Chapter 5
Seed Dispersal by Howler Monkeys: Current Knowledge, Conservation Implications, and Future Directions

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Abstract Primate seed dispersal has been increasingly recognized as having a potentially profound impact on tropical forest regeneration and plant species composition. Confirming and quantifying this impact, however, has proven to be an important challenge. We review the literature on seed dispersal by howler monkeys (*Alouatta* spp.) throughout their geographical range and assess the impact for plant populations and communities. Howler monkeys spend ca. 50 % of their feeding time eating fruits from many plant species and different life forms. For some plant species they are probably the only or primary dispersal agent (e.g., fruits with large seeds and/or with hard indehiscent husks), especially in anthropogenically disturbed forests, where other large-bodied frugivores tend to be absent or are locally extinct. In this regard, howlers contribute to secondary succession, aiding in the restoration of degraded habitats. *Alouatta* spp. swallow most (>90 %) of the seeds they handle, defecating them undamaged. Studies indicate that passage through the howler gut has a positive effect on rates of seed germination. In addition, studies of secondary dispersal indicate that seeds voided in howler dung attract secondary seed dispersers such as rodents and dung beetles. Also, nutrients in the dung may enhance seedling establishment. Although certain components of howler seed dispersal such as seed shadows, post-dispersal seed fate, and seeds/seedlings survival need to be better studied, current information suggests that howler monkeys are effective seed dispersers for many plant species, with important consequences for plant communities and forest regeneration.

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M.M. Kowalewski et al. (eds.), *Howler Monkeys*, Developments in Primatology:
Progress and Prospects, DOI 10.1007/978-1-4939-1960-4_5

Resumen La dispersión de semillas por primates puede tener un gran impacto potencial sobre la regeneración y composición de especies de plantas en bosques tropicales. Sin embargo, la confirmación y cuantificación de dicho impacto ha constituido un importante reto. Nosotros hacemos una revisión de la literatura sobre dispersión de semillas por monos aulladores (*Alouatta* spp.) en su rango de distribución geográfica y evaluamos su impacto sobre las poblaciones y comunidades de plantas. Encontramos que los aulladores dedican ca. 50 % de su tiempo a alimentarse de frutos de muchas especies de plantas y varias formas de vida. Ellos pueden ser los únicos o principales dispersores primarios para algunas especies (por ejemplo, frutos con semillas grandes y/o con exocarpo duro e indehiscente), especialmente en bosques perturbados, donde otros frugívoros de tamaño grande tienden a desaparecer. De hecho, estos primates pueden contribuir a la sucesión secundaria, ayudando a la restauración de hábitats degradados. Ellos tragan la mayoría de las semillas que manipulan, defecándolas sin dañarlas. Usualmente, el paso por el tracto digestivo tiene un efecto positivo en la germinación. Además, las semillas que se encuentran en las heces de monos aulladores pueden ser dispersadas por dispersores secundarios como roedores y escarabajos. Sus heces enriquecen el suelo y pueden favorecer el establecimiento de plántulas. Aunque algunos componentes de este mutualismo, como el destino final de las semillas dispersadas y la supervivencia de semillas/plántulas, necesitan ser mejor estudiados, la información actual sugiere que los monos aulladores son dispersores efectivos para muchas especies de plantas, con importantes consecuencias para las comunidades vegetales y la regeneración de bosques.

Keywords Forest regeneration • Seed-dispersing animals • Seed dispersal effectiveness

5.1 Introduction

More than 60 % and up to 94 % of woody plant species in tropical forests have their seeds dispersed through endozoochory by frugivorous animals. Hence, studying the interactions between frugivores and plants is critical for understanding the dynamics of these ecosystems (Jordano 2000). Frugivory and the consequent dispersal of seeds constitute a key ecological interaction that is mostly mutualistic, and that has important ecological, evolutionary, and conservation implications for both the animal and plant species involved, as well as for the ecosystems in which they occur (Herrera 2002; Schupp et al. 2010).

From a plant's perspective, seed dispersal has three main, non-mutually exclusive, advantages (Howe and Smallwood 1982): (1) escape from areas of high mortality; (2) colonization of suitable sites which occur at random locations; and (3) directed dispersal to suitable sites. The 'escape hypothesis', which was derived from the mechanistic part of the Janzen–Connell hypothesis (Janzen 1970; Connell 1971), predicts that seed/seedling mortality will be higher under the parent plant, due to predators and/or pathogens that act in a density- and/or distance-dependent fashion, resulting in greater recruitment with increasing distance from the parent plant. In turn, according to the ‘colonization hypothesis’, widespread dispersal of seeds may be critical for some species, because it allows the arrival of at least some seeds into favorable sites, whose occurrence is unpredictable in space and time. Finally, according to the ‘directed dispersal hypothesis’, some dispersal vectors, and in particular animal vectors, can promote the arrival of seeds into specific non-random habitats (or microsites), where survival of seeds/seedlings will be predictably higher.

As mentioned above, these and other advantages of seed dispersal are not mutually exclusive, and the relative importance of each is species- and context-dependent (Andresen 2000; Vulinec and Lambert 2009; Chaves et al. 2011). In this regard, the theoretical framework most extensively used to assess the contribution of seed dispersal agents to plant fitness is the ‘Seed Dispersal Effectiveness’ framework (Schupp 1993; Schupp et al. 2010). Dispersal effectiveness is defined in terms of the contribution that dispersal agents make to the reproduction of a given plant species (Schupp et al. 2010). However, seed dispersal not only affects plant demography or the number of saplings present in a given area (e.g., recruitment); it can also play an important role in determining the spatial distribution of individuals in a given population, and it can have important consequences at the plant community level (Schupp et al. 2010; Russo and Chapman 2011). Regarding the latter, seed dispersal not only plays a role in determining the species composition of local plant communities through its effect on individual species, but it will also affect emerging properties such as community structure and diversity (Schupp et al. 2010; Russo and Chapman 2011).

In tropical forests, the most prominent taxa of seed-dispersing frugivores are birds, bats, and primates (Fleming and Kress 2011). While the former two have been the focus of seed dispersal studies for many decades, it has only been during the last two decades that primates have been recognized as important seed dispersers, with an increasing number of evidences from species within the Strepsirrhini and Haplorrhini suborders of primates (Chapman 1995; Lambert and Garber 1998; Koné et al. 2008; Chaves et al. 2011; Russo and Chapman 2011; Stevenson 2011; González-Zamora et al. 2014). This may reflect the fact that although many primates act as seed dispersers, they also act as seed predators. Seed consumption is reported in a large number of primate taxa including *Lagothrix*, *Ateles*, and *Alouatta* (Stevenson et al. 2002). In addition, since larger bodied primates tend to disperse many seeds together in a large fecal clump (Chapman 1989; Russo et al. 2006; González-Zamora et al. 2012, 2014), which may attract fungal pathogens or other seed predators (rodents), post-dispersal survivorship of voided seeds can be low (Howe and Smallwood 1982).

Frugivorous primates can disperse viable seeds of many plant species. However, evidence shows that the effects of seed dispersal on plant populations and communities can be highly variable among and within primate species (see Russo and Chapman 2011 for a thorough review). Primate species also differ in their vulnerability to disturbances such as hunting or habitat loss. While some primate species are highly sensitive, others are known to be particularly resilient (e.g. howler monkeys in the Neotropics; Arroyo-Rodríguez and Dias 2010; Estrada 2014), becoming the main or only seed dispersal agent for many plant species in areas where other frugivores have disappeared (Andresen 2000).

This chapter focuses on seed dispersal by howler monkeys (*Alouatta* spp.) throughout their geographical range. As is the case with primates in general, studies of seed dispersal by howler monkeys have focused on one or a few aspects of the seed dispersal process (e.g., frugivory, seed-handling, gut-passage effects, seed deposition patterns, post-dispersal seed fate, among others; Table 5.1). Thus, clearly establishing the effects of howler monkey seed dispersal on plant populations (demography, spatial distribution), and on plant communities (composition, structure, diversity), has been difficult.

As an attempt to fill these gaps of information, we first assess the effects of seed dispersal by howler monkey on plant populations. To do so, we follow the seed dispersal effectiveness framework by identifying general patterns of the two primary components of effectiveness, i.e., quantity and quality of dispersal. Then, we discuss how seed dispersal by howler monkeys also can affect the spatial distribution of plant individuals in a population. At present, however, we know very little regarding the degree to which seeds dispersed by howlers actually survive the seedling, sapling, and pole stages of development and live to become fruiting and reproductive adults. In the second section, we evaluate the impact that howler monkey seed dispersal may have on plant community properties. Finally, in the last section we draw some conclusions on the roles that howler monkeys may play in forest conservation and restoration. Although this genus represents a radiation of some 12 species (Cortés-Ortiz et al. 2014), this review is focused on 6 howler monkey species due to the lack of data on the remaining species (Table 5.1).

5.2 Implications of Howler Monkey Seed Dispersal for Plant Populations

5.2.1 Seed Dispersal Effectiveness and its Effects on Demography

Seed dispersal effectiveness depends on both the quantity and the quality of seed dispersal (Schupp 1993). Dispersal quantity is simply given by the number of seeds that are dispersed. In turn, the number of dispersed seeds depends on the number of visits to the plant by a disperser and the number of seeds swallowed per visit. The quality component is given by the probability that a dispersed seed germinates and the developing sapling survives to become a reproductive adult. The quality of seed dispersal is determined by two sub-components: the quality of the treatment given to the seed in the animal's mouth/gut, and the quality of seed deposition (Schupp 1993). This latter is influenced by primary dispersal, as well as in many cases secondary dispersal.

Table 5.1 Aspects of seed dispersal by howler monkeys (*Alouatta* spp.) studied throughout their geographic range in both continuous forest (CF) and forest fragments (FF). References are indicated inside parentheses

	A. caraya		*A. fusca*	*A. guariba*		*A. palliata*		*A. pigra*		*A. seniculus*		*A. puruensis*	*A. macconnelli*
Aspects	CF	FF	CF	CF	FF	CF	FF	CF	FF	CF	FF	CF	CF
Frugivory [a]	–	Argentina (4[b], 51[b])	–	Brazil (49)	–	Costa Rica (13) Mexico (15, 16, 22)	–	Guatemala (25) Mexico (22, 28)	Mexico (28)	Colombia (33, 35, 48)	Colombia (50)	Peru (47)	Brazil (29) French Guiana (38, 39, 41, 44)
Seeds in feces	Brazil (7)	Argentina (4[b])	–	Brazil (11)	–	Costa Rica (13, 14) Mexico (15, 16, 22)	Mexico (23)	Guatemala (25) Mexico (22, 28)	Mexico (28)	Colombia (33, 34, 35)	Colombia (36, 37)	Peru (47)	Brazil (29, 30, 31, 32) French Guiana (40, 42, 43, 44, 45)
Gut passage time	–	Argentina (1)	–	–	–	Costa Rica (14) Mexico (15, 16, 18, 19)	Mexico (18, 19)	–	–	Colombia (33, 34)	–	–	French Guiana (40)
Gut passage effect on seed germination	–	Argentina (1, 3, 5[b])	Brazil (8, 9, 10)	Brazil (11)	Brazil (12)	Mexico (15, 17, 18, 19)	Mexico (17, 18, 19, 21)	Mexico (27, 28)	Mexico (27, 28)	Colombia (34)	–	–	Brazil (30) French Guiana (40, 44)
Ranging patterns[a]	–	Argentina (5[b])	–	–	–	Mexico (15, 17, 18, 19, 22)	Mexico (17, 18, 19)	Mexico (22)	Belize (24)	Colombia (33, 35, 48)	–	–	Brazil (29) French Guiana (38, 39, 40, 41)

(continued)

Table 5.1 (continued)

Aspects	*A. caraya*		*A. fusca*	*A. guariba*		*A. palliata*		*A. pigra*		*A. seniculus*		*A. puruensis*	*A. macconnelli*
	CF	FF	CF	CF	FF	CF	FF	CF	FF	CF	FF	CF	CF
Defecation pattern	Brazil (7)	Argentina (1, 3, 5[b])	–	Brazil (11)	–	Costa Rica (14)	Mexico (23)	Guatemala (26)	–	Colombia (35, 33)	–	Peru (47)	Brazil (31) French Guiana (40, 41, 43, 45, 46)
Seed dispersal distance	–	Argentina (1, 3, 5[b])	–	Brazil (11)	–	Mexico (15, 16, 18, 19)	Mexico (18, 19)	–	–	Colombia (33, 35)	–	–	French Guiana (40)
Post-dispersal seed fate	–	Argentina (2)	–	–	–	Costa Rica (13, 14) Mexico (16)	Mexico (20)	Guatemala (25, 26)	–	–	Colombia (36, 37)	Peru (47)	Brazil (30, 31, 32) French Guiana (42, 43, 44, 45)
Seedling/ sapling recruitment	–	Argentina (6[b])	–	–	–	Mexico (15)	Mexico (23)	Mexico (27, 28)	Belize (24) Mexico (27, 28)	–	–	–	Brazil (32) French Guiana (41)

References: (1) Bravo et al. (1995), (2) Bravo and Zunino (1998), (3) Bravo and Zunino (2000), (4) Bravo (2008), (5) Bravo (2009), (6) Bravo (2012b), (7) Moura and McConkey (2007), (8) de Figueiredo (1993), (9) Pedroni and Sanchez (1997), (10) De Figueiredo and Longatti (1997), (11) Martins (2006), (12) Graeff et al. (2007), (13) Chapman (1989), (14) Wehncke et al. (2004), (15) Estrada and Coates-Estrada (1984), (16) Estrada and Coates-Estrada (1991), (17) Serio-Silva and Rico-Gray (2002a), (18) Serio-Silva and Rico-Gray (2002b), (19) Serio-Silva and Rico-Gray (2003), (20) Martinez-Mota et al. Martínez-Mota et al. (2004), (21) Righini (2004), (22) Amato and Estrada (2010), (23) Anzures-Dadda et al. (2011), (24) Marsh and Loiselle (2003), (25) Ponce (2004), (26) Ponce et al. (2006), (27) Gonzalez-Di Pierro et al. (2011), (28) González-Di Pierro (2011), (29) Santamaría (1999), (30) Andresen (2001), (31) Andresen (2002a), (32) Andresen and Levey (2004), (33) Yumoto et al. (1999), (34) Stevenson et al. (2002), (35) Giraldo et al. (2007), (36) Santos-Heredia et al. (2010), (37) Santos-Heredia et al. (2011), (38) Julliot and Sabatier (1993); (39) Julliot 1996av (40) Julliot 1996b, (41) Julliot 1997, (42) Feer (1999), (43) Feer et al. (2001), (44) Feer and Forget (2002), (45) Pouvelle et al. (2009), (46) Ratiarison and Forget (2011), (47) Andresen (1999, (48) Stevenson et al. (2000), (49) Martins (2008), (50) Palma et al. (2011), (51) Bravo (2012a)

–: Unavailable data

[a] We only included in this review those studies focusing on howler monkey seed dispersal. Consequently the lists of studies addressing frugivory and ranging patterns, presented here, are not comprehensive. For additional information on these aspects please refer to other chapters in this volume

[b] Study carried out on an island

5.2.1.1 Quantity of Seed Dispersal

Considering that the number of visits to a particular feeding site is directly related to the abundance of the dispersers, their dietary preferences, and the reliability of visitation (Schupp 1993), howler monkeys can contribute notably to this component of seed dispersal effectiveness. First, because of their high population densities (densities vary widely, but values of up to 283 ind/km^2 have been reported) (reviewed in IUCN 2012), howler monkeys constitute one of the most common vertebrate species in many Neotropical forests (Peres 1997; Garber et al. 2006). Second, although howler monkeys have been typically considered the most folivorous of Neotropical primates, they spend approximately half of their feeding time consuming ripe fruits when this resource is available (reviewed by Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; see also Dias and Rangel-Negrin 2014), generally being 'as frugivorous as possible and as folivorous as necessary' (Silver et al. 1998). Finally, howler monkeys spend most of their time feeding on the fruits of a small number of plant families (e.g. Moreaceae, Fabaceae, Lauraceae and Sapotaceae; Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Dias and Rangel-Negrin 2014). These species are consistently used year after year (e.g. Estrada and Coates-Estrada 1984), such that howler monkeys can be considered highly reliable seed dispersers for these plant taxa. Therefore, these evidences indicate that howlers are able to disperse very large quantities of seeds.

The number of seeds dispersed per visit depends on the number of seeds handled and swallowed per visit and the probability of dispersing a handled seed (Schupp 1993). In general, howler monkeys disperse, through defecation, most of the seeds they handle. Also, there is a trend showing that, in general, the larger the frugivorous animal, the higher the amount of fruits (and seeds) it can handle, and the larger the size of fruits/seeds it is able to swallow (e.g., Cramer et al. 2007). However, some important exceptions have been published (e.g., tamarin monkeys: Lambert and Garber 1998).

Studies indicate that howlers disperse large numbers of seeds from both small-seeded species and from large-seeded (>10 mm) plant species (Tables 5.2 and 5.3). For example, Andresen (2002a) found that up to 560 seeds >3 mm long can be found in a defecation sample of *A. macconnelli* in Brazil, although 20 % of the defecation samples with seeds had less than 30 seeds. Similarly, Giraldo et al. (2007) analyzed 60 fecal samples of *A. seniculus* in Colombia, finding 290,174 seeds (1–33 mm long), of which 99.9 % belonged to three small-seeded light-demanding tree species (*Ficus* spp., *Cecropia telealba*, and *Miconia acuminifera*). Martins (2006) assessed seeds larger than 2 mm in length and reported an average of 18 seeds (range: 1–97 seeds) per fecal sample (from 1 or 2 tree species) in 147 fecal samples of *A. guariba* in a semideciduous forest in Brazil. In Argentina, one *A. caraya* group can remove up to 1,070 fruits from a tree of *Ocotea diospyrifolia* (Lauraceae) in a day (Bravo 2012a). *Ocotea diospyrifolia* seeds are 13.2 mm long (7 mm in diameter) and the howlers were reported to swallow 100 % of removed seeds.

The ability to swallow large seeds (up to 4.6 cm length; Table 5.2) that are unlikely to be swallowed by smaller frugivorous animals makes the dispersal services offered

Table 5.2 Ranging pattern and gut passage time (GPT) of howler monkeys (*Alouatta* spp.), and characteristics of seeds in monkeys' feces

Howler species and references[a]	Ranging pattern[b]		GPT (hour)	Characteristics of seeds in monkeys' feces[c]			
	DR (m)	HR (ha)		No. spp. (*n*)	Seed length (cm)	SDD (m)	% FWS (*n*)
A. caraya							
1	–	–	24	–	–	5–290	–
3	–	–	–	–	–	20–1,200	–
4	–	–	–	–	0.9–1.4	–	–
5	500–600	–	–	–	–	0–360	–
7	–	–	–	19 (19)	0.6–1.9	–	–
A. fusca							
9	–	–	–	–	1.5	–	–
A. guariba							
11	–	–	19	14 (147)	–	> 100	45 (66)
A. macconnelli							
29	688	21	–	12 (103)	1.1–2.2	–	80 (103)
30	–	–	–	–	1.8	–	–
31	–	–	–	137 (263)	1–3.3	–	9–61 (263)
32	–	–	–	–	0.4–2.7	–	–
38, 39, 40, 41	–	45	35	86 (236)	<0.1–4	0–550	–
42	–	–	–	47 (100)	up to 4.6	–	–
43, 44	–	–	–	–	2.5	–	–
45	–	–	–	37 (–)	–	–	–
46	–	–	–	–	–	–	–
A. palliata							
13	–	–	–	12 (53)	<0.1–2.5	–	15 (53)
14	–	–	16–25	8 (–)	<0.1–2.4	–	46 (68)
15	10–893	60	18	15 (250)	<0.1–3.6	10–811	–
16	–	–	18–20	28 (–)	<0.1–3	10–1,000	–
17, 18, 19	–	10–75	20–30	–	–	65.7–217 means	–
22	127 (±66)	6	–	31 (167)	4	–	–
23	–	–	–	13 (–)	0.4–3.3	–	–
A. pigra							
24	–	1–4	–	–	–	–	–
25, 26	–	–	–	2 (–)	0.1–1.5	–	–
22	202 (±149)	33	–	13 (156)	2.1	–	–
27, 28	–	–	–	8 (–)	1–3	–	–
A. s. puruensis							
47	–	–	–	14 (27)	–	–	21 (27)

(continued)

Table 5.2 (continued)

Howler species and references[a]	Ranging pattern[b]		GPT (hour)	Characteristics of seeds in monkeys' feces[c]			
	DR (m)	HR (ha)		No. spp. (*n*)	Seed length (cm)	SDD (m)	% FWS (*n*)
A. seniculus							
33	560–1,660	17	19–20	8 (–)	0.8–2.1	up to 1,875	0.65 (153)
34, 48	633 (±261)	79	35	80 (–)	<0.1–3.2	–	–
35	554	8–14	–	9–13 (60)	<0.1–3.4	116 (±92)	–
36	–	–	–	–	0.68	–	–
37	–	–	–	–	0.8–1.4	–	–

[a] References are the same as in Table 5.1

[b] Day range (DR) and home range (HR)

[c] Number of species (no. spp.) in *n* fecal samples, seed length, seed dispersal distances (SDD) and percentage of *n* fecal samples without seeds (%FWS)

– unavailable data

by howler monkeys particularly relevant for large-seeded plants (Julliot 1996a; Andresen 2002a; Bravo 2009; Anzures-Dadda et al. 2011). For example, 83 % of the large-seeded fruit species (i.e., 5–25 mm in length) in the Paraná flooded forest (e.g., Lauraceae species) are dispersed by *A. caraya* (Bravo 2009). Also, genera such as *Garcinia* and *Inga* and many Sapotaceae species have seeds >3 cm long and are commonly found in howler monkeys' defecations (Table 5.3). Ramos-Obregon (2007) found that howler monkeys disperse a larger biomass of seeds >4 mm (in width) than the smaller sympatric brown capuchins, and that the mass of seeds dispersed per fecal sample was also higher (12.1 g vs. 1.3 g). In addition, she found that adult howler monkeys defecated a larger biomass of seeds than juveniles (mean adult female: 15 g/sample, adult male: 12, and juvenile: 7), consistent with the idea that body size can limit seed dispersal abilities within a primate species (Stevenson et al. 2005). Given that juveniles, in general, eat the same species with the adults, this difference between age classes can be explained by higher seed spitting rates in juveniles than in adults.

Plant species with indehiscent hard-husked fruits also tend to have a limited assemblage of dispersers. This is due to the fact that small bats and avian frugivores have limited handling abilities to open protected fruits in comparison with primates and other mammals (Janson 1983). For such plant species, howler monkeys and non-flying mammals with biting and manipulative abilities will likely play a very important role in seed dispersal (Andresen 2000). This is again the case for most species in the Sapotaceae family, which are very diverse and dominant in the forests of the Guiana Shield and in Central Amazonia and are frequently dispersed by Guianan red howler monkeys (*A. macconnelli*; Julliot 1996b; Andresen 2002a). For example, during a 2-years period *A. macconnelli* in Brazil defecated seeds from 47 species of Sapotaceae with large seeds (average size ± SD: 19.6 ± 0.7 mm in length, and 11.2 ± 0.4 mm width; Andresen 2002a). Other species with hard indehiscent

Table 5.3 Plant taxa dispersed by howler monkeys (*Alouatta* spp.) throughout their geographic range[a]

Family	Species[b]	Life form	Howler species[c]	References [d]
Anacardiaceae	*Spondias* spp. (>2)	Tree	Apa, Api, Ase	13–15, 24, 34
	Tapirira peckoltiana	Tree	Ama	40
Annonaceae	*Duguetia* sp.	Tree	Ama	42
	Rollinia edulis	Tree	Ase	36
Apocynaceae	*Parahancornia fasciculata*	Tree	Ama	40–42
	Stemmadenia obovata	Tree	Apa	14
Aralicaceae	*Dendropanax* spp. (3)	Tree	Api, Ase	22, 34
	Schefflera paraensis	Tree	Ama	42
Arecaceae	*Iriartea deltoidea*	Palm	Ase	34
	Oenocarpus bataua	Palm	Ase	34
	Syagrus sancona	Palm	Ase	34
Boraginaceae	*Cordia* spp. (3)	Tree	Agu, Apa, Api	11, 14, 24
Bromeliaceae	*Bromelia plumieri*	Epyphite	Aca	7
Burseraceae	*Bursera simaruba*	Tree	Apa	13, 15
	Protium spp. (4)	Tree	Ase	33, 34
	Tetragastris sp.	Tree	Ama	42
Cannabaceae	*Celtis* spp. (2)	Tree	Agu, Ase	11, 34
Celastraceae	*Salacia* cf. *cordata*	Tree	Ama	40
Chrysobalanaceae	*Chrysobalanus icaco*	Shrub	Api	24
	Hirtella racemosa	Tree	Apa	13
Clusiaceae	*Garcinia* sp.	Tree	Ase	35
Dilleniaceae	*Doliocarpus* sp.	Liana	Ama	40, 42
Erythroxylaceae	*Erythroxylum* sp.	Tree	Aca	7
Fabaceae	*Cynometra retusa*	Tree	Apa, Api	22
	Dialium guianense	Tree	Apa	15
	Geoffroea striata	Tree	Aca	5
	Inga spp. (7)	Tree	Api, Ase	22, 24, 34
	Pithecelobium lanceolatum	Tree	Api	24
	Samanea saman	Tree	Apa	14
	Swartzia arborescens	Tree	Ase	34
Icacinaceae	*Dendrobangia boliviana*	Tree	Ama	40
Lamiaceae	*Vitex* sp.	Liana	Aca	7
Lauraceae	*Nectandra* spp. (3)	Tree	Aca, Apa	3, 5, 15
	Ocotea spp. (4)	Tree	Aca, Api	2, 4–5, 7, 22
Lecythidaceae	*Gustavia hexapétala*	Tree	Ase	34
Malpighiaceae	*Byrsonima gardneri*	Tree	Aca	7
Malvaceae	*Belotia mexicana*	Tree	Apa	15
	Guazuma ulmifolia	Tree	Api	24

(continued)

Table 5.3 (continued)

Family	Species[b]	Life form	Howler species[c]	References [d]
Melastomataceae	*Miconia* spp. (>2)	Tree	Aca, Api, Ase	7, 24, 35
Meliaceae	*Guarea* sp.	Tree	Apa	15
	Trichilia pleeana	Tree	Ase	34
Moraceae	*Bagasa guianensis*	Tree	Ama	40
	Brosimum spp. (4)	Tree	Aca, Apa, Api, Ase, Apu	7, 14–15, 22, 34, 47
	Castilla ulei	Tree	Ase	33, 34
	Clarisia racemosa	Tree	Ase, Apu	37, 47
	Ficus spp. (>22)	Tree	Aca, Apa, Api, Ase, Apu	1–3, 7, 13–14, 17–18, 20–21, 24, 26, 33–35, 47
	Maclura tinctoria	Tree	Apa	14
	Perebea spp. (2)	Tree	Ase	33, 34
	Poulsenia armata	Tree	Apa	15, 22
	Pseudolmedia spp. (4)	Tree	Apa, Api, Ase	15, 22, 33–34, 37
	Trophis racemosa	Tree	Api	24
Muntingiaceae	*Muntingia calabura*	Tree	Apa	13
Myristicaceae	*Virola* spp. (2)	Tree	Ama, Apu	41, 47
Myrtaceae	*Eugenia* spp. (3)	Tree	Aca, Agu	4, 5, 7, 11
	Psidium guajava	Tree	Aca	5
	Syzygium spp. (2)	Tree	Api	24
Olacaceae	*Minquartia guianensis*	Tree	Ama	41
Phytolaccaceae	*Phytolacca dioica*	Tree	Aca	3
	Trichostigma octandra	Liana	Api, Apu	22, 47
Polygalaceae	*Diclidanthera* sp.	Liana	Agu	11
	Coccoloba spp. (5)	Tree	Api, Ase	24, 33, 34
Primulaceae	*Cybianthus* sp.	Shrub	Aca	7
Quiinaceae	*Quiina obovata*	Shrub	Ama	41
Rhamnaceae	*Zizyphus* sp.	Tree	Aca	7
Rubiaceae	*Alibertia* sp.	Tree	Ase	34
	Genipa americana	Tree	Apa, Ase	13, 34
	Morinda panamensis	Tree	Api	24
	Psychotria carthagenensis	Tree	Aca	5
Salicaceae	*Banara arguta*	Tree	Aca	4, 5
	Zuelania guidonia	Tree	Apa	13
Sapindaceae	*Allophylus mollis*	Tree	Ase	35
	Cupania guatemalensis	Tree	Apa	13
	Paullinia spp. (2)	Liana	Aca	3, 5
	Talisia sp.	Tree	Ama	40

(continued)

Table 5.3 (continued)

Family	Species[b]	Life form	Howler species[c]	References [d]
Sapotaceae	*Chrysophyllum* spp. (2)	Tree	Ama, Apu	40–42, 44, 47
	Sideroxylon portoricense	Tree	Apa	15
	Ecclinusa lanceolata	Tree	Ama	40
	Manilkara spp. (2)	Tree	Apa	13, 15
	Micropholis spp. (5)	Tree	Ama, Apu	30, 40, 42, 47
	Pouteria spp. (>10)	Tree	Aca, Apa, Api, Ama	5, 15, 26, 40–42
Simaroubaceae	*Simarouba* spp. (2)	Tree	Api, Ase	24, 34
Smilacaceae	*Smilax* sp.	Vine	Apa	22
Solanaceae	*Solanum* sp.	Liana	Ama	42
Ulmaceae	*Ampelocera hottlei*	Tree	Apa, Api	15, 27
Urticaceae	*Cecropia* spp. (8)	Tree	Aca, Apa, Api, Ase, Ama	5, 7, 15, 22, 33, 34–35, 40
	Coussapoa spp. (3)	Tree	Apa, Ase, Apu	22, 34, 47
	Pourouma spp. (3)	Tree	Ase	33, 34
	Urera aurantiaca	Shrub	Aca	5
Violaceae	*Leonia glycycarpa*	Tree	Ase	34
Vitaceae	*Cissus* sp.	Liana	Aca, Api	5, 22

[a] Plant nomenclature followed the Missouri Botanical Garden nomenclatural update data base (http://mobot.org/W3T/search/vast.html). We only include plant taxa with seeds swallowed and/or defecated by howler monkeys for studies listed in Table 5.1. The species list, however, is not complete, as several papers only report the total number of species swallowed and/or defecated by howler monkeys, and not the complete species list

[b] For the plant genera with several species we only indicate the genus (and the number of species in parenthesis). The symbol '>' indicates that the number of species could be higher, as one or more studies report taxa identified only to genus level (e.g. *Ficus* sp.)

[c] Species of howler monkeys: Aca: *Alouatta caraya*; Agu: *A. guariba*; Ama: *A. macconnelli*; Apa: *A. palliata*; Api: *A. pigra*; Apu: *A. s. puruensis*; Ase: *A. seniculus*

[d] References are the same as in Table 5.1

husks and for which howler monkeys provide important dispersal services include *Dialium guianense*, *Inga* spp., *Genipa americana*, and *Gustavia hexapetala* (Table 5.3).

The number of seeds dispersed per visit also depends on the length of a visit, and howler monkeys tend to have long feeding bouts. For instance, the time fruit feeding in a single tree by a group of *A. palliata* in Los Tuxtlas, Mexico, can reach 40 min (mean ± SD, 19.0 ± 7.0 min; Dunn et al. 2012), whereas *A. caraya* in Argentina can spend up to 2 h feeding on fruit in a single laurel tree (*Ocotea diospyrifolia*; Bravo 2012a). In fact, *A. seniculus* in Colombia spends on average 14 min (±15.6, SD) per tree feeding on fruits, which represent longer feeding bouts than those reported for three other sympatric primates (mean bout length: *Cebus apella*: 8.4 ± 10.3 min, *Lagothrix lagothricha*: 7.8 ± 9.3 min, and *Ateles belzebuth*: 6.9 ± 9.0 min; Stevenson et al. 1998). As argued by these authors, the stronger group cohesion in howler monkeys compared to *Ateles* and *Lagothrix* results in larger feeding subgroup sizes and longer feeding bouts (more fruits consumed per group feeding bout). This stable grouping pattern can result in howlers exploiting larger food patches (to accommodate all group members; group size in *A. seniculus* in Colombia averaged 9.3 ± 0.9 individuals), allowing individuals to spend more time feeding on each food patch (Stevenson et al. 1998) and minimizing thus the energy cost related to traveling between food patches.

5.2.1.2 Quality of Seed Dispersal

Seed treatment in the mouth and gut determines both the proportion of seeds destroyed (due to mastication and/or digestion) and the germination ability (percentage of seeds that are not destroyed) (Schupp 1993; Schupp et al. 2010). In general, researchers have considered howler monkeys as high quality seed dispersers because, despite a long transit time (18–35 h), seeds remain viable after passing through their gut (e.g., Milton 1980; Estrada and Coates-Estrada 1984; de Figueiredo 1993; Julliot 1996a; Santamaría 1999; Gonzalez-Di Pierro et al. 2011). Howler monkeys generally swallow seeds and rarely chew or spit out seeds (e.g., *A. caraya*: Bravo 2009; *A. palliata*: Wehncke et al. 2004). Occasionally, however, howler monkeys include unripe fruits in their diet, and in these cases they act as seed predators by selecting seeds before they are fully mature and capable of germination. In some cases these seeds are digested in the gut (Giraldo et al. 2007). However, several studies of howlers indicate that individuals show a marked preference for consuming mature fruits (80–90 % of fruit feeding time: Estrada and Coates-Estrada 1984, 1991; Giraldo et al. 2007; Amato and Estrada 2010), which implies a reduced likelihood of seed predation.

Gut passage can also positively affect germination and early seedling establishment through at least two mechanisms (Traveset et al. 2007): (1) scarification (i.e., removal or thinning of the seed coat); and (2) deinhibition (i.e., separation of the seeds from the pulp). The scarification process increases the permeability of seeds, allowing the exchange of gases and water, which in turn triggers germination in many seed species (Traveset et al. 2007). It has been reported that gut passage in howler monkeys can have a positive, neutral, or negative effect on germination (Table 5.4). On the other hand, the impact of deinhibition has not been assessed for seeds dispersed by howler monkeys, and studies focusing on how howlers treat, process, and void seeds are needed to gain a better understanding of all possible implications of gut passage on seed germination. It is important to note that deinhibition occurs not only for defecated seeds, but also for seeds that are spat or dropped. Therefore, although howler monkeys disperse most seeds through defecation, in future studies it would be very useful to analyze the effect of pulp removal on seed fate, not only for defecated seeds, but also for spat and dropped seeds.

Another positive effect of gut passage on seed survival and germination is the control of insect larvae present in the ingested fruits/seeds. For example, the passage of seeds through the gut of howler monkeys can kill insect larvae that infest seeds of *Ocotea diospyrifolia* (Lauraceae), increasing the probability of seed survival and germination (Bravo 2008). In other cases, larvae are not killed, and seed dispersal by monkeys actually favors insect dispersal (Hernández 2011). Both phenomena are probably widespread, but have so far received little attention. Finally, gut passage may also have effects beyond germination, i.e., on seedling survival and growth; however, the available evidence on this topic is very limited (e.g., Gonzalez-Di Pierro et al. 2011; Table 5.1).

While the quality of seed treatment is relatively easy to quantify and has thus received more attention (Tables 5.1 and 5.4), the quality of seed deposition is much harder to evaluate, as it requires an assessment of seed and seedling fate through the primary and secondary post-dispersal and post-germination phases (Schupp et al. 2010). Seed deposition quality can be affected by many variables. Some of these can be directly linked to characteristics of the primary disperser (e.g., howlers), while others cannot. Variables affecting deposition quality, which can be directly associated to the primary disperser, include movement, foraging, and defecation patterns (whether seeds are voided singly or in large clumps), diet, social structure, and frugivore gut size and food passage rates (Schupp 1993). These aspects of animal behavior will determine many specific circumstances of seed deposition which are known to affect seed fate, such as: (1) presence/absence of dung surrounding the seeds; (2) amount and type of dung surrounding the seeds; (3) amount of seeds and number of seed species dispersed together; and (4) dispersal distance with respect to conspecific fruiting trees (Andresen 1999). Most of these variables will affect seed/seedling fate indirectly, i.e., through the effect they have on the behavior of secondary seed dispersers and/or predators and fungal pathogens, which in turn will determine what happens to a seed or seedling. These biotic post-dispersal agents will be discussed separately in the next section.

In terms of dispersal distances, howler monkeys are able to disperse seeds far from the parent plant due to their high daily travel distances (mean = 497 m, range = 50–1,564 m: Bicca-Marques 2003; also see Table 5.2) and long retention times (up to 35 h; Table 5.2). Evidence indicates that seeds dispersed by howler monkeys are deposited at distances of up to 1,000 m or more from the parent plant (Table 5.2). Nevertheless, howler monkeys may also defecate or drop fruits underneath conspecific fruiting trees; a reason why some authors have considered these primates as low-quality dispersers (e.g., Howe 1980).

In fact, due to their cohesive social structure, and their digestive physiology, howler monkeys spend most of their time resting in large sleeping trees [mean = 64.2 %, range = 8–97 %; from Cristóbal-Azkarate and Arroyo-Rodríguez (2007) and Bicca-Marques (2003) reviews]. After the resting period, and before moving to another tree, all or most of the individuals in the group usually defecate simultaneously (this occurs 2–4 times in a 24 h period; *A. palliata*: Wehncke et al. 2004; *A. s. puruensis*: Andresen 1999; *A. seniculus*: Giraldo et al. 2007). This behavior results in high amounts of feces and seeds being deposited in latrines located under the sleeping trees (e.g., Chapman 1989; Julliot 1996a, 1997; Andresen 2002a; Wehncke et al. 2004; Pouvelle et al. 2009, Table 5.2). For example, Wehncke et al. (2004) report that 67 % of *A. palliata* feces in a tropical dry forest in Costa

Table 5.4 Gut passage net effect on seed germination rates (i.e., percentage of defecated vs. control seeds that germinated in trials) and latency period of seeds[a]

Howler species	Country	Germination rate			Latency period			Germination trials[b]	Refs.[c]
		Higher	Similar	Lower	Shorter	Similar	Longer		
A. caraya	Argentina	1	0	0	1	0	0	Lab	1
A. caraya	Argentina	1	2	0	0	3	0	–	3
A. caraya	Argentina	0	3	1	3	1	0	Lab	5
A. fusca	Brazil	1	0	0	–	–	–	Lab	8
A. fusca	Brazil	1	0	0	–	–	–	Lab	9
A. fusca	Brazil	0	0	1	–	–	–	–	10
A. guariba	Brazil	3	1	1	0	3	1	Lab	11
A. guariba	Brazil	0	0	1	0	0	1	Lab	12
A. palliata	Mexico	5	1	0	3	2	0	Mix	15
A. palliata	Mexico	1	0	0	–	–	–	Field & Lab	17,18,19
A. palliata	Mexico	0	1	0	–	–	–	Field & Lab	21
A. pigra	Mexico	1[e]	0	0	1	0	0	Field	27, 28
A. macconnelli	Brazil	0	1	0	–	–	–	Field	30
A. macconnelli	French Guiana	4	7	6	2	12	1	Mix	40
A. macconnelli	French Guiana	0	1	0	–	–	–	Field	44
A. seniculus	Colombia	4	2	1	4	2	0	Mix	34
	Total percentages[d]	42 %	37 %	21 %	35 %	58 %	8 %		

[a] Cells indicate the number of plant species that showed a significant effect (positive or negative) and those that showed no effect of gut passage on germination rate and latency period

[b] Germination trials were performed in the field (Field), in the laboratory (Lab), and/or in the field by controlling some variables such as light, water and/or soil (Mix)

[c] References are the same as in Table 5.1

[d] Percentages are based on the number of plant species used for testing germination rates (52 species) and latency periods (40 species)

[e] Although the cumulative germination percentage of *Ampelocera hottlei* seeds after the 60 days trial was significantly higher for control seeds in fragments, in continuous forest this percentage was higher for ingested seeds

–unavailable data

Rica are deposited under sleeping trees. Similar percentages have been reported for *A. caraya* in Argentina (65 %, Bravo 2009). Larger percentages have been reported, but these are usually related to howler monkeys living in smaller habitat patches (e.g., 90 % of *A. caraya* feces are deposited in latrines in a small tropical dry forest patch in Argentina; Bravo and Zunino 2000).

Despite this large aggregation of feces and seeds under sleeping trees and/or underneath conspecific fruiting trees, howler monkeys can also disperse a substantial fraction (33–35 %) of seeds in individual scats distributed across the forest (e.g., scattered pattern; Wehncke et al. 2004; Bravo 2009). Furthermore, during periods in which howler monkeys are eating large amounts of leaves, relative to fruits, seeds are reported to be dispersed in low densities (Andresen 2002a). Therefore, seed deposition patterns produced by howler monkeys can be considered mixed, i.e., a fraction clumped and another one scattered. However, given that clumped fecal deposits generally contain many more seeds than scatted fecal deposits, and there exist very few studies on the seedling survivorship of seeds voided by howlers, the specific impact of howler monkeys as seed dispersers relative to other fruit eating tropical vertebrates remains unclear (Russo and Chapman 2011).

The clumped defecation and seed deposition pattern produced by howler monkeys may be important in terms of soil nutrient enrichment. Evidence indicates that latrines are enriched in nutrients (e.g., N, P, and several minerals) compared to surrounding areas (Feeley 2005; Pouvelle et al. 2008; Neves et al. 2010), and may have positive effects on establishment, growth, and survival of seedlings arising from howler-dispersed seeds. For example, Bravo (2012b) found that the *per capita* survival of saplings taller than 1 m was higher in latrines than in control sites. This result is unlikely to be solely related to a higher rate of seed arrival and the possible saturation of biotic mortality agents, but is probably also affected by the higher nutrient availability in latrines (Russo and Augspurger 2004; Bravo 2012b). Thus, consistent with the 'directed dispersal hypothesis' (Howe and Smallwood 1982), howler monkeys may be depositing a large proportion of seeds in specific non-random habitats (i.e., latrines), where survival of seeds/seedlings could be relatively high. In fact, Bravo (2012b) also reports four times more saplings (and from more species) in latrines of *A. caraya* than in randomly selected areas within the forest, and that saplings >1 m tall of three tree species (*Ocotea diopyrifolia*, *Nectandra megapotamica*, and *Eugenia punicifolia*) have higher densities in latrines than below parent trees. Nevertheless, available evidence on this topic is very scarce and needs to be investigated more deeply.

5.2.1.3 Post-dispersal Seed Fate: Seed Predation and Secondary Seed Dispersal

Seed predation and secondary seed dispersal are considered key processes in the seed dispersal cycle (Wang and Smith 2002). These processes can greatly alter the initial seed shadow created by the primary seed dispersal agent, thus affecting the patterns of seedling recruitment (Forget et al. 2005; Russo and Chapman 2011).

The behavior of seed predators and secondary dispersers is often directly affected by the particular characteristics of the seed deposition patterns produced by the primary seed dispersal agent. For howler monkeys in particular, seed density and the presence/amount of dung in individual dung piles, as well as the overall seed/dung density produced by scatter vs. clumped defecation patterns, are known to affect post-dispersal seed fate (Chapman 1989; Andresen 2002a, b; Wehncke et al. 2004; Santos-Heredia et al. 2010).

Rodents, ants, and dung beetles are known to be attracted to howler monkey defecations and to affect, positively or negatively, the fate of the seeds in them (e.g., Chapman 1989; Estrada and Coates-Estrada 1991; Andresen 1999, 2001; Martínez-Mota et al. 2004; Wehncke et al. 2004). While granivorous rodents and ants may act both as seed predators and secondary seed dispersers by actively searching for seeds in defecations, dung beetles act solely as secondary seed dispersers, as they search and use the fecal material, and move and bury accidentally seeds imbedded in it (Andresen and Feer 2005).

In general, rodents are known to be highly efficient in locating seeds dispersed by monkeys, and removal rates of 90 % or more are not uncommon (Chapman 1989; Estrada and Coates-Estrada 1991; Andresen 1999). Moreover, seeds embedded in relatively large quantities of feces have a higher probability of removal by rodents than seeds in small quantities or without feces (Chapman 1989; Andresen 1999, 2002a; Wehncke et al. 2004). Seed density can be another factor affecting seed removal by rodents, but much variation exists among microhabitats, seed species, and/or seasons/years (see Hulme 2002 and references therein). Although seed removal by rodents has been traditionally considered equivalent to seed predation, it is clear now that not all seeds removed by rodents are consumed. Depending on the rodent species, the seed species, and the overall fruit availability in a given moment, the probability of secondary seed dispersal by rodents, rather than predation, can be quite high (Forget et al. 1998; Feer and Forget 2002).

Secondary seed dispersal by dung beetles is characterized by burial and/or small horizontal movements (generally <1 m, Andresen and Feer 2005; Vulinec and Lambert 2009) of the seeds imbedded in the fecal material. In general, Neotropical dung beetles bury small and large seeds (up to approximately 3 cm), but there is a negative relationship between seed size and the percentage of seeds buried (Estrada and Coates-Estrada 1991; Feer 1999; Andresen and Feer 2005). Burial depth also varies greatly, but in general, most seeds are buried <5 cm (e.g., Andresen and Feer 2005). Seed burial by dung beetles greatly increases the probability of seed survival (Estrada and Coates-Estrada 1991; Andresen 1999, 2001, 2002b; Santos-Heredia et al. 2010) and, while seed burial may in some cases hinder seedling emergence (Feer 1999), it has been shown to have a significant net positive effect on seedling establishment of large-seeded species (Andresen 2001; Andresen and Levey 2004). In particular, twice as many seedlings emerged from seeds buried by beetles compared to defecated seeds that remained on the surface (Andresen and Levey 2004).

As with rodents, seeds surrounded by larger amounts of dung (as is often the case with seeds defecated by howler monkeys compared to seeds defecated by other frugivorous mammals including some other primates such as tamarins; Garber 1986) also have a higher probability of being removed by dung beetles (Andresen and Feer 2005). However, seed density per fecal clump does not seem to affect the probability of seed burial by dung beetles (Andresen 2002a; Culot et al. 2009). Regarding the influence of defecation patterns (clumped vs. scattered), results are not conclusive. Some studies report no significant effect of the defecation pattern on seed burial by dung beetles (Andresen 2002a; Ponce et al. 2006), but one study has reported increased seed burial rates for the clumped defecation pattern, but only for spider monkey dung, and not so for howler monkey dung (Santos-Heredia et al. 2010).

Although less studied, ants are likely to play very important roles as both predators and secondary dispersers of seeds defecated by howler monkeys, in particular of small seed species (<3 mm). A very extensive literature exists on seed predation and seed dispersal by ants in many different ecosystems. These studies illustrate how important these insects can be in plant–animal interactions (see Beattie and Hughes 2002 and references therein). For seeds defecated by howler monkeys, one study has shown that ants transport seeds to moist sites, rich in organic material, such as cracks in bark, ant gardens, and tunnel-like nests (Martínez-Mota et al. 2004). As argued by Martínez-Mota et al. (2004), these microsites may favor germination of some important epiphytic fig trees (*Ficus* spp.) and may thus constitute an example of directed seed dispersal.

Finally, post-dispersal seed fate is not only affected by rodents, dung beetles, and ants. Other biotic factors, such as pathogens (e.g., fungi) and other insect predators (e.g., bruchid beetles) also are responsible for the death of many dispersed seeds (Jones 1994). For example, Lambert (2002a, b) demonstrated that red-tailed guenons (*Cercopithecus ascanius schmidti*) consume fruits and spit out cleaned seeds of the tree *Strychnos mitis*, and that these seeds are significantly less likely to be attacked by seed predators and fungus than the unprocessed seeds. Further studies are needed to assess the impact of insect predators and fungus on post-dispersal fate of seeds dispersed by howler monkeys.

5.2.2 *Effects on the Spatial Distribution of Individuals in a Plant Population*

The implications of primary seed dispersal at the level of plant populations go beyond determining the number of seeds that are dispersed and affecting the probability those seeds have on producing a reproductive adult. While effective dispersal is necessary for the successful recruitment of new individuals, dispersal will also play an important role in determining the spatial distributions of those recruits, and possibly the spatial structuring of reproductive adults in a population or metapopulation. The spatial distribution of dispersed seeds is generally assessed by describing the seed shadow (number of seeds at different distances from the parent plant) and/or estimating the seed dispersal kernel (probability distribution of dispersed seeds relative to distance). Although the shape and size of seed shadows are recognized as having profound implications for population/metapopulation dynamics and community structure (see below), accurately estimating seed shadows, particularly for vertebrate-dispersed trees, remains an important challenge (Russo et al. 2006).

One of the main difficulties researchers face is how to incorporate complex animal behavior and their spatially explicit movement patterns, when estimating seed dispersal shadows (Russo and Augspurger 2004). Yet, the behaviors and movements of dispersers are known to create highly structured seed deposition patterns, often with no distance relationship to the parent plant (Schupp et al. 2002). Studies on tamarins, spider monkeys, and tapirs show evidence of how these animals, through their behavior and movement patterns, are responsible for the spatial distribution of individuals for some of the plant species they disperse (Garber 1986; Fragoso et al. 2003; Russo and Augspurger 2004).

No study has yet explicitly assessed the seed shadows created by howler monkeys for particular plant species, and only one has focused on the possible implications (Bravo 2012b). However, the potential impact that howler monkeys are having through their seed dispersal on the spatial distribution of local plants is repeatedly mentioned by authors. Indeed, since the seminal study by Milton (1980), it has been suggested that seed dispersal by howler monkeys could create a patchy spatial distribution of preferred fruit-tree species. Studies reporting ranging and defecation patterns for these primates (e.g., Julliot 1996a; Andresen 2002a; Bravo 2009), together with studies quantifying seedling abundance in howler latrines (e.g., Julliot 1997; Anzures-Dadda et al. 2011; Bravo 2012b), suggest that seed dispersal by howler monkeys may have strong effects on the spatial distribution of howler-preferred plants. This constitutes a very important avenue for future research, in particular for those plant species for which howler monkeys constitute the only or main seed dispersal agent.

5.3 Implications of Howler Monkey Seed Dispersal for Plant Communities

At the plant community level, howler monkeys are considered important seed dispersers because they can disperse the seeds of many plant species from different life forms (e.g., trees, lianas, palms, and epiphytes; Tables 5.2 and 5.3). Although most studies have reported fruit diets consisting of less than 40 species (Bicca-Marques 2003), studies of *A. macconnelli* indicate that in some areas howler monkeys are able to disperse the seeds of more than 100 plant species (110 species, French Guiana: Julliot and Sabatier 1993; Julliot 1996a; 137 species, Central Amazonia: Andresen 2002a). In general, howler monkeys can feed and disperse a fewer number of plant species than other primates in pristine habitats. For instance, in Tinigua Park, during the same year of observations, red howlers fed on 52 species, while capuchins fed on 106, woolly monkeys on 137, and spider monkeys on 97 (Stevenson et al. 2000, 2002). However, the number of species dispersed depends, in part, on local tree diversity and, hence, in forests with fewer tree species or due to their smaller home range howler monkeys may disperse seeds of a small number of fruit species (Ramos-Obregon 2007). The length of the study can also affect the number of species reported in the diet of primates. Many plant species fruit every two years, while most primate research studies last one year or less. Not surprisingly, the studies reporting >100 fruit species in howler monkey diet had a duration of two years.

As already mentioned, howler monkeys, as well as other arboreal mammals and a few large birds species such as toucans, may serve as the main dispersers of large-seeded plants (>10 mm, seed length) and/or plants with hard indehiscent husks. These plants may constitute a large proportion of the total tree species richness and stem density (e.g., Sapotaceae in Central Amazonia and the Guiana Shield); therefore, by dispersing seeds of these species, howler monkeys may affect the abundance and distribution of structurally important tropical plant populations, directly impacting the structure of plant communities and forest dynamics.

Seed dispersal by howler monkeys also may have important implications for the maintenance of high tree species diversity in tropical forests. For other primate species, in particular highly frugivorous atelines, it has been shown that primate density is positively associated with the diversity of regenerating plants (Stevenson 2011). Although the effect of less frugivorous primates, such as howler monkeys, is probably less strong, the effect of these primates still remains positive in models that predict the diversity of regenerating plants (Stevenson 2011).

Howler monkeys and other primates may promote species diversity not only through effective seed dispersal, but also through the highly structured seed shadow they produce (see above). Due to their behavior and ranging patterns, the seed shadow created by howler monkeys is characterized by areas of very high seed density in latrines, which are used repeatedly over time (Julliot 1997; Bravo 2009). It has been argued that such patterns of seed dispersal will create dissemination limitation for other potential plant recruitment sites, and consequently recruitment limitation, which is defined as the failure to establish seedlings in a suitable site (Schupp et al. 2002). In turn, recruitment limitation is one of the main mechanisms that are assumed to prevent competitive exclusion by superior competitors, and thus favoring the coexistence of many plant species (see Schupp et al. 2002 and references therein). Nevertheless, much research is still needed to clearly establish the relative importance of different aspects of recruitment limitation (Terborgh et al. 2011), as well as to ascertain its role in the maintenance of high plant species richness.

5.4 Implications of Howler Monkey Seed Dispersal for Conservation and Restoration

Large-bodied, seed-dispersers have been shown to be particularly vulnerable to hunting pressure and habitat destruction, with potentially severe cascading effects for plant regeneration (Peres and Palacios 2007; Stoner et al. 2007; Wilkie et al. 2011). Studies increasingly show that such disturbances disrupt plant-animal dispersal systems, causing changes in plant recruitment, and potentially changing forest composition and structure in sites without primates and/or with lower primate population sizes (Chapman and Onderdonk 1998; Stevenson and Aldana 2008; Gonzalez-Di Pierro et al. 2011; Stevenson 2011). In this sense, understanding the long-term effects that primate disappearance and/or population declines could have on the composition and structure of plant communities represents an important challenge for ecologists, primatologists, and conservation biologists (Chapman 1989; Russo and Chapman 2011; Stevenson 2011).

In this chapter we have shown that howler monkeys can have negative effects on seed dispersal. For example, they can deposit a large number of seeds in clumps, which can result in high seed and seedling mortality. Also, in some cases, howler monkeys can act as seed predators. Nevertheless, the positive effects are more frequently reported, indicating that they play an important role in Neotropical forest regeneration due to a combination of factors: (1) they are one of the most abundant frugivorous arboreal mammals; (2) they can spend ca. 50 % of their monthly or yearly feeding time consuming fruits, swallowing most of the seeds they handle, and defecating them undamaged; (3) gut passage rarely has a negative effect on germination and often has a positive one; (4) their behavior and ranging patterns create a highly structured seed shadow, i.e., a spatially heterogeneous distribution of seeds, that may enhance plant species diversity; (5) they disperse seeds of many plant species from different life forms, including trees, lianas, palms, and epiphytes; (6) they are likely to be the main seed dispersers of certain tree species (e.g., large-seeded species and/or with indehiscent hard-husked fruits), especially in small forest fragments in which other primates are absent; and (7) their dung enriches the soil (that is commonly poor in many tropical forests), and attracts secondary seed dispersers that move the seeds to microsites with higher probability of survival and seedling establishment.

Howler monkeys not only play an important role as seed dispersers in conserved habitats, but they can also be playing a crucial role in disturbed habitats. Unlike most large Neotropical mammal species, howler monkeys are highly resilient to disturbance, being able to maintain populations in disturbed habitats, such as forest fragments, secondary forests, and some types of agroecosystems (Vulinec et al. 2006; Williams-Guillén et al. 2006; Arroyo-Rodríguez and Dias 2010; Zárate et al. 2014). For example, in a small fragment in the Orinoco basin in Colombia without other large atelines, howler monkeys were estimated to disperse approximately 40,900 g of dry weight of seeds per km^2 in 4 months (Ramos-Obregon 2007), equivalent to the dispersal rate of more frugivorous ateline primates at other sites (Stevenson 2007). Thus, it has been increasingly recognized that howler monkeys play a key role for local plant regeneration in disturbed habitats (e.g. Gonzalez-Di Pierro et al. 2011). However, in smaller and/or disturbed habitat patches, howler monkeys tend to spend a lower percentage of time feeding on fruits (Dias and Rangel-Negrin 2014) and exploit a smaller number of plant species (Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007). This has also been found for other frugivorous primate species (e.g. *Ateles geoffroyi*; González-Zamora et al. 2009). Thus, in terms of the quantity of seeds dispersed, as well as the number of species dispersed, the role played by howler monkeys as seed dispersers at both the plant population and the plant community level appears to be lower in highly disturbed habitats. Nevertheless, the role played by these primates in such habitats will depend on the extent to which their populations are able to compensate for lost dispersal services due to the local extinction of other seed-dispersing animals and may thus be proportionally large. Such compensatory role, however, still remains to be assessed in future studies.

Howler monkeys can transport seeds among different forest types and conditions (e.g., continuous and fragmented forests, old-growth and secondary forests), contributing to secondary succession and thus aiding in the restoration of degraded habitats (e.g., Giraldo et al. 2007). Particularly relevant for forest restoration in degraded habitats is the fact that howler monkeys disperse seeds of both pioneer and old-growth forest species. Abundant dispersal of light-demanding and pioneer tree species, such as *Ficus*, *Cecropia*, *Inga*, and many liana species (Julliot 1996a; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Pouvelle et al. 2009) could favor rapid recruitment of vegetation in open areas. At the same time, dispersal of long-lived pioneer and old-growth forest species could favor the incorporation of such species in the seed and seedling bank, allowing for the continuation of succession.

Finally, soil nutrient enrichment through defecation is an important factor that may affect forest regeneration, particularly in degraded areas. Only three studies are available on this topic (Feeley 2005; Pouvelle et al. 2008; Neves et al. 2010), and all agree that howler monkeys' dung contributes considerably to the horizontal and vertical redistribution of nutrients. For example, the clumped defecation pattern of howler monkeys can enrich the soil in nutrients such as phosphorus and nitrogenous, which are important for vegetation growth (Feeley 2005). Also the physical characteristics of the soil are improved due to increased activity of the soil microbial and microfaunal communities (Neves et al. 2010). Whether the improvement of soil characteristics in defecation sites actually translates into positive effects for plants (seedling survival, establishment, growth), either in conserved or disturbed habitats, is still unknown. This is a highly promising avenue for future research.

5.5 New Directions for Future Research

Overall, we found that several aspects of seed dispersal by howler monkeys (*Alouatta* spp.) have been studied throughout their geographic range (Table 5.1), but there are some important questions that need to be addressed to improve our understanding on the importance of howler monkeys as seed dispersers. First, we found that current evidence comes exclusively from studies of eight of 14–18 howler monkey species, and therefore studies of other species are needed to accurately determine (e.g., through meta-analyses) whether there are inter-specific differences in their contribution as seed dispersers. This is likely given differences in diet found across the genus *Alouatta* (see Dias and Rangel-Negrin 2014). Second, most studies have so far focused on well-conserved forests. Thus, more research is needed in fragmented/degraded forests in order to assess, for example, if seed dispersal effectiveness can be lower in these habitats, if primate disappearance and/or population declines can negatively affect forest regeneration, and the potential compensatory role of howlers in sites lacking other dispersal agents. Third, while the quantity component of seed dispersal has received much attention, some aspects of the quality component require further research (Table 5.1). These include: (1) the effect of pulp removal (deinhibition) on seed fate, not only for defecated seeds, but also for spat and dropped seeds; (2) the effect of gut passage on the control of insect larvae present in the ingested fruits/seeds; and (3) the impact of gut passage on seedling survival and growth.

Regarding the impact of howler monkeys on the spatial distribution of plants, no study to date has yet explicitly assessed the seed shadows created by howler monkeys for particular plant species. Also, the post-dispersal seed fate is not well understood. Studies are needed to fully assess the importance of ants, dung beetles, rodents, insect predators, and fungal pathogens in determining the fate of small-seeded species dispersed by howler monkeys and other primates. Finally, more investigation is also needed to assess the differences between clumped (e.g., in latrines) and scattered seed deposition patterns on seeds/seedlings survival and plant recruitment. Also, an interesting hypothesis that needs to be tested in future research is whether seed dispersal by howler monkeys creates a patchy spatial distribution of preferred fruit-tree species, creating food gardens within the forests (Milton 1980). This is possible if seeds deposited in latrines regenerate in greater density than seeds deposited in other areas, but evidence on this topic is scarce, and it is still unclear whether the improvement of soil characteristics in latrines actually translates into positive effects for plants (seedling survival, establishment, growth).

Acknowledgments The Centro de Investigaciones en Ecosistemas (Universidad Nacional Autónoma de México) provided logistical support to V.A.R. and E.A., and CONICET (Consejo Nacional de Investigaciones Científicas y Tecnológicas, Argentina) and the Universidad de Buenos Aires provided financial support to S.P.B. Banco de la República (Colombia), Primate Conservation, Margot Marsh Fund, Colciencias, Ecopetrol, and Universidad de Los Andes have provided funds to P.R.S.

References

Amato KR, Estrada A (2010) Seed dispersal patterns in two closely related howler monkey species (*Alouatta palliata* and *A. pigra*): a preliminary report of differences in fruit consumption, traveling behavior, and associated dung beetle assemblages. Neotrop Primates 17:59–66

Andresen E (1999) Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rainforest. Biotropica 31:145–158

Andresen E (2000) Ecological roles of mammals: the case of seed dispersal. In: Entwistle A, Dunstone N (eds) Future priorities for the conservation of mammalian diversity: has the panda had its day? Cambridge University Press, Cambridge

Andresen E (2001) Effects of dung presence, dung amount, and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. J Trop Ecol 17:61–78

Andresen E (2002a) Primary seed dispersal by red howler monkeys and the effect of defecation pattern on the fate of dispersed seeds. Biotropica 34:261–272

Andresen E (2002b) Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. Ecol Entomol 27:257–270

Andresen E, Feer F (2005) The role of dung beetles as secondary seed dispersers and their effect on plant regeneration in tropical rainforests. In: Forget P-M, Lambert J, Hulme P, Vander Wall SB (eds) Seed fate: predation, dispersal and seedling establishment. CAB, Wallingford

Andresen E, Levey DJ (2004) Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia 139:145–154

Anzures-Dadda A, Andresen E, Martinez ML, Manson RH (2011) Absence of howlers (*Alouatta palliata*) influences tree seedling densities in tropical rain forest fragments in southern Mexico. Int J Primatol 32:634–651

Arroyo-Rodríguez V, Dias PAD (2010) Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am J Primatol 71:1–16

Beattie AJ, Hughes L (2002) Ant-plant interactions. In: Herrera CM, Pellmyr O (eds) Plant-animal interactions. An evolutionary approach. Blackwell, Oxford

Bicca-Marques JC (2003) How do howler monkeys cope with habitat fragmentation. In: Marsh LK (ed) Primates in fragments: ecology and conservation. Kluwer Academic, New York

Bravo SP (2008) Seed dispersal and ingestion of insect-infested seeds by black howler monkeys in flooded forests of the Paraná river, Argentina. Biotropica 40:47–476

Bravo SP (2009) Implications of behavior and gut passage for seed dispersal quality: the case of black and gold howler monkeys. Biotropica 41:751–758

Bravo SP (2012a) From which *Ocotea diospyrifolia* trees does *Alouatta caraya* (Primates, Atelidae) eat fruits? J Trop Ecol 28:417–420

Bravo SP (2012b) The impact of seed dispersal by black and gold howler monkeys on forest regeneration. Ecol Res 27:311–321

Bravo SP, Zunino GE (1998) Effects of black howler monkey (*Alouatta caraya*) seed ingestion on insect larvae. Am J Primatol 45:411–415

Bravo SP, Zunino GE (2000) Germination of seeds from three species dispersed by black howler monkeys (*Alouatta caraya*). Folia Primatol 71:342–345

Bravo SP, Kowalewski MM, Zunino GE (1995) Dispersión y germinación de semillas de *Ficus monckii* por el mono aullador negro (*Alouatta caraya*). Bol Primatol Latin 5:25–27

Chapman CA (1989) Primate seed dispersal: the fate of dispersed seeds. Biotropica 21:148–154

Chapman CA (1995) Primate seed dispersal: coevolution and conservation implications. Evol Anthropol 4:74–82

Chapman CA, Onderdonk DA (1998) Forests without primates: primate/plant codependency. Am J Primatol 45:127–141

Chaves OM, Stoner KE, Arroyo-Rodríguez V, Estrada A (2011) Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in southern Mexico. Int J Primatol 32:177–192

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Center for Agricultural Publication and Documentation, Wageningen

Cortés-Ortiz L, Rylands AB, Mittermeier RA (2014) The taxonomy of howler monkeys: integrating old and new knowledge from morphological and genetic studies. In: Kowalewski M, Garber P, Cortés-Ortiz L, Urbani B, Youlatos D (eds) Howler monkeys: adaptive radiation, systematics, and morphology. Springer, New York

Cramer JM, Mesquita RCG, Williamson GB (2007) Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biol Conserv 137:415–423

Cristóbal-Azkarate J, Arroyo-Rodríguez V (2007) Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. Am J Primatol 69:1013–1029

Culot L, Huynen MC, Gérard P, Heymann EW (2009) Short-term post-dispersal fate of seeds defecated by two small primate species (*Saguinus mystax* and *Saguinus fuscicollis*) in the Amazonian forest of Peru. J Trop Ecol 25:229–238 de Figueiredo RA (1993) Ingestion of *Ficus enormis* seeds by howler monkeys (*Alouatta fusca*) in Brazil: effects on seed germination. J Trop Ecol 9:541–543

de Figueiredo RA, Longatti CA (1997) Ecological aspects of the dispersal of a melastomataceae by Marmosets and Howler monkeys (Primates: Platyrrhini) in a semideciduous forest of southeastern Brazil. Revue d'Ecologie (La Terre et la Vie) 52:3–8

Dias PAD, Rangel-Negrin A (2014) Diets of howler monkeys. In: Kowalewski M, Garber P, Cortés-Ortiz L, Urbani B, Youlatos D (eds) Howler monkeys: behavior, ecology and conservation (pp. 21–56). Springer, New York

Dunn JC, Asensio N, Arroyo-Rodríguez V, Schnitzer S, Cristóbal-Azkarate J (2012) The ranging costs of a fallback food: liana consumption supplements diet but increases foraging effort in howler monkeys. Biotropica 44(5):705–714. doi:10.1111/j.1744-7429.2012.00856.x

Estrada A (2014) Conservation of *Alouatta*: social and economic drivers of habitat loss, information vacuum and mitigating population declines. In: Kowalewski M, Garber P, Cortés-Ortiz L, Urbani B, Youlatos D (eds) Howler monkeys: behavior, ecology and conservation (pp. 383–409). Springer, New York

Estrada A, Coates-Estrada R (1984) Fruit eating and seed dispersal by howlers (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. Am J Primatol 6:77–91

Estrada A, Coates-Estrada R (1991) Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. J Trop Ecol 7:459–474

Feeley K (2005) The role of clumped defecation in the spatial distribution of soil nutrients and the availability of nutrients for plant uptake. J Trop Ecol 21:99–102

Feer F (1999) Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. J Trop Ecol 15:129–142

Feer F, Forget P-M (2002) Spatio-temporal variations in post-dispersal seed fate. Biotropica 34:555–566

Feer F, Julliot C, Simmen B, Forget P-M, Bayart F, Chauvet S (2001) Recruitment, a multi-stage process with unpredictable result: The case of a Sapotaceasae in French Guianan forest. Revue d'Ecologie (La Terre et la Vie) 56:119–145

Fleming TH, Kress WJ (2011) A brief history of fruits and frugivores. Acta Oecol 37:521–530

Forget P-M, Milleron T, Feer F (1998) Patterns in post-dispersal seed removal by Neotropical rodents and seed fate in relation to seed size. In: Newbery DM, Prins HHT, Brown ND (eds) Dynamics of tropical communities. Blackwell Science, Oxford

Forget P-M, Lambert J, Hulme P, Vander Wall SB (2005) Seed fate. Predation, dispersal and seedling establishment. CABI, Wallingford

Fragoso JMV, Silvus KM, Correa JA (2003) Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. Ecology 84:1998–2006

Garber PA (1986) The ecology of seed dispersal in two species of Callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). Am J Primatol 10:155–170

Garber PA, Estrada A, Pavelka MSM (2006) New perspectives in the study of Mesoamerican primates: concluding comments and conservation priorities. In: Estrada A, Garber PA, Pavelka M, Luecke L (eds) New perspectives in the study of Mesoamerican primates. Springer, New York

Giraldo P, Gómez-Posada C, Martinez J, Kattan G (2007) Resource use and seed dispersal by red howler monkeys (*Alouatta seniculus*) in a Colombian Andean forest. Neotrop Primates 14:55–64

González-Di Pierro AM (2011) Presencia de *Alouatta pigra* y regeneración en fragmentos forestales de la Selva Lacandona, Ph.D. Thesis, Universidad Nacional Autónoma de México, Morelia, Michoacán

Gonzalez-Di Pierro AM, Benítez-Malvido J, Mendez-Toribio M, Zermeno I, Arroyo-Rodríguez V, Stoner KE, Estrada A (2011) Effects of the physical environment and primate gut passage on the early establishment of *Ampelocera hottlei* standley in rain forest fragments. Biotropica 43:459–466

González-Zamora A, Arroyo-Rodríguez V, Chavez O, Sanchez-Lopez S, Stoner KE, Riba-Hernández P (2009) Diet of spider monkeys (*Ateles geoffroyi*) in Mesoamerica: current knowledge and future directions. Am J Primatol 71:8–20

González-Zamora A, Arroyo-Rodríguez V, Oyama AK, Sork V, Chapman CA, Stoner KE (2012) Sleeping sites and latrines of spider monkeys in continuous and fragmented rainforests: implications for seed dispersal and forest regeneration. PLoS One 7:e46852

González-Zamora A, Arroyo-Rodríguez V, Escobar F, Rös M, Oyama K, Ibarra-Manríquez G, Stoner KE, Chapman CA (2014) Contagious deposition of seeds in spider monkeys' sleeping trees limits effective seed dispersal in fragmented landscapes. PloS ONE 9:e89346

Graeff VG, Bicca-Marques JC, Astarita LV (2007) Viability and germination of seeds of iguana hackberry, *Celtis iguanaea* (Jacq) Sargent, ingested by brown howler monkeys, *Alouatta guariba clamitans* Cabrera, 1940. A Primatologia no Brasil 10:363–374

Hernández A (2011) Internal dispersal of seed-inhabiting insects by vertebrate frugivores: a review and prospects. Integr Zool 6:213–221

Herrera CM (2002) Seed dispersal by vertebrates. In: Herrera CM, Pellmyr O (eds) Plant-animal interactions. An evolutionary approach. Blackwell, Oxford

Howe HF (1980) Monkey dispersal and waste of a Neotropical fruit. Ecology 61:944–959

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Ann Rev Ecol Syst 13:201–228

Hulme PE (2002) Seed-eaters: seed dispersal, destruction and demography. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CAB International, Wallingford

IUCN (2012) *Alouatta*. In: IUCN 2012. IUCN Red list of threatened species. Version 2012.2. www.iucnredlist.org. Downloaded on 06 November 2012

Janson CH (1983) Adaptation of fruit morphology to dispersal agents in a Neotropical forest. Science 219:187–189

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528

Jones MB (1994) Secondary seed removal by ants, beetles, and rodents in a Neotropical moist forest, M.Sc. Thesis. University of Florida, Gainesville

Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford

Julliot C (1996a) Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. Int J Primatol 17:239–258

Julliot C (1996b) Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. Am J Primatol 40:261–282

Julliot C (1997) Impact of seed dispersal by red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. J Ecol 85:431–440

Julliot C, Sabatier D (1993) Diet of the red howler monkey (*Alouatta seniculus*) in French Guiana. Int J Primatol 14:527–550

Koné I, Lambert JE, Refisch J, Bakayoko A (2008) Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d'Ivoire: implications for the conservation of forest fragments. Trop Conserv Sci 1:293–306

Lambert J (2002a) Red-Tailed Guenons (*Cercopithecus ascanius*) and *Strychnos mitis*: evidence for plant benefits beyond seed dispersal. Int J Primatol 22:189–201

Lambert J (2002b) Exploring the link between animal frugivory and plant strategies: the case of primate fruit processing and post-dispersal seed fate. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, Wallingford

Lambert JE, Garber PA (1998) Evolutionary and ecological implications of primate seed dispersal. Am J Primatol 45:9–28

Marsh LK, Loiselle BA (2003) Recruitment of black howler fruit trees in fragmented forests of northern Belize. Int J Primatol 24:65–86

Martínez-Mota R, Serio-Silva JC, Rico-Gray V (2004) The role of canopy ants in removing *Ficus perforata* seeds from howler monkey (*Alouatta palliata mexicana*) feces at Los Tuxtlas, Mexico. Biotropica 36:429–432

Martins MM (2006) Comparative seed dispersal effectiveness of sympatric *Alouatta guariba* and *Brachyteles arachnoides* in southeastern Brazil. Biotropica 38:57–63

Martins MM (2008) Fruit diet of *Alouatta guariba* and *Brachyteles arachnoides* in Southeastern Brazil: comparison of fruit type, color, and seed size. Primates 49:1–8

Milton K (1980) The foraging strategy of howler monkeys. A study in primate economics. Columbia University Press, New York

Moura ACDA, McConkey KR (2007) The capuchin, the howler, and the caatinga: seed dispersal by monkeys in a threatened Brazilian forest. Am J Primatol 69:220–226

Neves N, Feer F, Salmon S, Chateil C, Ponge JF (2010) The impact of red howler monkey latrines on the distribution of main nutrients and topsoil components in tropical rain forests. Aus Ecol 35:545–559

Palma AC, Vélez A, Gómez-Posada C, López H, Zárate-Caicedo DA, Stevenson PR (2011) Use of space, activity patterns, and foraging behavior of red howler monkeys (*Alouatta seniculus*) in an Andean forest fragment in Colombia. Am J Primatol 73:1062–1071

Pedroni F, Sanchez M (1997) Dispersao de sementes de *Pereskia aculeata* Muller (Cactaceae) num fragmento florestal no sudeste do Brasil. Rev Brasil Biol 57:479–486

Peres CA (1997) Primate community structure at twenty western Amazonian flooded and unflooded forests. J Trop Ecol 13:381–405

Peres CA, Palacios E (2007) Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. Biotropica 39:304–315

Ponce G (2004) Dispersión de semillas por mono araña (*Ateles geoffroyi*), saraguato negro (*Alouatta pigra*) y escarabajos coprófagos en el Parque Nacional Tikal, Guatemala, B.Sc. Thesis, Universidad del Valle de Guatemala, Guatemala

Ponce G, Andresen E, Cano E, Cuaron AD (2006) Primary seed dispersal by primates and secondary seed dispersal by dung beetles in Tikal, Guatemala. Biotropica 38:390–397

Pouvelle S, Feer F, Ponge J-F (2008) Topsoil as affected by dung deposition under resting places of red howler monkey (*Alouatta seniculus*). Pedosphere 18:691–698

Pouvelle S, Jouard S, Feer F, Tully T, Ponge J-F (2009) The latrine effect: Impact of howler monkeys on the distribution of small seeds in a tropical rain-forest soil. J Trop Ecol 25:239–248

Ramos-Obregon J (2007) Comparación de la cantidad y el tipo de semillas dispersadas por *Cebus apella* y *Alouatta seniculus* en un bosque fragmentado, San Martín; Meta, BSc. Thesis. Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogota

Ratiarison S, Forget P-M (2011) Fruit availability, frugivore satiation and seed removal in 2 primate-dispersed tree species. Integr Zool 6:178–194

Righini N (2004) Germinación de semillas de *Ficus perforata* ingeridas por monos aulladores (*Alouatta palliata mexicana*) y monos araña (*Ateles geoffroyi vellerosus*). Lab Prim Newslett 43:19–20

Russo SE, Augspurger CK (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecol Lett 7:1058–1067

Russo SE, Chapman CA (2011) Primate seed dispersal: Linking behavioral ecology with forest community structure. In: Campbell CJ, Fuentes AF, MacKinnon KC, Panger M, Bearder S (eds) Primates in perspective, 2nd edn. Oxford University Press, Oxford

Russo SE, Portnoy S, Augspurger CK (2006) Incorporating animal behavior into seed dispersal models: implications for seed shadows and an example for a primate-dispersed tree. Ecology 87:3160–3174

Santamaría M (1999) Ecologia e comportamento de *Alouatta seniculus* em uma mata de terra firme na Amazonia Central, M.Sc. Thesis. Universidade Federal de Minas Gerais, Brazil

Santos-Heredia C, Andresen E, Zarate DA (2010) Secondary seed dispersal by dung beetles in a Colombian rain forest: effects of dung type and defecation pattern on seed fate. J Trop Ecol 26:355–364

Santos-Heredia C, Andresen E, Stevenson P (2011) Secondary seed dispersal by dung beetles in an Amazonian forest fragment of Colombia: influence of dung type and edge effect. Integr Zool 6:399–408

Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107:15–29

Schupp EW, Milleron T, Russo SE (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, Wallingford

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a conceptual review. New Phytol 188:333–353

Serio-Silva JC, Rico-Gray V (2002a) Influence of microclimate at different canopy heights on the germination of *Ficus* (Urostigma) seeds dispersed by Mexican howler monkeys (*Alouatta palliata mexicana*). Interciencia 27:186–190

Serio-Silva JC, Rico-Gray V (2002b) Interacting effects of forest fragmentation and howler monkey foraging on germination and dispersal of fig seeds. Oryx 36:266–271

Serio-Silva JC, Rico-Gray V (2003) Howler monkeys (*Alouatta palliata mexicana*) as seed dispersers of strangler figs in disturbed and preserved habitat in southern Veracruz, Mexico. In: Marsh LK (ed) Primates in fragments: ecology and conservation. Kluwer Academic, New York

Silver SC, Ostro LET, Yeager CP, Horwich R (1998) Feeding ecology of the black howler monkey (*Alouatta pigra*) in Northern Belize. Am J Primatol 45:263–279

Stevenson PR (2007) Estimates of the number of seeds dispersed by a population of primates in a lowland forest in western Amazonia. In: Dennis AJ, Schupp EW, Green RJ, Westcott DW (eds) Seed dispersal: theory and its application in a changing world. CAB International, Wallingford

Stevenson PR (2011) The abundance of large Ateline monkeys is positively associated with the diversity of plants regenerating in Neotropical forests. Biotropica 43:512–519

Stevenson PR, Aldana AM (2008) Potential effects of Ateline extinction and forest fragmentation on plant diversity and composition in the western Orinoco Basin, Colombia. Int J Primatol 29:365–377

Stevenson PR, Quiñones MJ, Ahumada JA (1998) Effects of fruit patch availability on feeding subgroup size and spacing patterns in four primate species, at Tinigua National Park, Colombia. Int J Primatol 19:313–324

Stevenson PR, Quiñones MJ, Ahumada JA (2000) The relationship between temporal variation in fruit abundance and ecological overlap among four Neotropical primates in Colombia. Biotropica 32:533–544

Stevenson PR, Castellanos MC, Pizarro JC, Garavito M (2002) Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia. Int J Primatol 23:1187–1204

Stevenson PR, Pineda M, Samper T (2005) Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park, Colombia. Oikos 110:435–440

Stoner KE, Riba-Hernandez P, Vulinec K, Lambert JE (2007) The role of mammals in creating and modifying seed shadows in tropical forests and some possible consequences of their elimination. Biotropica 39:316–327

Terborgh J, Alvarez-Loayza P, Dexter K, Cornejo F, Carrasco C (2011) Decomposing dispersal limitation: limits on fecundity or seed distribution? J Ecol 99:935–944

Traveset A, Robertson AW, Rodríguez-Pérez J (2007) A review on the role of endozoochory in seed germination. In: Dennis AJ, Schupp EW, Green RJ, Westcott DA (eds) See dispersal. Theory and its application in a changing world. CABI, Wallingford

Vulinec K, Lambert JE (2009) Neutral and niche perspectives and the role of primates as seed dispersers: a case study from Rio Paratari, Brazil. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American primates. Comparative perspectives in the study of behavior, ecology, and conservation, Developments in primatology: progress and prospects. Springer, New York

Vulinec K, Lambert JE, Mellow DJ (2006) Primate and dung beetle communities in secondary growth rain forests: Implications for conservation of seed dispersal systems. Int J Primatol 27:855–879

Wang B, Smith T (2002) Closing the seed dispersal loop. Trends Ecol Evol 17:379–385

Wehncke EV, Valdez CN, Dominguez CA (2004) Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: consequences for seed dispersal effectiveness. J Trop Ecol 20:535–543

Wilkie DS, Bennett EL, Peres CA, Cunningham SA (2011) The empty forest revisited. Ann New York Acad Sci 1223:120–128

Williams-Guillén K, McCann C, Martínez-Sánchez JC, Koontz F (2006) Resource availability and habitat use by mantled howling monkeys in a Nicaraguan coffee plantation: can agroforests serve as core habitat for a forest mammal? Anim Conserv 9:331–338

Yumoto T, Kimura K, Nishimura A (1999) Estimation of the retention times and distances of seed dispersed by two monkey species, *Alouatta seniculus* and *Lagothrix lagotricha*, in a Colombian forest. Ecol Res 14:179–191

Zárate DA, Andresen E, Estrada A, Serio-Silva CJ (2014) Black howler monkey (Alouatta pigra) activity, foraging and seed dispersal patterns in shaded cocoa plantations versus rainforest in southern Mexico. Am J Primatol 76:890–899