

Post-dispersal seed predation by Atlantic Forest squirrels monitoring lowland tapir latrines

ANA CAROLINA SRBEK-ARAUJO^{1,2*}, CRISTINA JAQUES DA CUNHA¹ & JAMES JOSEPH ROPER³

¹*Laboratório de Ecologia e Conservação de Biodiversidade (LECBio), Programa de Pós-graduação em Ecologia de Ecossistemas, Universidade Vila Velha – UVV, Rua Comissário José Dantas de Melo, n° 21, Bairro Boa Vista, Vila Velha, Espírito Santo, CEP 29.102-920, Brazil*

²*Instituto SerraDiCal de Pesquisa e Conservação, Belo Horizonte, Minas Gerais, Brazil*

³*Laboratório de Dinâmicas Populacionais e Conservação de Vertebrados (DPeC), Programa de Pós-graduação em Ecologia de Ecossistemas, Universidade Vila Velha – UVV, Rua Comissário José Dantas de Melo, n° 21, Bairro Boa Vista, Vila Velha, Espírito Santo, CEP 29.102-920, Brazil*

Abstract: Here we describe novel post-dispersal seed predation by Atlantic Forest squirrels (*Guerlinguetus ingrami*). We show that the squirrel preys on seeds defecated by lowland tapirs (*Tapirus terrestris*) in the Atlantic Forest, southeastern Brazil. The squirrel consumed seeds in tapir feces at a latrine, including *Spondias macrocarpa*, *S. venulosa* and *Elaeis guineensis*. In videos and photographs taken by a camera trap, squirrels are clearly seen removing and eating seeds from tapir fecal pellets. Squirrels are known to be both seed dispersers (primary and secondary) and predators, and seed dispersal and predation are important for plant community structure. We demonstrate that as seed predators, squirrels seem to monitor and opportunistically take advantage of seeds dispersed by other mammals, thereby reducing primary dispersal effectiveness and compromising the ecosystem service provided by other dispersers. Squirrels may take advantage of latrines when other food sources are locally unavailable. Also, tapirs, because they travel large distances while foraging, often predictably return to latrines, thereby providing squirrels with an otherwise unavailable resource. If seeds become very abundant in latrines, perhaps squirrels then hoard (secondary dispersal) the excess. If the behavior described is a general trend, the pattern is likely to be often repeated, especially in tropical forests with similar mammalian assemblages, and this complex dynamic will require further study to better understand consequences of post-dispersal seed predation.

Key words: Animal-plant interaction, camera trapping, ecological antagonism, South American tapir, Southeastern squirrel, tapir latrine.

Seed dispersal by animals often favors plant germination, survival and recruitment (Janzen 1970). Dispersal has been a strong driving force of natural selection and, today, plant distribution patterns and community structure are often a consequence of dispersal (Bleher & Bohing-Gaese

2001; Howe & Miriti 2004; Janzen 1970). Benefits of dispersal may include passage through the digestive tract (which can favor germination), reaching new and appropriate locations in which to germinate, and reduction in density-dependent seed predation near the parent plant (Howe &

*Corresponding Author; e-mail: srbekaraujo@hotmail.com

Miriti 2004; Janzen 1970; Sanchez-Cordero & Martínez-Gallardo 1998; Schupp 1988). Because seeds often become food in their own right, seed predation can reduce or eliminate the benefits of seed dispersal (Janzen 1970; Terborgh 1988).

Terrestrial mammals are the main seed predators and dispersers in tropical forests (O'Farrill *et al.* 2013; Sanchez-Cordero & Martinez-Gallardo 1998; Wright *et al.* 2000). Many species of mammals are selective in the fruits or seeds they consume and may be very important for the plant reproductive cycle. Changes in plant-animal interactions have potentially important consequences for plant community structure (Janzen 1970; Galetti *et al.* 2015). For example, small rodents may overcompensate the local extinction of large frugivores thereby increasing their (and possibly overall) impact of seed predation on the plant community (Galetti *et al.* 2015); and the absence of megafauna today may have influenced the distributions and life histories of many plants that were previously dispersed by large-bodied, now extinct, frugivores (Janzen & Martin 1982; O'Farrill *et al.* 2013). Current mammalian seed dispersers and predators can range in size from small rodents to the largest extant native disperser in neotropical forests, the lowland tapir (*Tapirus terrestris* (Linnaeus 1758). Animals along this size gradient may all play important roles in the reproductive cycle of many plants due to seed dispersal and predation (Dirzo & Miranda 1990; Fragoso 1997; Galetti *et al.* 2015; Gautier-Hion *et al.* 1985; Janzen 1970; Terborgh 1988).

Here we report on a novel interaction between seed dispersal by lowland tapirs followed by seed predation by Atlantic Forest squirrels (*Guerlinguetus ingrami* (Thomas 1901), previously *Sciurus ingrami*) in the coastal lowland Atlantic Forest (Tabuleiro forest) of southeastern Brazil. This coastal lowland forest is among the most diverse ecosystems, especially with respect to plants, within the domain of the Atlantic Forest (Gonzalez-Garay & Rizzini 2003). The Atlantic Forest domain is also among the most threatened with habitat loss, fragmentation and other anthropogenic consequences of the large and growing human population in the world (Morellato & Haddad 2000).

Observations of both dispersal and predation of seeds took place in the Sooretama Biological Reserve (SBR, 18°53'–19°55'S and 39°55'–40°15'W), in the state of Espírito Santo. The SBR is a Federal Reserve comprising ca. 242 km² adjacent

to another three protected areas, which together form the Linhares-Sooretama Block of nearly continuous native vegetation formations (ca. 500 km²). This region contains approximately 10% of the entire remaining forested area of the state (based on data available in FSOSMA & INPE 2014).

A camera trap (Bushnell Trophy Cam HD Aggressor-Bushnell Inc., Overland Park, USA) was placed and aimed at a tapir latrine near the northern limit of the SBR (18°58'S and 40°06'W) on 18 March 2016 until 25 September 2016. The camera was configured to record a 10 second video clip and two photographs at each capture event. Due to the nature of camera traps, it was impossible to determine how many individuals of tapirs (at least one female and one male) and squirrels visited the latrines. So here we simply document the interaction, in which we consider each day as an independent record, and we refer to photos and videos together as records.

We use the *t*-Test (one-tailed) to verify if the interval between the squirrel records after a tapir visit is different than the interval between the tapir records and the last visit by a squirrel.

Tapirs were recorded on 15 different days (7 days with fecal deposition), with a median interval of 9 days between records (minimum interval = 1 d, max = 27 d). Squirrels were recorded on a total of 27 days (6 days foraging on the ground but not at the latrine area, and 21 days visiting the latrine), with a median interval of 5 days (min = 1 d, max = 19 d). The last day the tapir visited the latrine was 22 July, and the last record of squirrel was on 26 August. The camera was removed after another 30 days and during which time neither tapirs nor squirrels were photographed again. Three other rodent species were recorded during the sample period: the spotted paca (*Cuniculus paca* (Linnaeus 1766), 29 records), the red-rumped agouti (*Dasyprocta leporina* (Linnaeus 1758), 2 records) and the hairy Atlantic spiny-rat (*Trinomys setosus* (Desmarest 1817), 1 record). Other mammals were recorded after 26 August: Southern tamandua (*Tamandua tetradactyla* (Linnaeus 1758)), nine-banded armadillo (*Dasybus novemcinctus* (Linnaeus 1758)), crested capuchin (*Sapajus robustus* (Kuhl 1820)), South American brocket (*Mazama* sp. (Rafinesque 1817)) and tapeti (*Sylvilagus brasiliensis* (Linnaeus 1758)), with additional visits by the spotted paca.

Only squirrels were interested in the latrine and all other species recorded, including the other

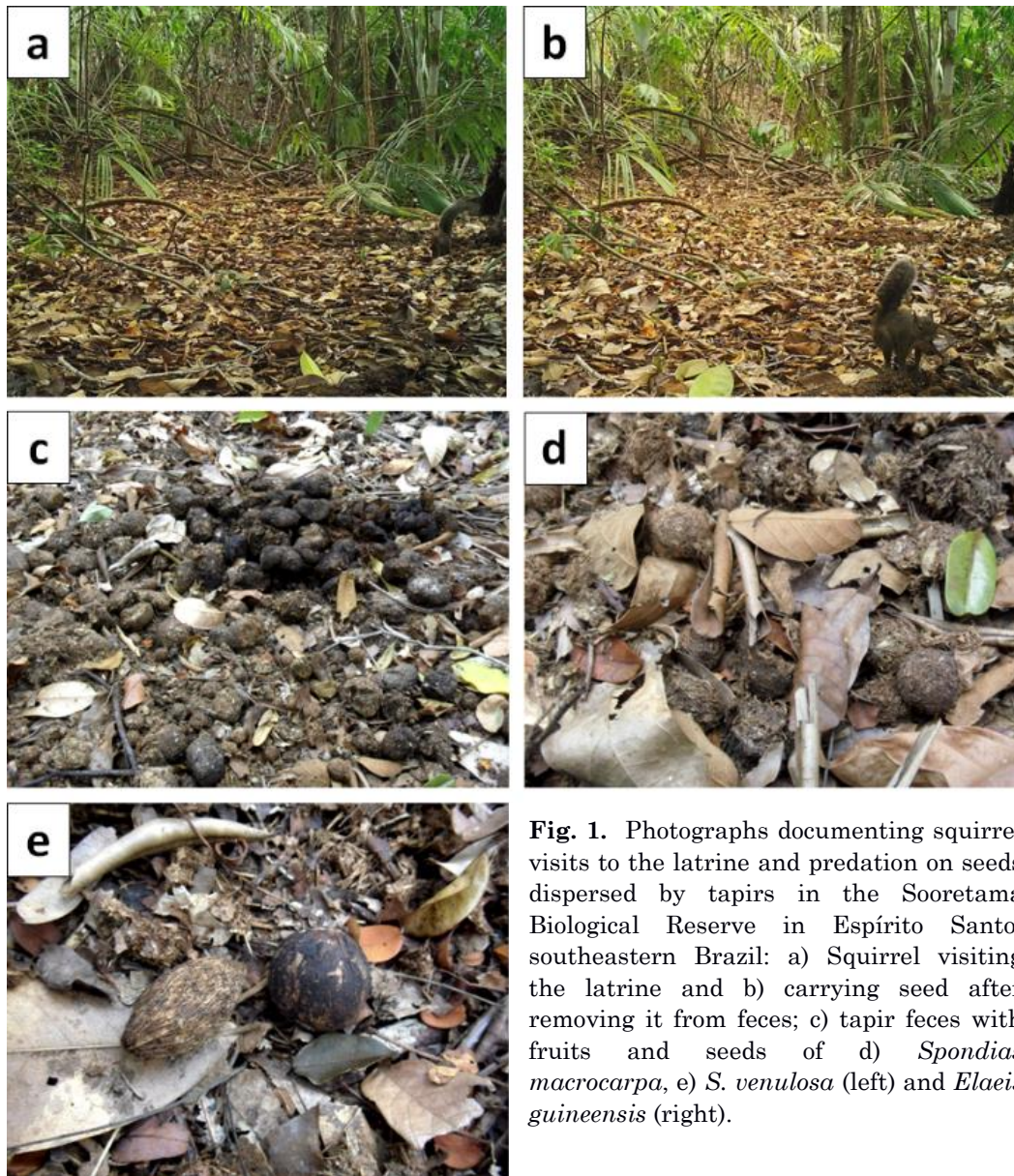


Fig. 1. Photographs documenting squirrel visits to the latrine and predation on seeds dispersed by tapirs in the Sooretama Biological Reserve in Espírito Santo, southeastern Brazil: a) Squirrel visiting the latrine and b) carrying seed after removing it from feces; c) tapir feces with fruits and seeds of d) *Spondias macrocarpa*, e) *S. venulosa* (left) and *Elaeis guineensis* (right).

three rodents, were indifferent to the latrine and simply passed by. On days squirrels visited the latrine, they were recorded in 1–23 events (median = 4) and actively foraged in the latrine feeding on fruits or seeds taken from the tapir feces (Fig. 1). In 77% of the videos after the first fecal deposition by tapir, the squirrel ate the seeds immediately after removing them from the fecal pellet, often close to the camera (other records were equally divided in ‘fruit removal’ and ‘search/inspection’). Also, squirrels appeared to monitor the latrine for the arrival of the tapir (perhaps by scent or by actively checking known latrines – the squirrel is

diurnal while the tapir is essentially crepuscular–nocturnal), because the squirrel tended to visit the latrine sooner after the tapir than expected at random (Fig. 2). The squirrel arrived at the latrine from 0 (the same day) to 8 days after the tapir (median 2 days, compared to 5 days when simply counting days between captures as described above; Fig. 2) and then continued to visit the latrine up to 28 days after the tapir". The median interval after a tapir visit and a visit by the squirrel (2 days) tended to be shorter than that between the last visit by a squirrel before the next visit by a tapir (3.6 days; one-tailed $t = 1.59$, $df = 19$, $P = 0.064$).

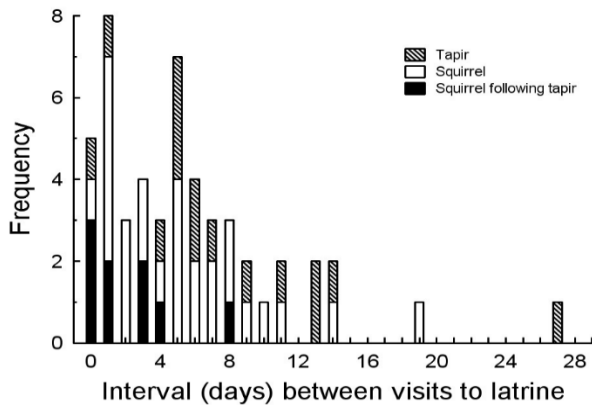


Fig. 2. Comparison of distributions of intervals, in days, between latrine visits by the tapir, by the squirrel overall, and by the squirrel immediately following the tapir visit. This figure shows that visits by the squirrel tend to quickly follow those of the tapir, where it quickly finds and consumes tapir-dispersed seeds.

After the last visit by the tapir (22 July), the squirrel visited the latrine and removed seeds on four different days (the last visit on 19 August). In the last visit, the squirrel inspected the area of the latrine and surroundings, removing a fruit from the latrine on a single occasion. It suggests the latrine probably had very few or almost no seeds on which to feed. On the very last record of squirrel (26 August; 35 days later the last record of tapir), the squirrel inspected the area, but the photos and videos do not showed the inspection of the latrine. Thus, squirrels visited the latrines soon after the tapirs, and apparently stopped visiting once seeds were exhausted from the feces.

During camera maintenance we inspected the latrine to collect seeds from the fecal pellets of the tapirs to identify the plant species they consumed. We found seeds of two species in the plant family Anacardiaceae (*Spondias macrocarpa* Engl., and *S. venulosa* (Engl.) Engl.) and one in the family Arecaceae, the Oil Palm (*Elaeis guineensis* Jacq.; Fig. 1). These seeds were clearly the object of squirrel interest in camera trapping records and on several occasions the squirrel consumed the seeds very close to the camera trap allowing to determine the shape and relative size of the seeds (Fig. 1). Husks and remains of these seeds (with marks from gnawing) were found in and around the latrine.

The Atlantic Forest squirrel is known to disperse and store seeds (scatter hoarding, Paschoal & Galetti 1995) and to consume seeds of

a variety of plants (Bordignon & Monteiro-Filho 1999; Paschoal & Galetti 1995). In contrast to other seed-storing species that usually collect fallen fruits and seeds on the ground (secondary dispersers; Vander Wall 1992), squirrels, being arboreal, are also primary dispersers that remove fruits and seeds from the source (Gautier-Hion *et al.* 1985). Here, instead of providing secondary dispersal (in a diplochoric dispersal system; Vander Wall & Longland 2004), we show that squirrels can be a post-dispersal seed predator that clearly consumes seeds dispersed by the tapir. While it is possible that the squirrel also disperses some seeds (especially if they are very abundant in the latrine), in our observations they appeared to consume most (if not all) seeds found in the tapir feces. In a previous study manipulating the seed composition in feces at simulated latrines of raccoon (*Procyon lotor* (Linnaeus 1758)), five mammal species were recorded actively foraging among the feces and the fox squirrel (*Sciurus niger* Linnaeus 1758) was one of them (Page *et al.* 2001). The present study, however, reports the first record of post-dispersal seed predation without manipulation of available resources in the latrine and with South American species.

Studies of the diet of lowland tapirs include a wide range of latitudes and habitats (e.g. Bueno *et al.* 2013; O'Farrill *et al.* 2013; Quiroga-Castro & Roldán 2001; Tófoli 2006) and they tend to disperse a wide variety of species. The few available seed germination studies show that tapirs can provide germination benefits or other advantages to dispersal. In a study of 12 species of seeds found in latrines, overall germination rate was around 17%, with two notable species having germination rates of $\geq 60\%$ (*Bromelia balansae* Mez and *Psidium guajava* L.) (Tófoli 2006). Elsewhere, using seeds from latrines, 73% of *Cryptocarya mandioccana* Meisn. and 64% of *Hyeronima alchorneoides* Allemão germinated (Bueno *et al.* 2013). Finally, in comparisons of different ways of treating the seeds of *Buchenavia tomentosa* Eichler, 40% of those that passed through the digestive tract of tapirs germinated, while only 25% germinated when cleaned by ants, yet 100% germinated when cleaned by researchers (Giombini *et al.* 2016). Thus, while germination rates after passage through the digestive tract may vary, the long-distance dispersal of large seeds between widely spaced latrines (O'Farrill *et al.* 2013) and the large number of seeds potentially carried by tapirs indicate that tapirs may often play an important role as seed dispersers. Thus,

tapirs may reduce seed predation rates of many mast-producing plants due to a density-dependent response that often occurs beneath the fruiting tree (Howe & Miriti 2004; Janzen 1970; Schupp 1988). However, if squirrels commonly monitor tapir activity, then the seed-predator squirrel may reduce the effectiveness of the seed-dispersing tapir, and is likely to do the same for other larger mammals, such as peccaries and some larger primates.

We describe novel Atlantic Forest squirrel predation on seeds dispersed by lowland tapirs and suggest that seed predation may remove most (if not all) seeds deposited in the latrines visited by the squirrels, compromising the ecosystem service provided by other dispersers. Although these data were collected by a single camera at one tapir latrine, it is unlikely that the squirrel behavior recorded here was that of a single squirrel. We must assume that if one squirrel behaves this way, the behavior is likely to be done by other squirrels. The nature of the visits and the evidence that the squirrel is aware of the tapir and quickly follows to uncover seeds in the feces implies a complex, observational behavior on the part of the squirrel. If this behavior is a general trend, and considering the ubiquity of the squirrel, the pattern is likely to be often repeated, especially in tropical forests with similar mammalian assemblages.

When seeds are extremely abundant, more than can be eaten at the time, squirrels often stock some fraction of the excess. However, in areas near tapir latrines and which may be far from the original source of the seeds, seed availability may be relatively low, in which case squirrels may completely consume those seeds. Clearly the density of tapirs, the relative abundance of fruits with seeds potentially useful to the tapir and the squirrel, the abundance of these seeds in the tapir feces, and the density of squirrels will influence the total negative impact of post-dispersal predation on seed dispersal by the tapirs. Future studies should address these issues. Also, because squirrels are nearly ubiquitous in tropical forests, we need to understand how common squirrel seed predation at latrines is to estimate how effective the squirrel is in eliminating benefits of dispersal by the tapir. Next, squirrels should be marked to determine whether their use of tapir latrines is facultative and only occurs by chance, or whether (as our data suggest) squirrels actively monitor tapirs to benefit from the seeds they have dispersed. Finally, future studies should determine whether other larger mammals (such as peccaries

and larger primates) are also monitored by squirrels for the same reason. This dynamic suggests that Atlantic Forest squirrels (and other squirrels) may often interact with seed dispersal by other mammals. Thus, seeds may escape predation beneath parent plants through dispersal, but may be consumed post-dispersal by other seed predators.

Acknowledgements

C. J. Cunha thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the research assistantship. A. C. Srbek-Araujo thanks Universidade Vila Velha (UVV 21/2015) and Fundação de Amparo à Pesquisa do Espírito Santo (FAPES 0607/2015) that supported this research. Finally, we thank Vale S.A./Instituto Ambiental Vale for financial support, and Sooretama Biological Reserve for permission to carry out our research on their lands (SISBIO 50048-3).

References

- Bleher, B. & K. Bohing-Gaese. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* **129**: 385–394.
- Bordignon, M. & E. L. A. Monteiro-Filho. 1999. Seasonal food resources of the Squirrel *Sciurus ingrami* in a secondary Araucaria forest in southern Brazil. *Studies on Neotropical Fauna and Environment* **34**: 137–140.
- Bueno, R. S., R. Guevara, M. C. Ribeiro, L. Culot, F. S. Bufalo & M. Galetti. 2013. Functional redundancy and complementarities of seed dispersal by the last neotropical megafrugivores. *PLoS One* **8**: 56252.
- Dirzo, R. & A. Miranda. 1990. Contemporary neotropical defaunation and forest structure, function, and diversity—a sequel to John Terborgh. *Conservation Biology* **4**: 444–447.
- Fragoso, J. M. V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology* **85**: 519–529.
- FSOSMA & INPE. 2014. *Atlas dos Remanescentes Florestais da Mata Atlântica - Período 2012–2013*. [Atlas of the Atlantic Forest Remnants - Period 2012–2013]. Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais, São Paulo. [https:// www.sosma.org.br/wp-content/uploads/2014/05/atlas_2012-2013_relatorio_tecnico_20141.pdf](https://www.sosma.org.br/wp-content/uploads/2014/05/atlas_2012-2013_relatorio_tecnico_20141.pdf) (accessed on 29 December 2014).

- Galetti, M., R. S. Bovendorp & R. Guevara. 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forest. *Global Ecology and Conservation* **3**: 824–830.
- Gautier-Hion, A., J. M. Duplantier, R. Quris, F. Feer, C. Sourd, J. P. Decoux & A. Moungazi. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65**: 324–337.
- Giombini, M. I., S. P. Bravo & D. S. Tosto. 2016. The key role of the largest extant Neotropical frugivore (*Tapirus terrestris*) in promoting admixture of plant genotypes across the landscape. *Biotropica* **48**: 499–508.
- Gonzalez-Garay, I. & C. M. Rizzini. 2003. *A Floresta Atlântica de Tabuleiros: diversidade funcional da cobertura arbórea*. [The lowland Atlantic Forest: functional diversity of the tree cover]. Vozes, Rio de Janeiro.
- Howe, H. F. & M. N. Miriti. 2004. When seed dispersal matters. *BioScience* **54**: 651–660.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forest. *American Naturalist* **104**: 501–528.
- Janzen, D. H. & P. S. Martin. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* **215**: 19–27.
- Morellato, L. P. C. & C. F. B. Haddad. 2000. Introduction: The Brazilian Atlantic Forest. *Biotropica* **32**: 786–792.
- O'Farrill, G., M. Galetti & A. Campos-Arceiz. 2013. Frugivory and seed dispersal by tapirs: an insight on their ecological role. *Integrative Zoology* **8**: 4–17.
- Page, L. K., R. K. Swihart & K. R. Kazacos. 2001. Seed preferences and foraging by granivores at raccoon latrines in the transmission dynamics of the raccoon roundworm (*Baylisascaris procyonis*). *Canadian Journal of Zoology* **79**: 616–622.
- Paschoal, M. & M. Galetti. 1995. Seasonal food use by the neotropical squirrel *Sciurus ingrami* in southeastern Brazil. *Biotropica* **27**: 268–273.
- Quiroga-Castro, V. D. & A. I. Roldán. 2001. The fate of *Attalea phalerata* (Palmae) seeds dispersed to a tapir latrine. *Biotropica* **33**: 472–477.
- Sanchez-Cordero, V. & R. Martinez-Gallardo. 1998. Post dispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in Mexico. *Journal of Tropical Ecology* **14**: 139–151.
- Schupp, E. W. 1988. Seed and early seedling predation in the forest under story and in treefall gaps. *Oikos* **51**: 71–78.
- Terborgh, J. 1988. The big things that run the world—a sequel to E O Wilson. *Conservation Biology* **2**: 402–403.
- Tófoli, C. F. D. 2006. Frugivoria e Dispersão de Sementes por *Tapirus terrestris* (Linnaeus, 1758) na paisagem Fragmentada do Pontal do Paranapanema. [Frugivory and Seed Dispersal by *Tapirus terrestris* (Linnaeus, 1758) in the Fragmented Landscape of Pontal do Paranapanema]. M.Sc. Thesis. Universidade de São Paulo, São Paulo, Brazil.
- Vander Wall, S. B. 1992. The role of animals in dispersing a “wind-dispersed” pine. *Ecology* **73**: 614–621.
- Vander Wall, S.B. & W.S. Longland. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology and Evolution* **19**: 155–161.
- Wright, S. J., H. Zeballos, I. Domínguez, M. M. Gallardo, M. C. Moreno & R. Ibañez. 2000. Poachers alter mammal abundance, seed dispersal and seed predation in neotropical forest. *Conservation Biology* **14**: 227–239.

(Received on 08.06.2017 and accepted after revisions, on 20.08.2017)