garber and Jelinek 2006; Fernández 2008; Hopkins 2008; Pereira 2008).

The ranging behavior of nine species of howlers has been studied from Mexico to southern Brazil and northeastern Argentina, but most studies involved the observation of a single social group. Therefore, our knowledge of within-population variability is quite limited because only a few researchers have monitored more than a single group in the same forest (Larose 1996; Ostro et al. 1999a; Arrowood et al. 2003; Bridgett 2006; Kowalewski 2007; Hopkins 2008; Agostini 2009; Gómez-Posada and Londoño 2012). In this chapter we present the results of the most comprehensive review of the literature so far to analyze the ecological and demographic factors that affect the ranging behavior of howler monkeys. Like previous studies, we evaluate whether group size, population density, habitat availability, and food consumption are proximate causes of home range size and day range length. We also included species, home range estimation method, and group biomass as possible explanatory variables, whose potential influence was never assessed in a genus-wide comprehensive review. We used generalized linear models (GLMs) because they analyze all variables simultaneously while modeling their possible effects independently, and fit the model to alternative distributions (not necessarily linear). In the second part of the chapter we discuss the cognitive challenges faced by howler monkeys when navigating between feeding and resting sites, and present the major findings of recent research.

9.1.1 Factors Affecting Home Range Size

The home range used by a primate group is limited by several factors, including the availability of suitable habitat and food, the density and size of neighboring conspecific groups, and the risk of predation. Because most forests represent a mosaic of habitat types that vary in floristic composition, density and spatial distribution of plant species, and their phenology, the total area of forest available does not necessarily match the area of "suitable habitat." To perform this analysis requires data on species (resource) distribution at a fine spatial scale, a quite complex and time-consuming task that gets impractical with increasing potential habitat area. Therefore, there is an almost complete absence of such detailed evaluations in the literature (the exceptions are restricted to tiny habitat patches, e.g., Bicca-Marques 1994; Prates 2007). As a consequence, most studies have used the size of the study area as a proxy of habitat availability in regression analyses. A strong positive relationship between habitat availability and home range size was evidenced both at the genus level ($n=39$ groups in 29 study sites, Bicca-Marques 2003, based on nine howler species according to the taxonomy adopted by Cortés-Ortiz et al. 2014) and at the species level for *A. palliata* in Los Tuxtlas, Mexico ($n=21$ measures of 19 groups in 10 study sites, Cristóbal-Azkarate and Arroyo-Rodríguez 2007). However, in forest fragments below a given size threshold possibly represented by the size of the home range of groups living in continuous forests or large fragments (that is, in habitats where there are no spatial constraints, without taking into account the influence of neighboring groups) home range size may be limited.

The distance to neighboring habitat patches may also affect home range size by changing the costs of moving across unsuitable or highly disturbed environments and their associated risks (e.g., exposure to predation or parasite infections). Regular travel on the ground for distances of up to about 100 m to reach isolated food patches has been observed in systematic studies of groups inhabiting forest fragments and anthropogenic habitats (*A. guariba clamitans*: Fortes 2008; *A. caraya*: Muhle 2008; Prates and Bicca-Marques 2008; *A. palliata*: Pozo-Montuy and Serio-Silva 2007; Pozo-Montuy et al. 2013). For instance, the home range of a group of *A. g. clamitans* studied by Fortes (2008) in the Brazilian state of Rio Grande do Sul comprised 3 very small fragments (0.2, 0.5 and 1.1 ha) isolated by 35–50 m of grassland that were crossed by the howlers on a daily basis. Similarly, the home range of a group of *A. palliata* in Tabasco, Mexico, included several trees scattered in a pastureland, to which the howlers traveled regularly to feed on fruits (Pozo-Montuy et al. 2013). The costs of adopting this strategy are illustrated by 2 events of predation, 1 by a coyote (Pozo-Montuy and Serio-Silva 2007, 499 h of observation) and the other by a domestic dog (V.B. Fortes, unpublished data, 654 h of observation). Unfortunately, data on the energy spent and on rates of predation or parasitic contamination under varying landscape scenarios are missing to allow a long-term cost-benefit analysis of ground travel at both the individual and the population level.

The number and age-sex composition of individuals living together in a social unit may also influence home range size by affecting the overall amount of food required to satiate all group members. Studies of groups in interbreeding populations suggest the existence of such relationship (*A. pigra*: six groups ranging from four to ten individuals, Ostro et al. 1999a; *A. seniculus*: five groups ranging from five to ten individuals, Gómez-Posada et al. 2007). However, this pattern was not observed in within-species comparisons among different study sites (see Table 9.1). Groups of *A. g. clamitans* with 7–8 individuals used near 70 ha in Misiones, Argentina (Agostini et al. 2010), but only 4–8 ha in study sites in southeast (Mendes 1989; Gaspar 1997) and south Brazil (Cunha 1994; Fortes 1999; Fialho 2000; Marques 2001). There are also cases in which smaller groups range over wider areas than larger ones. For instance, whereas a group of *A. seniculus* composed of 8 individuals had a home range of 182 ha in a continuous rainforest in Colombia (Palacios and Rodríguez 2001), a group of 18 individuals used only 3.7 ha in a bamboo forest fragment in the Andes (Gómez-Posada and Londoño 2012). Here, again, the isolation of howlers in forest fragments (especially small ones) plays a critical role by hampering dispersal and promoting the establishment of larger groups. Therefore, analyses of multiple groups sharing a forest several times larger than the maximum home range recorded for the species are more appropriate to assess the effect of group size and composition on home range size. However, because nutritional requirements vary among age-sex classes and female reproductive state (Serio-Silva et al. 1999; Raguet-Schofield 2010; Amato 2013), group biomass might be a better measure to relate with home range size.

Unlike the effect of group size or biomass, howler monkey population density is reported to have an inverse relationship with home range (Crockett and Eisenberg 1987; Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Studies carried out in large forest tracts (where there are no spatial constraints due to fragmentation) showed that the smallest home ranges are frequently found under the highest population densities (*A. g. clamitans*: Chiarello 1992; *A. caraya*: Kowalewski 2007; Bravo and Sallenave 2003; *A. seniculus*: Gómez-Posada and Londoño 2012), whereas the largest ones are found under very low densities (*A. g. clamitans*: Steinmetz 2000; Miranda 2004; Agostini 2009; *A. caraya*: Agostini 2009; *A. palliata*: Estrada 1984; Stoner 1996) (see Table 9.1). The largest home range ever reported for howlers (182 ha) was recorded in a continuous forest (>600,000 ha) where *A. seniculus* is found at a density of only 0.04 individuals per hectare (Palacios 2003).

Food availability and diet composition are probably the most assessed potential causes of howlers' use of space. The first studies addressing this issue proposed a negative relationship between the degree of folivory (contribution of leaves to the diet) and home range size based on the assumption that leaves are more abundant and evenly distributed than fruits (Milton 1981). This is clearly an oversimplification

Table 9.1 Variables describing use of space and the factors that may affect this use in different species of howler monkeys (*Alouatta* spp.)

References	Study length months (h)	Mean day range (*m*) ± SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
A. guariba clamitans													
1, 2	7 (493)	523	197–1,100	7.9	GC (25 × 25 m)	–	–	570	7	1.17	16	71	Rainforest
3, 4, 5	12 (718)	467	241–808	4.1	GC (25 × 25 m)	–	1.38 (33)[a]	250	6	1.19–1.77	6.5	80.4	Subtropical
6	12	393	155–741	3.9	–	–	–	35	7–10	–	41.7	50.4	Semideciduous
7	–	–	–	8.5	–	–	–	234	7–9	–	14.9	61.9	Subtropical
8	12 (408)	494	–	12.5	GC (50 × 50 m)	–	–	165	3–4	0.10	>44.7	49.5	Semideciduous
9	12 (835)	790	376–1,564	7.2	MCP (afl)	–	–	~1,000	7–9	–	16.2	58.8	Semideciduous
10^{1}	7 (454)	584	230–950	6.4	GC (10 × 10 m)	–	–	12	9	1.04	39.5	53.9	Semideciduous
10^{2}	7 (415)	481	235–735	4	GC (10 × 10 m)	–	–	27	8	1.50	58.9	30.1	Semideciduous
11	12 (~700)	608	235–1,527	11.6	GC (25 × 25 m)	–	–	80	4	–	14.7	62.7	Semideciduous
12	12	–	–	4.5	GC (25 × 25 m)	–	–	7,900	8–10	–	15	55	Subtropical
13	–	546	50–1,280	33 (41.6)	GC (MCP)	–	–	120,000	5–6	–	23	74	Subtropical
14, 15^{1}	12 (580)	958 ± 305	305–1,677	13.5	MCP	–	–	272	11	0.92–1.25[b]	16	55	Araucaria
15^{2}	12 (484)	769 ± 103	274–1,451	8.6	MCP	–	–	5,533	8	0.65–0.85[c]	47	34	Semideciduous
16	12	567	–	6.5	GC (25 × 25 m)	–	–	120	6	0.93	26	62	Semideciduous

17^{1}	12	582 ± 168	252–1,210[d]	19.5	GC (50 × 50 m)	1.8 (9)[e]	–	700	10	0.38	–	–	Araucaria
17^{2}	12	495 ± 207	–	14	GC (50 × 50 m)	2 (14)[e]	–	700	4.5	0.38	–	–	Araucaria
18	12 (560)	–	75–1,187	5	GC (25 × 25 m)	–	–	5	5–8	Max 1.60[f]	39	52	Semideciduous
19^{1}	12 (577)	709 ± 207	324–1,193	4.9	MCP	–	–	~1,000	5	1.10	9	78	Semideciduous
19^{2}	12 (623)	679 ± 274	92–1,463	5	MCP (afl)	–	–	20.2	6	2.20	35	59	Semideciduous
19^{3}	12 (654)	734 ± 228	349–1,273	1.8	MCP (afl)	–	–	1.8	7	3.30[f]	18	67	Semideciduous
20^{1}	12 (352)	759 ± 71	244–1,666	69.9 (70.3)	MCP (95% KDE)	7.4 (11)[g]	(41)[h]	165	7–8	0.10	24[i]	62[i]	Araucaria
20^{2}	12 (308)	744 ± 95	75–1,538	47.4 (31.6)	MCP (95% KDE)	2.1 (7)[g]	(99)[j]	165	4	0.10	–	–	Araucaria
21	12 (636)	520 ± 127	265–1,034	2.2	GC (20 × 20 m)	–	–	2.2	6	2.70[f]	15	78	Araucaria
Mean ± SD		**620 ± 142**	**50–1,677**	**13.00 ± 15.9**			**58 ± 36%**		**6.9 ± 2.0**	**1.17 ± 0.91**	**25.9 ± 14.3**	**59.8 ± 13.0**	
A. belzebul													
22	–	450	350–650	9.5	–	–	–	271	6–8	–	59	13	Subtropical
23	6 (401)	1,474	861–2,409	13.8 (10.9)	GC (25 × 25 m) (MCP)	0.3[k]	Low	33,100	7	2.0[l]	70.8	28.6	Rainforest
24	10 (1,203)	684 ± 215	269–1,300	17.8	GC (25 × 25 m)	–	–	20,000	6	–	42.8/43.9[m]	46.6/43.4[m]	Rainforest
25	14	–	–	10.6	GC	–	–	266.53	16	–	–	66.3	Rainforest
Mean ± SD		**869 ± 537**	**269–2,409**	**12.6 ± 3.7**					**9.0 ± 4.7**	**2**	**57.7 ± 13.8**	**38.2 ± 22.8**	
A. discolor													
26	10	761	167–1,425	50.1 (63.2)	GC (MCP)	–	–	10,000	7–9	–	55	25	Rainforest

(continued)

Table 9.1 (continued)

References	Study length months (h)	Mean day range (*m*) ± SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
Mean ± SD		**761**	**167–1,425**	**56.7**					**8**		**55**	**25**	
A. caraya													
27	–	345	130–1,200	5.5	–	–	–	12	6	–	–	–	Subtropical
27	–	–	–	6.3	–	–	–	12	6	–	–	–	Subtropical
28	–	341 ± 156	112–1,200	5.5	–	–	–	12	5.5	–	26.7	54.5	Subtropical
29, 30	12 (745)	454 ± 176	156–893	2	GC (20 × 20 m)	0.16[n]	–	2	15–17	Max 8.5[f]	29	61	Seminatural
31^1	17 (1,680)	513 ± 253	Min 85	1.7	GC (20 × 20 m)	1.3[o]	0.4	141	16	4.25	18[p]	64[p]	Subtropical
31^2	17 (1,680)	602 ± 350	Max 1,515	2.2	GC (20 × 20 m)	1.8[o]	0,4	141	21	4.25	–	–	Subtropical
32	12 (50)	–	–	6	–	1.5	–	170	5	0.82–1.02	–	–	Subtropical
32	(100)	280	120–500	5	–	1.6	–	170	3	0.82–1.02	–	–	Subtropical
33^1	(306)	564 ± 245	154–1,065	5.0 (3.2)	GC (MCP)	1 (20)[q]	1.25 (25)	1,050	11–9	2	–	–	Semideciduous
33^2	12 (288)	842 ± 364	416–1,638	18.8 (18.4)	GC (MCP)	Nule[q]	1.5 (8)	–	13–11	0.64	–	–	Semideciduous
34	12	684 ± 225	300–1,300	5.9 and 6.0	GC (20 × 20 m)	–	(70.5)[r]	400	10.5	3.48	24	46	Subtropical
35	12 (699)	371 ± 116	168–628	0.7	GC (15 × 15 m)	–	–	0.7	12–14	Max 20[f]	12.3	82.4	Seminatural
36	12 (830)	272 ± 99	113–540	1.3	Wfu	–	–	1.3	4–5	Max 3.85[f]	1.9	75.3	Seminatural
37^1	12 (383)	840 ± 95	62–1,582	93.8 (111.9)	MCP (95% KDE)	27.03 (24)[s]	(46)[t]/(6)[u]	165	12–14	0.15	19[v]	64[v]	Araucaria

37[2]	12 (351)	709 ± 59	228–1,308	17.8 (17.3)	MCP (95% KDE)	2.36 (14)[s]	(75)[w]/ (38)[x]	165	5–7	0.15	–	–	Araucaria
Mean ± SD		**524 ± 201**	**62–1,638**	**11.7 ± 23.3**			**38 ± 26%**		**9.8 ± 5.3**	**5.44 ± 6.38**	**18.7 ± 8.6**	**63.9 ± 11.3**	
A. seniculus													
38	10 (340)	706 ± 382	–	22	–	–	–	270	9–10	–	42	53	Rainforest
39	–	–	–	25	–	47.4–90.8	–	469	8	–	–	–	Rainforest
39	–	–	–	28.4	–	–	–	469	8	–	–	–	Rainforest
39	–	–	–	30	–	–	–	469	13	–	–	–	Rainforest
40, 41	10 (496)	1,150 ± 394	370–2,200	182	GC (100 × 100 m)	17[y]	0	–	8	0.04	52.3	35.3	Rainforest
42	–	–	–	14.5	–	–	–	–	9	–	–	–	Rainforest
42	–	–	–	21.5	–	–	–	–	10	–	–	–	Seminatural
43	6 (534)	–	469–878	21	–	–	–	–	–	–	–	–	Rainforest
44[1]	18 (705)	–	–	2.1	MCP	–	0.9[z]	110.7	13	3.8	–	–	Dry
44[2]	18 (556)	–	–	3.7	MCP	–	0.9[z]	110.7	18	3.8	–	–	Dry
44[3]	12 (311)	–	–	4.8	MCP	–	0.9[z]	110.7	17	3.8	–	–	Dry
44[4]	12 (260)	–	–	3.8	MCP	–	0.9[z]	110.7	13	3,8	–	–	Dry
Mean ± SD		**928 ± 313**	**370–2,200**	**29.9 ± 49.0**					**9.58 ± 1.86**	**0.04**	**47.2 ± 7.3**	**44.2 ± 12.5**	
A. juara													
45	12 (492)	320	–	7.5	–	–	–	1,240,000	8	–	47	46	Rainforest
46	–	–	–	6.7	–	–	–	–	5.5	–	–	–	Rainforest
Mean ± SD		**320**		**7.1 ± 0.6**					**6.8 ± 1.8**		**47**	**46**	

(continued)

Table 9.1 (continued)

References	Study length months (h)	Mean day range (m) ± SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
A. arctoidea													
47^{1}	14 (603)	–	Max 430	7.1	–	–	–	3,200	6–9	–	–	–	Dry
48	–	340	20–840	4–7	–	–	–	–	–	–	–	–	–
48	–	445	–	–	–	–	–	–	–	–	–	–	–
Mean ± SD		**393 ± 74**	**20–840**	**6.3 ± 1.1**					**7.5**				
A. pigra													
49^{1}	10	520 ± 185	–	10.4	DP	–	–	4,700	7	0.47	–	–	Semideciduous
49^{2}	10	648 ± 230	–	15.8	DP	–	–	4,700	10	0.47	–	–	Semideciduous
49^{3}	10	441 ± 176	–	9.3	DP	–	–	40,000	6	0.03	–	–	Rainforest
49^{4}	10	567 ± 263	–	20.2	DP	–	–	40,000	4,5	0.03	–	–	Rainfores
50^{1}	6 (290)	246 ± 108	0–383	2.2	DP	–	22.3	71	2	–	40^{aa}	56^{aa}	Semideciduous
50^{2}	–	485 ± 190	128–716	4	DP	–	12.3	71	6	–	–	–	Semideciduous
50^{3}	–	476 ± 180	180–814	4.1	DP	–	–	71	3	–	–	–	Semideciduous
50^{4}	–	576 ± 182	182–856	2.8	DP	–	–	71	4	–	–	–	Semideciduous
51	12	–	–	14 ± 5.1 (8–21)^{bb}	GC (100 × 100 m)	–	(54 ± 32)^{bb}	385	–	0,39	–	–	Rainforest
Mean ± SD		**491 ± 129**	**0–1,015**	**9.2 ± 6.4**			**30 ± 22%**		**5.9 ± 2.3**	**0.25 ± 0.25**	**40**	**56**	
A. palliata													
52	14 (2071)	596	207–1,261	9.9	–	–	–	10	13	–	13	69	Rainforest
53, 54^{1}	10	488 ± 152	104–792^{d}	31.1	MCP	–	–	1,600	17	1.13	47	44	Rainforest
53, 54^{2}	10	392 ± 127	–	31.7	MCP	–	–	1,600	17	1.13	37	53	Rainforest

55, 56^1	12	123 ± 101	11–503	60	GC (100 × 100 m)	–	–	700	16	0.22	51	49	Rainforest
57^1	60	148	10–893	–	–	–	–	700	16	–	–	–	Rainforest
58, 59	24 (394)	–	–	108	GC (120 × 120 m)	–	–	10,800	40	–	29	49	Dry deciduous
60^1	6 (324)	374/390[cc]	–	30.5[dd]	GC (10 × 10 m)	–	–	10,800	28	–	–	–	Dry deciduous
60^2	6 (304)	407	–	–	–	–	–	10,800	20–22	–	–	–	Dry deciduous
60^3	6 (241)	362/331[cc]	–	46[dd]	GC (10 × 10 m)	–	–	10,800	14–11	–	–	—	Dry deciduous
60^4	6 (291)	306	–	–	–	–	–	10,800	10	–	–	–	Dry deciduous
60^5	6 (275)	184/262[cc]	–	17.8[dd]	GC (10 × 10 m)	–	–	10,800	7–4	–	–	–	Dry deciduous
60^6	6 (302)	322	–	–	–	–	–	10,800	6	–	–	–	Dry deciduous
61^1	15 (140)	–	–	54	GC (100 × 100 m)	–	–	1,200	20–23	0.07–0.15	17	72	Rainforest
61^2	15 (208)	–	–	35	GC (100 × 100 m)	–	–	1,200	11–14	0.07–0.15	29	65	Rainforest
62	12	326	161–475	3.6	Wfu	–	–	3.6	7	1.94[f]	54.3	40.6	Rainforest
63^1	12 (1,300)	752 ± 292	–	21.9 (20.3)	MCP (DP)	–	(0)[ee]	125	25.9	0.56	34.8[ff]	55.8[ff]	Semideciduous
63^2	–	568 ± 256	–	15.8 (13.7)[gg]	MCP (DP)	–	(7)[ee]	125	15.3	0.56	–	–	Semideciduous
63^3	–	572 ± 301	–	21.3 (17.3)	MCP (DP)	–	(5)	125	20.2	0.56	–	–	Semideciduous
64^1	10 (1,010)	453 ± 189	109–958	26	95% MCP	–	22.61 ha	1,600	13.6 ± 2.8	–	41.3 ± 27.9[hh]	47.2 ± 22.1[hh]	Rainforest
64^2	10 (1,001)	771 ± 440	81–2,850	44	95% MCP	–	18.90 ha	1,600	23.4 ± 1.2	–	–	–	Rainforest

(continued)

Table 9.1 (continued)

References	Study length months (h)	Mean day range (m) ± SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
64^3	6 (219)	474 ± 229	130–828	29	95% MCP	–	17.98 ha	1,600	16.8 ± 2.9	–	–	–	Rainforest
64^4	6 (416)	288 ± 233	0.05–974	18	95% MCP	–	9.01 ha	1,600	9.0 ± 2.1	–	–	–	Rainforest
Mean ± SD		**432 ± 172**	**0.05–2,850**	**33.3 ± 23.9**			**36 ± 33%**		**16.1 ± 8.6**	**0.70 ± 0.60**	**35.3 ± 13.7**	**54.5 ± 10.8**	

Only studies longer than 6 months are included

References and Study sites: (1, 2) Mendes (1985, 1989)—Caratinga Biological Station, Brazil; (3, 4, 5) Chiarello (1992, 1993, 1994)—Santa Genebra Municipal Reserve, Brazil; (6) Cunha (1994)—Itapuã State Park, Brazil; (7) Gaspar (1997)—Campinas, Brazil; (8) Martins (1997)—Rio Claro Farm, Lençóis Paulista, Brazil; (9) Fortes (1999)—Campo de Instrução de Santa Maria, Brazil; (10^1) Fialho (2000)—Morro da Extrema, Porto Alegre, Brazil (Encosta troop); (10^2) Fialho (2000)—Lami, Porto Alegre, Brazil (Restinga troop); (11) Limeira (1996)—Amazonas Farm, Rio de Janeiro, Brazil; (12) Lunardelli (2000)—Parque Estadual da Cantareira, São Paulo, Brasil; (13) Steinmetz (2000)—Intervales State Park, Brazil; (14, 15^1) Marques (1996, 2001)—Aracuri Ecological Station, Brazil; (15^2) Marques (2001)—Itapuã State Park, Brazil; (16) Oliveira (2003)—Água Branca Farm, SP, Brazil; (17^1) Miranda (2004)—Chácara Payquerê, Balsa Nova, PR, Brazil (Forninho troop); (17^2) Miranda (2004)—(Patropi troop); (18) Koch (2008)—Barra do Ribeiro, Rio Grande do Sul, Brasil; (19^1) Fortes (2008)—Campo de Instrução de Santa Maria, Brazil (G troop); (19^2) Fortes (2008)—(M troop); (19^3) Fortes (2008)—(P troop); (20^1) Agostini (2009)—El Piñalito Provincial Park, Misiones, Argentina (Cosacos troop); (20^2) Agostini (2009)—(Gitanos troop); (21) Guzzo (2009)—Ipê, Rio Grande do Sul, Brazil; (22) Bonvicino (1989)—Fazenda Pacatuba, Paraíba, Brazil; (23) Jardim (1997)—Estação Científica Ferreira Penna, Brazil; (24) Pinto et al. (2003)—Cauaxi Ranch, Paragominas, Brazil; (25) Porfírio de Souza (2005)—RPPN Pacatuba, Paraíba, Brazil; (26) Pinto (2002)—Paranaíta, MT, Brazil; (27) Zunino (1986)—Northeastern Argentina; (28) Zunino (1989)—Northeastern Argentina; (29, 30) Bicca-Marques (1993, 1994)—Estância Casa Branca, Rio Grande do Sul, Brazil; (31^1) Bravo and Sallenave (2003)—Brasilera Island, Argentina (Gringos troop); (31^2) Bravo and Sallenave (2003)—(Enfermitos troop); (32) Aguiar et al. (2003)—Balsa Nova, Paraná, Brazil; (33^1) Ludwig (2006)—Mutum Island, Paraná river, Brazil (GM troop); (33^2) Ludwig (2006)—Porto Rico, Paraná, Brazil (GP troop); (34) Kowalewski (2007)—Brasilera Island, Argentina; (35) Prates (2007)—Alegrete, Rio Grande do Sul, Brasil; (36) Muhle (2008)—Tupaciretã, Rio Grande do Sul, Brazil; (37^1) Agostini (2009)—El Piñalito Provincial Park, Misiones, Argentina (Orishas troop); (37^2) Agostini (2009)—(Reviro troop); (38) Gaulin and Gaulin (1982)—Finca Merenberg, Colombia; (39) Izawa and Nishimura (1988)—Serranía La Macarena, Colombia; (40, 41) Palacios and Rodríguez (2001), Palacios (2003)—Caparú Biological Station, Colombia; (42) Morales-Jimenez (2003)—Otun Quimbaya Sanctuary, Risaralda, Colombia; (43) Santamaría and Rylands (2003)—Biol. Dyn. Forest Frag. Proj., Amazonas, Brazil; (44^1) Gómez-Posada and Londoño (2012)—LMO forest fragment, Quindío, Colombia (Matapalo troop); (44^2) Gómez-Posada and Londoño (2012)—(Ocaso troop); (44^3) Gómez-Posada and Londoño (2012)—(troop 4); (44^4) Gómez-Posada and Londoño (2012)—(troop 5); (45) Queiroz (1995)—Mamirauá Ecological Station, Amazonas, Brazil; (46) Soini (1986)—Cahuana Field Station, Pacaya-Samiria N.R., Peru; (47^1) Neville (1972)—Hato Masaguaral ranch, Venezuela (troop 1); (48) Sekulic (1982)—Hato Masaguaral, Venezuela; (49^1) Ostro et al. (1999a)—Community Baboon Sanctuary, Belize (C1 troop); (49^2) Ostro et al. (1999a)—(C2 troop); (49^3) Ostro et al. (1999a)—(E1 troop); (49^4)

Ostro et al. (1999a, 1999b)—(E2 troop); (50^{1}) Bridgett (2006)—Monkey River, Belize (troop A); (50^{2}) Bridgett (2006)—(troop B); (50^{3}) Bridgett (2006)—(troop N); (50^{4}) Bridgett (2006)—(troop Q); (51) Gavazzi et al. (2008)—Lamanai, Belize; (52) Glander (1978)—Hacienda La Pacifica, Guanacaste, Costa Rica; (53, 54)^{1} Milton (1977, 1980)—Barro Colorado Island, Panama (Lutz Ravine troop); (53,54)^{2} Milton (1977, 1980)—(Old Forest troop); (55, 56)^{1} Estrada (1982, 1984)—Los Tuxtlas Station, Mexico (troop S); (57^{1}) Estrada and Coates-Estrada (1984)—Los Tuxtlas Station, Mexico (troop S); (58, 59) Chapman (1987, 1988)—Santa Rosa National Park, Costa Rica; (60^{1}) Larose (1996)—Santa Rosa National Park, Costa Rica (SN troop, 1991); (60^{2}) Larose (1996)—(SN troop, 1992); (60^{3}) Larose (1996)—(EX troop, 1991); (60^{4}) Larose (1996)—(EX troop, 1992); (60^{5}) Larose (1996)—(SE troop, 1991); (60^{6}) Larose (1996)—(SE troop, 1992); information on population density in Santa Rosa National Park is from Fedigan et al. (1985); (61^{1}) Stoner (1996)—La Selva Biological Reserve, Costa Rica (troop 1); (61^{2}) Stoner (1996)—(troop 2); (62) Estrada et al. (1999)—Los Tuxtlas, Mexico; (63^{1}) Williams-Guilén 2003—Finca La Luz, Nicaragua (troop 1); (63^{2}) Williams-Guilén 2003—(troop 2); (63^{3}) Williams-Guilén 2003—(troop 3); (64^{1}) Hopkins (2008)—Barro Colorado Island, Panama (troop 8); (64^{2}) Hopkins (2008)—(troop 2); (64^{3}) Hopkins (2008)—(troop 6); (64^{4}) Hopkins (2008)—(troop 7)

Notes: [a]5 neighboring groups; [b]Schneider and Marques (1999); [c]Buss (2001); [d]both groups considered together; [e]quadrats used in more than 30% of daily routes; [f]only one group; [g]fixed kernel 50%; [h]with Orishas and Reviro (black howler groups); [i]both groups averaged (fruits include 7% consumption of Araucaria seeds); [j]with Orishas (black howler group);[k]quadrats used in more than 30% of observations; [l]Ferrari and Lopes (1996); [m]unlogged/logged forest; [n]quadrats used more than 70% of sampling days; [o]exclusive (actively defended) area; [p]both groups averaged; [q]quadrats used in ≥10% records; [r]3 neighbor groups; [s]fixed kernel 50%; [t]with Cosacos and Gitanos (brown howlers groups); [u]with Reviro; [v]both groups averaged; [w]with Cosacos (brown howlers group); [x]with Orishas; [y]30.8% time records; [z]Overlap index (Di Bitetti 2001); [aa]4 groups averaged; [bb]average for 22 groups; [cc]both years (1991/1992) averaged; [dd]for the whole study period; [ee]small tips of their home ranges overlapped with other (non-studied) groups; [ff]3 groups averaged; [gg]only 9 months; [hh]troops 8 and 2 averaged

Abbreviations: *HR* home range, *GC* grid cell counting, *MCP* minimum convex polygon, *afl* adjusted to forest limit, *wfu* whole fragment was used, *DP* digitized polygons, *KDE* kernel density estimates of food availability that does not take into account seasonal and habitat differences in plant species density, dispersion, phenology, crop productivity, and howler monkey dietary selectivity in terms of plant species and stage of development of preferred leaves and fruits (see chapters on diet, digestion and nutritional ecology in this volume). A study of *A. palliata* at Los Tuxtlas, Mexico, illustrates this point. A group composed of 14 individuals studied by Estrada (1984) used one of the largest home ranges ever reported for *Alouatta* spp. (ca. 60 ha, see Table 9.1) despite ingesting a diet rich in leaves (49% of feeding records). Estrada (1984) attributed this finding to a foraging pattern based on young leaves (39%) of patchily distributed tree species. According to him, the study group traveled extensively among scattered 1-ha quadrats during periods of high leaf consumption. Because the other three groups studied in the same site followed a similar pattern, Estrada (1984) could not evaluate how the exploitation of more clumped leaf sources would influence home range use. The scarcity of data on the distance among food patches in most studies carried out in the last four decades, with the exception of those recent ones focusing on the cognitive aspects of foraging, represents an additional limitation for testing the relationship between the degree of folivory and home range size.

9.1.2 Factors Affecting Day Range

Day range may also be influenced by factors such as group size, size, density and distribution of food sources, location of neighboring groups (territorial encounters) and, possibly, predation risk. Unlike the positive relationship found between fragment size and home range described above, fragment size was not a good predictor of the average length of the daily path in a genus-wide analysis carried out by Bicca-Marques (2003). His analysis showed that groups using small home ranges in forest fragments may travel as much as groups inhabiting larger habitat patches (Table 9.1). This finding seems to be related to a pattern of travel to scattered resources, the monitoring of the phenology of potential food sources distributed throughout the home range and/or the monitoring of home range boundaries.

Consistent with Bicca-Marques' (2003) results, Fortes (2008) observed similar day ranges in 3 study groups of *A. g. clamitans* that inhabited forest fragments of discrepant sizes: 1.8 ha (mean ± SD = 734 ± 228 m), 20 ha (679 ± 274 m), and ~1,000 ha (709 ± 207 m). The group inhabiting the smallest area moved back-and-forth on the ground between the 3 isolated small fragments 49 times in 59 sampling days. As a result, day ranges longer than 1,000 m were more common there (14%) than in the largest fragment (7%). In 23 complete days of observation the former group moved from one fragment to another. About half (43.5%) of these fragment changes occurred when diet richness started to stabilize (indicated by the species accumulation curve), whereas the remaining 56.5% happened before stabilization. This strategy allowed the group to include new items in the diet as indicated by the low values of Jaccard similarity index between the diet composition observed in fragments used in sequence (Fortes and Bicca-Marques 2012). Therefore, tracking the spatial availability of food resources and obtaining a balanced diet and/or avoiding the ingestion of an overload of the same secondary compounds appear to be critical factors in howler ranging behavior, irrespective of fragment size. The positive relationship found between mean day range and average number of plant species used as food sources per day by Bicca-Marques (2003) lends support to this hypothesis.

A positive relationship between group size and day range has been proposed for predominantly frugivorous species based on the assumption that larger groups deplete fruit patches faster than smaller ones (Chapman et al. 1995; Chapman and Chapman 2000; but see Sussman and Garber 2011 for a critique of the Ecological Constraints Model). Although howlers are better described as folivorous–frugivorous (Crockett and Eisenberg 1987), they may behave as predominantly frugivorous under certain circumstances, either during the year (*A. belzebul*: Jardim 1997) or certain seasons or months (*A. g. clamitans*: Koch 2008; *A. caraya*: Bicca-Marques and Calegaro-Marques 1994; A. *pigra*: Pavelka and Knopff 2004). In addition, their preferred leaf sources may also be depletable (Snaith and Chapman 2007). Therefore, it is also possible to predict that howler group size has a direct influence on day range, particularly when exploiting scattered and depletable food sources.

Again, contrasting results have been found. Studies that failed to demonstrate a positive relationship for howlers in general (among other folivorous primates) attributed this result to a weak or absent food competition and/or a reliance on alternative, fallback food items, such as mature leaves (Isbell 1991; Janson and Goldsmith 1995). A significant relationship was found in four out of seven studies that evaluated this aspect at the species level, particularly in *A. palliata* (Larose 1996; Williams-Guilén 2003; Hopkins 2011), the howler monkey that forms the largest groups and presents the wider variation in group size (see Di Fiore et al. 2011). The fourth study that found this relationship involved a population of *A. pigra* at the Community Baboon Sanctuary (Ostro et al. 1999a). However, studies on this species at the Cockscomb Basin Wildlife Sanctuary (Ostro et al. 1999a) and Lamanai (Arrowood et al. 2003) failed to find such relationship. At Lamanai day range was predicted by group spread, a relationship compatible with the occurrence of feeding competition (Arrowood et al. 2003). Therefore, it is possible that the strength of the relationship between group size and day range is context-specific, depending on site characteristics (e.g., size, spatial distribution, and productivity of nearby feeding patches; Chapman and Chapman 2000) and population density. Unfortunately, analyses integrating this information are rare in *Alouatta* studies (Bridgett 2006 is an exception). Bridgett (2006) mapped the location of 201 trees and collected phenological samples to evaluate fruit availability within the home ranges of 4 groups of *A. pigra* in Belize. He calculated a coefficient of dispersion of fruiting trees for each home range and related it to the groups' ranging patterns.

Milton (1980) states that howlers are travel minimizers because of energetic constraints imposed by a diet rich in leaves that are low in ready energy, an assumption that leads to the prediction that day range should be inversely related to the contribution of leaves to the diet. However, howlers have been observed to travel over longer distances during periods of both high frugivory (*A. g. clamitans*: Mendes 1989;

Martins 1997; Fortes 1999; Marques 2001; Oliveira 2003; *A. pigra*: Bridgett 2006; *A. caraya*: Agostini et al. 2010) and high folivory (*A. g. clamitans*: Limeira 1996; *A. palliata*: Estrada 1984). Zunino (1986) addresses the complexity of this relationship by proposing two main behavioral strategies related to the Optimal Foraging Hypothesis: high cost-high reward and low cost-low reward (Zunino 1986).

The adoption of a high cost-high reward strategy would be expected during periods when howlers are feeding on fruit, a food item richer in ready energy than leaves. This strategy was observed by Pavelka and Knopff (2004) in *A. pigra*, in which time moving increased from 5.4% in the season of low fruit consumption (14%) to 9.4% in the season of high fruit consumption (67%). Similarly, a group of *A. g. clamitans* inhabiting an Araucaria forest (Aracuri Ecological Station) in southern Brazil showed the longest day ranges (mean ± SD = 1,200 ± 182 m, maximum = 1,512 m, $n = 11$ days) when traveling between scattered Brazilian pine trees (*Araucaria angustifolia*) to consume their seeds (Marques 2001). These displacements occurred during the Fall, when the howlers could be expected to save energy to cope with the low ambient temperatures (mean minimum temperature = 11 °C) and the needs of thermoregulation (Bicca-Marques and Azevedo 2004). However, in accordance with the high cost-high reward strategy, the seeds of *A. angustifolia* are fourfold richer in carbohydrates (total carbohydrates = 38.7 $\text{g} \times 100\ \text{g}^{-1}$; Cordenunsi et al. 2004) than the most consumed fruit by the study group (*Campomanesia xanthocarpa*, Myrtaceae; total carbohydrates = 8.9 $\text{g} \times 100\ \text{g}^{-1}$; Vallilo et al. 2008), thereby possibly offsetting an increase in travel costs.

On the other hand, a low cost-low reward strategy would be expected when howlers rely mostly on leaves (particularly mature ones), a food item containing less readily available energy (Milton 1979). This strategy was observed by Limeira (1996), who reports a negative correlation between the consumption of mature leaves and day range in *A. g. clamitans*. However, her study group also presented a positive correlation between day range and the consumption of young leaves from an important source, *Apuleia leiocarpa* (Fabaceae), a pattern similar to that previously reported by Estrada (1984) for *A. palliata*.

Again, it is important to consider that these strategies were proposed based on the oversimplified idea that fruits would be more sparsely distributed than leaves in time and space. For instance, other studies have shown that when fruit sources are clumped or hyperabundant in the environment, howlers may travel over shorter distances while "camping" at productive sites and feeding intensively on fruit for several days (Fialho 2000; Palacios and Rodríguez 2001; Oliveira 2003; Miranda 2004; Kowalewski 2007); that is, adopting a strategy of low energy expenditure even with a high energy intake.

Finally, some studies found no relationship between diet composition and day range. This result was observed in groups showing a low level of fruit consumption throughout the year (*A. palliata*: Chapman 1988; *A. g. clamitans*: Chiarello 1993) and in a group of the latter species that fed heavily on highly abundant fruit species that fruit asynchronously (*Syagrus romanzoffiana*, Arecaceae, and *Ficus* spp., Moraceae) throughout the year in a seasonal forest (Itapuã State Park) in south Brazil (Marques 2001). These studies highlight that day range may vary among habitats and times of the year in response to spatiotemporal chances in the availability of particular food items.

9.1.3 Hypotheses

Given the lack of consistent trends and the complexity of the relationships between ecological and demographic factors and the patterns of ranging behavior in *Alouatta* spp. discussed above, we tested whether home range size is affected by (1a) fragment size, (1b) population density, (1c) group size, and (1d) group biomass, and whether day range length is affected by (2a) fragment size, (2b) population density, (2c) group size, and the contribution of (2d) fruits and (2e) leaves to the diet. We also included species and method of estimating home range as factors, due to evidence showing that home range size differs among howler species (Bicca-Marques 2003) and that estimates may vary widely among methods (Grueter et al. 2009; Gula and Theuerkauf 2013) as discussed below.

9.1.4 Methods

We compiled data on the ranging behavior of nine howler monkey species from 56 studies that provided information on home range size and/or day range length and a set of potential predictive demographic and ecological variables (Table 9.1). We limited the review to studies lasting at least 6 six months and that covered more than 1 season to reduce the potential influence of seasonality on the results. We used GLMs to assess whether group size and biomass, population density, fragment size, and the contribution of fruits and leaves to the diet were good predictors of home range size or day range length. We also included species identity and home range estimating method as factors in the models. Group biomass was calculated multiplying the relative contribution of each age-sex class for the group size by the mean biomass of that class according to the literature (Glander 1980; Ford and Davis 1992; Smith and Jungers 1997; Glander 2005; Di Fiore et al. 2011). When there was no information on body mass for a given species we used data from its closest congener for which this information is available.

We began by adjusting the complete model (including all possible explanatory variables) for each of the dependent variables (home range size or day range length) based on the lower values of AIC (Matthiopoulos 2010). For the analysis of home range we also tested a model excluding the variable fragment size because its effect was negligible in the first model. Although there is a high correlation ($r_S = 0.89$) between time invested consuming fruits and leaves, we decided to test a model for day range including both variables because they are not perfectly complementary and each item has its own suspected influence on howler movement (energy balance vs. nutrient mixing or toxin avoidance). The significance of the fitted terms and their interactions was assessed using the Wald statistic (McCullagh and Nelder 1989).

Traditionally, home range size was estimated either by the Minimum Convex Polygon (MCP; e.g., Milton 1980) or the Grid Cell (GC; e.g., Estrada 1982) method. The MCP method is calculated by measuring the area inside the convex polygon that results from the connection of the extreme locations of the group's range. This method is highly sensitive to the number of recorded locations and to the occurrence of outliers (group excursions to areas rarely visited) and, therefore, tends to overestimate the area of the home range, especially if it has an irregular shape (Grueter et al. 2009; Fieberg and Börger 2012). The GC method is calculated by overlaying a grid of cells of a particular area on a field map of the study site and counting the number of cells visited by the group. The method tends to overestimate the area of the home range when cell size is large and to underestimate it when cell size is small (Kool and Croft 1992; Grueter et al. 2009). The definition of an optimal grid size should take group spread into account, a parameter that increases with increasing group size and that may be affected by the productivity and dispersion of feeding patches. Therefore, although 10 × 10 m cells as used by Larose (1996) are likely to be small, 25 × 25 (Chiarello 1993), 50 × 50 (Pinto et al. 2003), 100 × 100 (Palacios and Rodríguez 2001), or 120 × 120 m (Chapman 1987) cells may be adequate under different circumstances. We suggest the use of the maximum reliable group spread (calculated as the maximum reliable perpendicular distance of the line transect census technique, see NRC 1981) to determine cell size in each study.

Digitized Polygons (DP) are created by mapping day range paths with a strip buffer zone at each side of the path. The polygon is traced using an MCP and all lacunae (areas outside the paths) inside this polygon are excluded. Similar to the other methods, the estimated area of the home range increases with increasing sample size. However, this method appears to generate more realistic estimates because it does not include areas inside the polygon based on mathematical assumptions (as the 95% MCP does), excludes areas not visited by the animals, and takes into account group spread for calculating the width of the buffer zone. The remaining subjectivity concerns the definition of the width of the buffer zone and the size of the lacunae to exclude, a decision that is made by the researcher (Ostro et al. 1999b).

The use of probabilistic techniques, such as kernel density estimates (KDE), is more recent and restricted to fewer studies (Hopkins 2008; Agostini 2009). This method provides the probability of finding a group at a particular location on a plane (probability density function), but has the limitation of increasing the probability of excluding areas used by the howlers (such as corridors between habitat patches) by splitting the home range into multiple small polygons (Fieberg 2007; Fieberg and Börger 2012). Despite these limitations, the use of different methods to calculate the home range of study groups of three howler species produced quite similar estimates (*A. pigra*: Williams-Guilén 2003; *A. g. clamitans*: Ludwig 2006; Agostini 2009; *A. caraya*: Agostini 2009).

We used the Kruskal-Wallis analysis of variance to compare home range and day range among species because of missing data in the data sets included in both models. We analyzed the relationship between pairs of variables (frugivory vs. folivory and intraspecific home range variance vs. sample size) via Spearman rank correlation test. All tests were performed using Statistica 10.0 (Statsoft 2011) and considered a level of significance of 0.05.

9.1.5 Testing the Hypotheses

The home range of study groups varied from 0.7 to 182 ha (median = 10 ha, mean ± SD = 19 ± 27 ha, $n = 85$ groups). Thus, a more than 200-fold difference in size separates the smallest (0.7 ha in *A. caraya*, Prates and Bicca-Marques 2008) from the largest (182 ha in *A. seniculus*, Palacios and Rodríguez 2001) home range. This difference is explained by the area of habitat available for the *A. caraya* group and possibly by the presence of competing primate species and a lower howler population density in the study site of *A. seniculus*. Home range size differed significantly among howler species ($H = 25.94$, $p < 0.0005$, $\phi = 7$, $n = 85$, *A. discolor* was excluded from the analysis because of small sample size), being significantly larger in *A. palliata* (33 ± 24 ha; Dunn *post-hoc* test, $Z_{\text{crit}} = 3.1$, $p < 0.05$). Within-species variance was large (Fig. 9.1) and directly influenced by sample size (Spearman rank correlation $r_s = 0.78$, $p = 0.02$, $n = 8$ species).

The model excluded *A. belzebul*, *A. discolor*, and *A. juara* because their data sets were limited to only one or two study groups each and because there are missing data for some variables. For the remaining six species, fragment size (1a), group size (1c), and group biomass (1d) did not show a consistent effect on home range size, whereas population density (1b) showed a negative relationship with this variable (Table 9.2). According to this model, the home range of *A. seniculus* was significantly smaller than those of the other howlers, independent of other factors. However, this occurred because only two studies fulfilled the data requirements to be included in the model, and one of them (Gómez-Posada and Londoño 2012) involved four groups with quite small home ranges in a bamboo forest fragment. In fact, the median home range for *A. seniculus* (considering all data) is 21 ha, only inferior to that of *A. palliata* (30 ha) and the single estimate available for *A. discolor* (57 ha).

The inverse relationship between population density (1b) and home range size and the results for *A. seniculus* are maintained after excluding fragment size from the model. However, this new model shows that the method used to estimate home range has a significant effect on the results. Whereas the Grid Cell method with smaller quadrats (≤50 × 50 m) tends to result in lower home range estimates, the use of larger quadrats (≥100 × 100 m) tends to produce higher values, independent of other factors. There was also a significant interaction between species and method, with studies on *A. palliata* using the Grid Cell method (either ≤50 × 50 or ≥100 × 100 m) estimating larger home ranges, and studies on *A. caraya* using the MCP method (adjusted to the borders of the fragment) estimating smaller ones. This model showed that *A. g. clamitans* uses larger home ranges, independent of other factors, a result that probably derives from the restricted *A. palliata* data set included in the model.

Day range varied from 0 m in *A. pigra* to 2,850 m in *A. palliata* (median = 494 m, mean ± SD = 506 ± 190 m, $n = 72$ groups; Table 9.1). Mean day range at the species level ranged from 320 m in *A. juara* in the Mamirauá Sustainable Development Reserve (only 1 study group; Queiroz 1995) to 928 m (SD = 314 m, $n = 2$ groups) in *A. seniculus* (Fig. 9.2), and it varied among species ($H = 18.84$, $p = 0.004$, $\phi = 6$, $n = 70$; *A. juara* and *A. discolor* were excluded from the analysis because of small sample sizes). A *post-hoc* Dunn test showed that the average day range of *A. g.*

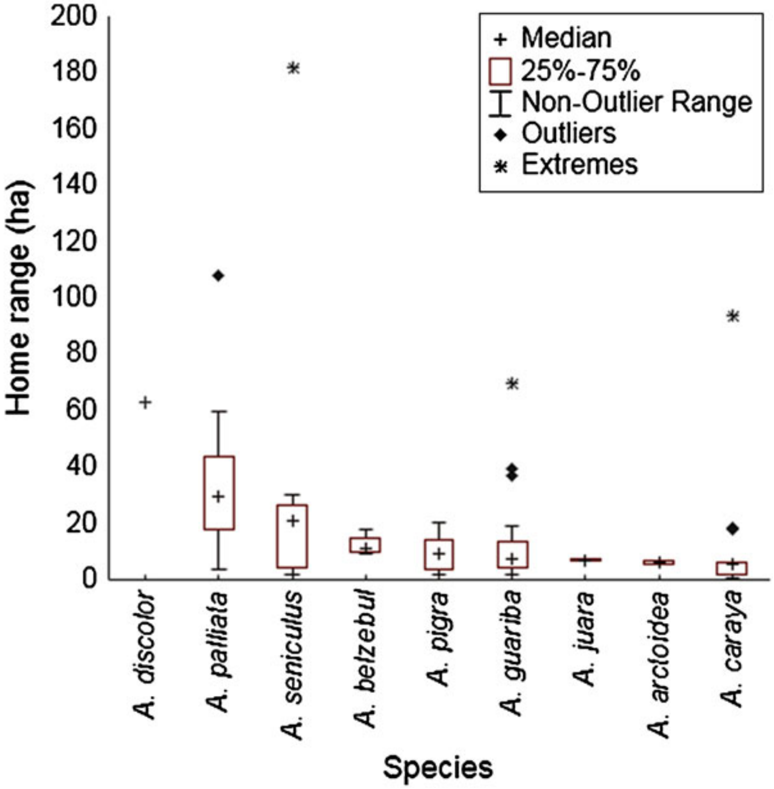

Fig. 9.1 Home range of howler monkey species (data set from Table 22.1)

clamitans (mean ± SD = 620 ± 142 m) is significantly longer than that of *A. palliata* (432 ± 172 m; $Z_{\text{calc}} = 3.34$, $Z_{\text{crit}} = 3.04$, $p < 0.05$).

The model for day range considered only three howler species—*A. g. clamitans*, *A. palliata*, and *A. caraya*—due to missing data for the others. Fragment area (2a) did not show a significant effect on day range, but both population density (2b) and group size (2c) did, independent of other factors. Whereas the first showed a negative relationship with day range, the latter showed a positive relationship. Finally, the degrees of frugivory (2d) and folivory (2e) showed negative relationships with day range, although the first was stronger (Table 9.3). Species identity also had a significant influence on day range: *A. g. clamitans* showed longer day ranges than *A. palliata*, irrespective of other factors, thereby corroborating the results of the nonparametric tests presented above.

Table 9.2 Summary of the effects included in the generalized linear model explaining home range size in howlers (distribution: gamma, link function: log, $n = 51$)

Effect	Level of effect	Estimate ± SE	Wald statistics	*p*
Complete model (AIC = 348.84; ϕ = 33)				
Intercept		1.91344 ± 1.931702	0.98119	0.321906
Fragment size		0 ± 0.000014	0.10850	0.741860
Population density		**−0.15924 ± 0.029479**	**27.17776**	**0.000000**
Group size		−0.06458 ± 0.063438	1.03646	0.308645
Group biomass		0.10893 ± 0.083227	1.71316	0.190576
Species	*A. g. clamitans*	0.86996 ± 0.459839	3.57924	0.058506
	A. palliata	0.88412 ± 1.828717	0.23374	0.628767
	A. pigra	−2.01215 ± 2.105268	0.91349	0.339189
	A. seniculus	**−1.00607 ± 0.472254**	**4.53845**	**0.033142**
	A. arctoidea	0.23217 ± 0.502308	0.21364	0.643928
Method	GC1	−0.04576 ± 2.026468	0.04414	0.833590
	GC2	1.41431 ± 6.228192	0.05157	0.820360
	MCP	0.62634 ± 2.065563	0.09195	0.761716
	DP	−0.01407 ± 0.331608	0.00180	0.966151
Model excluding fragment size (AIC = 346.95; ϕ = 34)				
Intercept		**2.53658 ± 0.400594**	**40.09465**	**0.000000**
Population density		**−0.15939 ± 0.029498**	**29.19520**	**0.000000**
Group size		−0.06211 ± 0.062795	0.97834	0.322609
Group biomass		0.010385 ± 0.081541	1.62220	0.202786
Species	***A. g. clamitans***	**0.93322 ± 0.417365**	**4.99957**	**0.025354**
	A. palliata	0.29521 ± 0.350976	0.70745	0.400291
	A. pigra	−2.38405 ± 1.794564	1.76487	0.184019
	A. seniculus	**−0.92651 ± 0.411093**	**5.07952**	**0.024210**
	A. arctoidea	0.30007 ± 0.460813	0.42403	0.514931
Method	**GC1**	**−1.08896 ± 0.218783**	**24.77422**	**0.000001**
	GC2	**3.45885 ± 0.447073**	**59.85576**	**0.000000**
	MCP	−0.05084 ± 0.196393	0.06701	0.795743
	DP	−0.02969 ± 0.327449	0.00822	0.927765
Species*Method	***A. palliata* × *A. caraya*/ GC1 x MCP ad**	**1.36880 ± 0.258815**	**27.97049**	**0.000000**
	***A. palliata* × *A. caraya*/ GC2 x MCP ad**	**−2.75546 ± 0.522078**	**27.85587**	**0.000000**

Significant effects are in bold

GC1 grid cell (≤50 × 50 m), *GC2* grid cell (≥100 × 100 m), *MCP* minimum convex polygon, *MCP ad* minimum convex polygon adjusted to fragment borders, *DP* digitized polygon

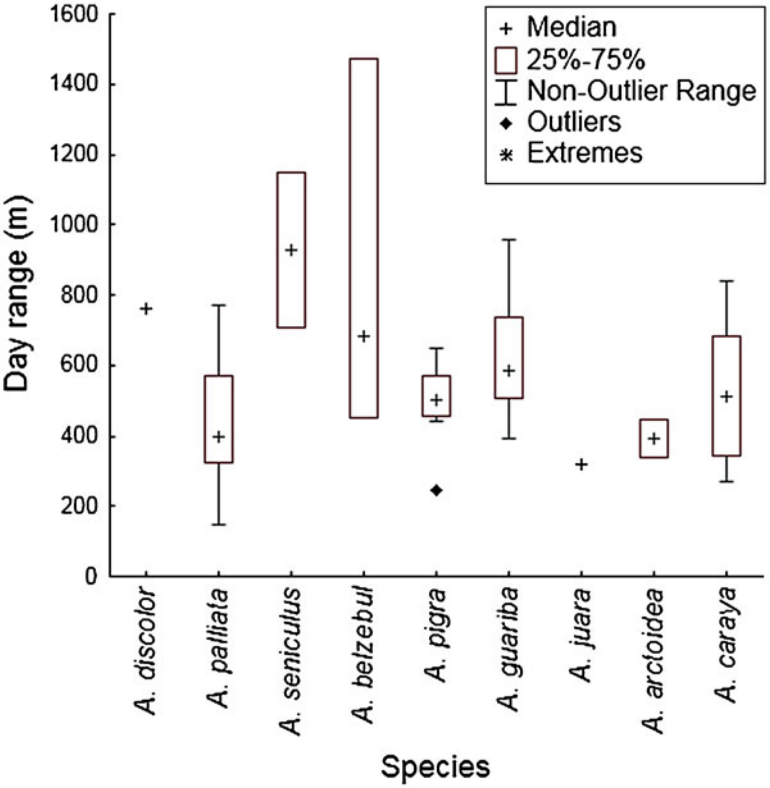

Fig. 9.2 Day range of howler monkey species (data set from Table 22.1)

Table 9.3 Summary of the effects included in the generalized linear model explaining day range length in howlers (distribution: normal, link function: log, $n = 24$, $\phi = 16$, AIC = 312.1)

Effect	Level of effect	Estimate ± SD	Wald statistics	*p*
Intercept		**6.9990 ± 0.57898**	**146.1329**	**0.000000**
Fragment size		0 ± 0.00003	0.3107	0.577281
Population density		**−0.0505 ± 0.01896**	**7.1047**	**0.007688**
Group size		**0.0414 ± 0.01551**	**7.1119**	**0.007657**
% Frugivory		**−0.0142 ± 0.00588**	**5.8128**	**0.015910**
% Folivory		**−0.0123 ± 0.00625**	**3.8861**	**0.048687**
Species	***A. g. clamitans***	**0.3508 ± 0.09040**	**15.0560**	**0.000104**
	A. palliata	**−0.5385 ± 0.14922**	**13.0226**	**0.000308**

Significant effects are in bold

9.1.6 Understanding the Ranging Behavior of Howler Monkeys

Howler population density is an important factor influencing howlers' use of space. In the presence of a high density of conspecific groups howler home ranges are usually smaller (Bravo and Sallenave 2003; Kowalewski 2007; Gómez-Posada and Londoño 2012) than those observed in study sites where howler density is lower (Estrada 1984; Steinmetz 2000; Palacios and Rodríguez 2001; Miranda 2004; Agostini 2009). However, the lack of detailed data on resource availability and distribution at most study sites does not allow to determine whether population density is the proximate cause or just a consequence of habitat carrying capacity and/or shrinking (see the chapter by Behie and Pavelka 2014). In any case, social groups need to use home ranges large enough to fulfill their nutritional requirements for enabling their long-term survival.

On the other hand, the area of forest is not a critical factor, despite the predictable effects of habitat loss at one extreme of the range of habitat availability. The influence of the area of potential habitat available on home range is relaxed because at the other extreme of the range, continuous forests or large forest tracts may be inhabited by groups using either large (Steinmetz 2000; Palacios and Rodríguez 2001; Agostini 2009) or small home ranges (Queiroz 1995; Ostro et al. 1999a; Ludwig 2006; Fortes 2008). The latter situation is often found under high population densities as discussed above. The fact that stable howler groups have been observed occupying small home ranges in fragments smaller than 10 ha (Estrada et al. 1999; Fortes 2008; Guzzo 2009; Muhle 2008), sometimes during many years (Bicca-Marques 1994; Prates 2007; Zunino et al. 2007), highlights their adaptation to conditions of constrained space.

Howlers do not use their home ranges homogeneously by concentrating their activities in core areas; that is, those portions of the home range exploited at a higher frequency than expected by chance. This pattern has been observed irrespective of habitat availability or home range size. For instance, the group of *A. seniculus* studied by Palacios and Rodríguez (2001) that ranged over 182 ha used a core area of ca. 8–9%, a similar proportion to that reported for *A. caraya* in a 2-ha home range by Bicca-Marques (1994). However, the criteria used to define core areas have differed widely among studies (quadrats used ≥10% time records: Ludwig 2006; ≥30% time records: Jardim 1997; Palacios and Rodríguez 2001; quadrats visited in ≥30% of daily routes: Miranda 2004; ≥70% of daily routes: Bicca-Marques 1994; ≥50% kernel density: Agostini 2009). More critical than the actual size of the core area, a description of howlers' use of space shall integrate information on the activities performed at highly used sectors of the home range, the number and spatial arrangement of these areas, the causes of the avoidance or reduced use of others, and the potential costs (including travel) of each ranging strategy.

Core areas may be associated to preferred sleeping sites, as suggested by Chivers (1969) based on a 3-month study of *A. palliata* on Barro Colorado Island, Panama (a single core area of night positions located in the center of the home range), and

Jardim (1997) in her study of *A. belzebul* in the Caxiuanã Biological Station, state of Pará, Brazil (multiple clusters of sleeping trees distributed mainly at the periphery of the home range). Few studies have quantitatively analyzed the spatial distribution of sleeping sites (e.g., Bicca-Marques 1994; Jardim 1997; Bravo 2009). While both groups of *A. caraya* studied by Bravo and Sallenave (2003) used a single sleeping tree in about 50% of the nights, no sleeping site of the group of *A. g. clamitans* studied by Fortes (1999) was used for more than 8% of nights (21 out of 51 sleeping trees were used just once), suggesting contrasting strategies of sleeping site use. The scarcity of the database on sleeping site selection, spatial distribution and use compromises testing hypotheses on the influence of the proximity to feeding sites, parasite or predator avoidance, thermoregulation, or social contact (see Anderson 1998).

Our model showed that population density has an inverse relationship with day range. This is a surprising finding because the need of defending/advertising the home range and its valuable resources against neighboring groups via border patrolling should be expected to increase as the population grows. However, this outcome is compatible with a low level of between-group contest competition for food among howlers (Isbell 1991). Therefore, the positive correlations found between day range and the frequency of group confrontations in *A. caraya* (Bravo and Sallenave 2003; Kowalewski 2007) and *A. palliata* (Hopkins 2008) might be related to contexts of mate monitoring instead of food competition or “territory” defense as stated by Kowalewski and Garber (2010) and Fernández et al. (2013). Comparative studies of the vocal communication, especially the frequency and spatial distribution (core area vs. periphery of the home range) of loud calling sessions, among species and varying contexts of population density, group size and resource availability and distribution, might be particularly insightful for understanding how howler groups cope with the social and ecological pressures of an increasing population density.

The influence of group size on day range is compatible with the contention that larger groups demand more food to satiate their group members and, therefore, may need to travel farther to fulfill their nutritional requirements. There is certainly a trade-off between the benefits of a larger group (e.g., predator protection and information-sharing) and the costs of additional travel or increased within-group competition (Chapman et al. 1995; Chapman and Chapman 2000) for food and/or mating opportunities. In the context of mating competition it is possible that between-group competition plays a critical role in the relationship between group size and day range. According to Kowalewski (2007), adult males cooperate to defend their mating partners during intergroup encounters. Therefore, larger groups may be expected to engage in group confrontations and seek contact with females from neighboring groups more frequently than smaller groups containing fewer males.

The negative relationship between day range and the contribution of fruit to the diet may be a consequence of a preference for exploiting highly productive and/or clumped fruiting sources, in whose vicinity howlers may “camp”, a foraging strategy that challenges the high cost-high reward strategy proposed by Zunino (1986). On the other hand, the negative relationship between folivory and day range corroborates Milton’s (1998) findings that howlers cope well with plant toxins and that they do not need to travel much to avoid an overload of the same secondary metabolites. However, according to Bicca-Marques (2003), there is a positive relationship between day range and diet diversity. Additionally, Fernández et al. (2012) show that the percentage of time (or feeding records) devoted to the consumption of a food item is not a good proxy for the biomass, energy, and nutrients ingested. Consequently, the use of broad categories, such as fruit and leaves, instead of the analysis of the nutritional and energy contents of ingested food items may compromise our interpretation of the actual foraging strategies adopted by howlers.

Finally, home range overlap is an important aspect of howler use of space that has been partially neglected because of logistical difficulties. The collection of accurate data on this variable requires a long-term monitoring of several habituated neighboring groups. However, because most studies have focused on a single social group, overlap has been estimated based on eventual sightings of neighboring groups inside the focal group's home range. Estimates of home range overlap are available in less than one third of the publications listed in Table 9.1 (*A. g. clamitans*: Chiarello 1993; Agostini 2009; *A. palliata*: Williams-Guilén 2003; Hopkins 2008; *A. belzebul*: Jardim 1997; *A. pigra*: Bridgett 2006; Gavazzi et al. 2008; *A. seniculus*: Palacios and Rodríguez 2001; Gómez-Posada and Londoño 2012; *A. caraya*: Bravo and Sallenave 2003; Ludwig 2006; Kowalewski 2007; Agostini 2009). Whereas overlap is nil in forest fragments inhabited by a single group or extremely low or absent in areas with low population densities (e.g., *A. seniculus,* Eastern Colombia: Palacios and Rodríguez 2001), it may be quite high (70%) under high population densities (e.g., *A. caraya*, Brasilera Island, Argentina: Kowalewski 2007).

9.2 Spatial Cognition

Alouatta is one of the most studied Neotropical primate genera in the wild, and the first to have its patterns of use of space described (ca. 80 years ago by C.R. Carpenter). Despite many tens of thousands of observation hours throughout its distribution since the classical monograph published by Carpenter (1934), only a handful of studies have addressed the cognitive challenges that howler monkeys face in navigating within their home ranges. Their small home ranges (often <30 ha), short day ranges (rarely >1,000 m), and cohesive foraging may have contributed to this situation by suggesting that they should face simpler spatial challenges than species ranging over larger areas (Clutton-Brock and Harvey 1977; Milton 1981). However, howlers are constantly challenged by the need to find appropriate food items to compose a nutritionally balanced diet (Righini and Garber 2012), a physiological need that shall be a critical selective force for the evolution of their spatial skills. These challenges exist even when the targeted resources are not fruits or seeds, but new leaves (Estrada 1984; Limeira 1996) or flowers (Fortes 1999; Marques 2001) of important food species, since in most cases these food sources do not present an uniform spatial distribution and their availability varies temporally, requiring howlers to be able to track their occurrence in the forest.

Although it is still unknown the kind of spatial information that howlers perceive, encode, and recall for guiding their movements within the tridimensional canopy milieu and the strategies that they adopt to increase their foraging efficiency, the importance of spatial knowledge to howler navigation can also be assessed by observing the travel patterns of groups confronted with unfamiliar areas, such as translocated groups. In this sense, groups of *A. pigra* showed a more exploratory travel pattern soon after release in a new site by shifting the location of their monthly ranges and exploring a larger number of new areas each month than did established groups (Ostro et al. 1999a, 2000).

Milton (1981) reports that howlers use a goal-directed travel pattern when moving between feeding trees by using specific routes at a higher frequency than expected by chance. She suggests that they rely on (1) “pivotal trees,” a small number of trees that are visited regularly during consecutive days or in the same day, and (2) “arboreal pathways,” travel routes (>100 m in length) that are repeatedly used to travel between “pivotal trees.” These “arboreal pathways” connect food patches and appear to be part of a strategy aimed at minimizing travel, which also allows them to monitor the phenological status of potential feeding trees (Milton 1981, 2000). She also suggests that the small set of “pivotal trees” (often feeding sources) used by mantled howlers during several days “[…] seemed to give the monkeys a base from which they could move out in various directions and search for other resources” (Milton 1980: 103), and that they seem to know when to visit these trees to find the necessary resources (Milton 2000).

Despite Carpenter’s and Milton’s reports, the first studies specifically designed to address the cognitive bases of howler monkey navigation only began to be conducted more than two decades after the publication of Milton’s seminal papers (Milton and May 1976; Milton 1980, 1981, 1993). These studies tested predictions such as (1) howlers minimize (“optimize”) the distance traveled by using straight-line movements to the nearest available tree of a few target species; (2) they monitor the availability of large and/or preferred food sources, and exploit the most productive trees available; (3) they repeatedly use travel pathways that include large trees that provide more food and from where they enjoy enhanced visibility of the surroundings, thereby reducing the need for memory load; and (4) they use these tall (high-visibility) trees where different routes intersect as nodes or decision points, an indication of a topological mental representation (*A. caraya*: Ventura 2004, 2005; Fernández 2008; *A. palliata*: Garber and Jelinek 2006; Hopkins 2008, 2011; *A. g. clamitans*: Pereira 2008).

The use of straight-line routes to the nearest target (feeding or sleeping) tree was partially supported by these studies as discussed below. The circuit index (CI: actual distance traveled/most efficient route distance; Garber and Hannon 1993) is a good proxy for path directedness, and offers a measure of the frequency of use of the shortest route to the next target (Garber and Jelinek 2006; Hopkins 2008; Fernández 2008). The indices recorded by Garber and Jelinek (2006) during 15 days of observation show routes close to linearity, at most 9% longer than the possible most efficient route (CI = 1.05). Possibly because ranging patterns vary temporally in response to changes in food availability, Hopkins (2011) recorded a higher circuit index (CI = 1.37–2.66) for the same species at a different site, whereas the highest amplitude was found for *A. caraya* (CI = 1.05–11.93) in Argentina (Ventura 2004, 2005).

In southern Brazil, brown howlers visited the nearest tree of target food species in 41% of the observations ($n = 160$ trees, 20 days of data collection). However, they used "less-direct" routes (traveled longer distances) when feeding on fruit of *Ficus organensis* by selecting the most productive trees and bypassing less-productive sources of the same species (Pereira 2008). This strategy might be related to a preference for foraging in areas with higher resource availability (trees with larger diameter at breast height), or to the selection of routes crossing areas with higher canopy connectivity (Hopkins 2011). This strategy can also be interpreted as evidence of spatial knowledge because these trees were usually outside the monkeys' potential field of view (Garber 1989; Janson 1998; Cunningham and Janson 2007). Additional evidence of spatial knowledge comes from the ability of howlers to reach the same target feeding and resting sites ("pivotal trees," sensu Milton 1980) from different directions and distances (Garber and Jelinek 2006; Pereira 2008).

Studies have also confirmed that howlers adopt strategies compatible with an efficient monitoring of preferred and most important food sources (Milton 1981, 2000; Garber and Jelinek 2006; Hopkins 2008, 2011; Pereira 2008). Brown howlers traveled farther and visited more trees when feeding on unripe than on ripe fruit of *F. organensis* (Pereira 2008), suggesting that they were keeping track of unripe fruit availability as a way of predicting future ripe fruit production, as suggested by Di Fiore (2003) for woolly monkeys (*Lagothrix lagotricha poeppigii*), and Janmaat et al. (2006) for sooty mangabeys (*Cercocebus atys atys*) and grey-cheeked mangabeys (*Lophocebus albigena johnstoni*). Howlers also usually travel along the same, highly predictable routes (*A. caraya*: Bicca-Marques and Calegaro-Marques 1995; Pereira 2004; Fernández 2008; *A. discolor*: Pinto 2002; *A. g. clamitans*: Limeira 1996; Fortes 1999; Marques 2001; Pereira 2008; *A. palliata*: Garber and Jelinek 2006; Hopkins 2008), an evidence of travel optimization using the available spatial knowledge (route-based spatial representation), that may, on the other hand, increase their vulnerability to some kinds of predators (Quintino and Bicca-Marques 2013). According to Garber and Jelinek (2006), howlers travel significantly shorter distances when reusing the same tree sequences than when selecting new tree sequences and directions.

The more frequent use of a few larger trees that provide wider visibility, especially in the low- and middle-canopy levels (Garber and Jelinek 2006; Pereira 2008), supports the idea that howlers use these trees as decision (or detection) nodes. Current evidence supports the idea that howlers do not need to remember neither the positions of a large number of trees in their home range, nor the availability of food. Remembering a limited number of route segments that lead to nodes, and their distances, is sufficient to allow howlers to monitor a series of potential feeding places. This task requires less cognitive processing than a continuous updating of a mental map that includes several landscape features and their current relationships (Barton 2000; Di Fiore and Suarez 2007). These findings are consistent with the idea of a topological, or route-based, mental representation (sensu Dyer 1991). It is also important to highlight that patterns of howler monkey spatial exploration were very consistent across these studies, despite the fact that they were conducted in areas varying in habitat availability and floristic and structural characteristics (from tropical evergreen to subtropical deciduous forests, and from continuous to gallery forests and forest fragments).

Finally, a recent study examined how age, sex, reproductive status, and dominance rank influence leadership of progressions in two groups of *A. caraya*. According to Fernández et al. (2013), leadership is based on age. Adult black-and-gold howler monkeys lead group progressions. This pattern agrees with previous studies on *A. caraya* (Bicca-Marques and Calegaro-Marques 1997), *A. palliata* (Costello 1991), and other primates (Boinski 1991; Janson and Di Bitetti 1997; Fashing 2001; Barelli et al. 2008), and is believed to be associated with a deficient knowledge of the home range by immature individuals (Janson and van Schaik 1993). However, the observation that *A. caraya* males lead the group in intergroup encounters is also consistent with a male mate defense hypothesis (Fernández et al. 2013). Studies on the ontogeny of ranging behavior and analyses of individual movement patterns across behavioral contexts (e.g., feeding, resting and intergroup encounters) are particularly useful for testing these hypotheses.

9.3 Conclusions and Prospects

Studies on the ranging behavior of howler monkeys are highly biased toward a few taxa (*A. palliata*, *A. pigra*, *A. seniculus*, *A. caraya* and *A. g. clamitans*) and have shown that some patterns are highly conservative among species (such as the short, often <1,000-m long day ranges), whereas others are more variable both within- and between-species (such as the size of the home range). Research on howler spatial cognition is new and has been restricted to three taxa (*A. palliata*, *A. caraya*, and *A. g. clamitans*), thereby limiting our ability to evaluate the influence of species, foraging syndrome, habitat structure, and resource availability among other factors on the strategy adopted by howler groups to navigate within their home range.

Our modeling allowed us to confirm that population density is an important factor influencing howlers' use of space, showing a negative relationship with both home range size and day range length, and that *A. palliata* groups tend to use larger home ranges than the other howlers. Although within-study comparisons of methods for estimating home range have produced similar results as reported above, our model identified significant differences derived from the size of the quadrats chosen for the Grid Cell method as well as significant species*method interactions. These differences in the sensitivity of the methods compromise comparisons and highlight the need of standardization.

Despite the natural increase in sample size from the time of Bicca-Marques's (2003) review to the present study, the difference found in the effect of habitat availability (fragment size) on home range size may have resulted from differences in the statistical methods applied. Whereas the linear regression analysis ran by

Bicca-Marques (2003) may have been driven by the spatial limitation imposed to howlers at the lower extreme of the range of habitat availability, our modeling appears to have been influenced by the fact that howler groups rarely use home ranges >50 ha (indeed, they are often <30 ha) irrespective of the area of habitat available. Therefore, instead of contradictory, these analyses may be highlighting distinct characteristics of the data set.

The expected positive effect of group size on day range was also supported by our model, but the proximate causes of this relationship remain unknown. This finding is compatible with both within- and between-group competition for food or mates, respectively. A detailed mapping of the spatial distribution of potential food sources, including an assessment of the distances between actual feeding and resting sites, together with an accurate monitoring of their phenology within the home ranges of several groups of the same population would be insightful to better interpret the ranging behavior of howler monkeys living under varying scenarios of group size, population density, food availability, and habitat carrying capacity.

The unexpected negative relationships between both the degree of folivory and frugivory with day range found in our model suggest that interpretations based on general assumptions of temporal and spatial availability and quality of gross categories of food (e.g., fruit vs. leaves) are too simplistic. Data on the number of sources of fruit, leaves, flowers, and other food items exploited on a daily basis, and their respective contributions to the diet, are needed to evaluate whether energy balance, nutrient mixing, and/or toxin avoidance play a significant role in the pattern of daily ranging behavior. Unfortunately, only a handful of studies report this kind of data, whose integration with recent approaches of nutritional ecology (Raubenheimer et al. 2009, 2012; Felton et al. 2009) shall be particularly enlightening. It is possible that these negative relationships resulted from the frequently high foraging investment (e.g., >50% of feeding time) of howlers on a few top species (see Bicca-Marques 2003; Chaves and Bicca-Marques 2013). This hypothesis would be supported by data showing that, on a daily basis, diet species richness is inversely related to the difference in the contribution of leaves and fruits, an open issue for future research. Evidence from studies on spatial cognition confirming that howlers present a high degree of fidelity to particular routes, feeding and resting trees and that they tend to favor more productive trees to visit is compatible with this hypothesis.

In sum, despite tens of thousands of observation hours of howler monkeys and the large amount of data amassed on their ecology and behavior as evidenced in our comprehensive review, there are still many gaps in our knowledge of basic aspects of their natural history that compromise our understanding of their pattern of use of space and information on some species and study regions is virtually nill. Future studies focusing on any aspect of the ranging behavior discussed in this chapter that, in addition to the potential causal variables that we have evaluated, also integrate detailed analyses of resource availability (via fine-scale assessments of habitat floristic composition, species density and spatial distribution, phenology, and crop productivity), daily diet species richness, the amount of biomass ingested of each food item and its energy and nutritional value among others will be better equipped to appropriately test hypotheses about the ecological and social causes of the patterns of range use and the cognitive challenges faced by howler monkeys for navigating within their home ranges in order to get access to a balanced diet. A study with this approach conducted simultaneously on multiple neighboring groups in the same interbreeding population will be particularly welcome.

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