

# The effect of passage through the gut of the Greater Rhea (*Rhea americana*) on germination of tree seeds: implications for forest restoration

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**Abstract.** Long-distance dispersal of seeds is an important process for maintaining genetic connectivity between forest fragments and for promoting fast re-colonisation of deforested land. Based on the hypothesis that the Greater Rhea (*Rhea americana*), a large flightless bird native to South America, could play a major role as a disperser of tree seeds, we evaluated whether passage of seeds through its digestive tract affected germination of six tree species native to central Argentina. We determined the proportion of seeds that germinated in a climate-controlled chamber for untreated (control) seeds, as found under seeding trees, seeds that passed through the digestive tract of captive Greater Rheas, and seeds treated with optimum pre-germination treatments for seedling production. Our results showed that the germination response to passage through the gut reached or surpassed the optimum germination treatments in three species of tree, was similar to control treatments and lower than optimum treatments in two species, and lower than all alternative treatments in one species of tree. We conclude that Greater Rheas are one of the few remaining large-bodied native animals with potential to disperse seeds of large fruits effectively, thus reinforcing the importance of restoring former populations of Greater Rhea.

## Introduction

Large seed-eating animals retain seeds within the gut for a longer time than small animals. The latter, including many perching birds, typically deposit a large proportion of ingested seeds under the parental trees, where the possibilities of succeeding are reduced through competition and predation. Conversely, many large seed-eating animals disperse seeds over long distances, which enhances the possibility of success of the seeds through reduced competition and predation (Alcántara *et al.* 2000; Pakeman 2001; Aerts *et al.* 2006). In Central and South America, most large native fauna disappeared 8000–15 000 years ago, possibly from indigenous hunting, or climate change or a combination of the two (Barnosky *et al.* 2004). In Central America, introduced livestock appears to be functioning as seed dispersers (Janzen and Martin 1982) and the only abundant large animals that have been identified as potential long-distance dispersers in central Argentina are also introduced livestock (e.g. Peinetti *et al.* 1993; Campos and Ojeda 1997; Campos *et al.* 2008). However, small isolated populations of two fairly large herbivores still inhabit central Argentina: the Guanaco (*Lama guanacoë*) and the Greater Rhea (*Rhea americana*), both of which could play an important but as yet unknown role in seed dispersal.

The Greater Rhea could be an efficient disperser because it is a large, flightless, herbivorous bird that eats fruits and seeds of a wide range of sizes (Martella *et al.* 1996; Pereira *et al.* 2003; Pratolongo *et al.* 2003). Populations of Greater Rhea have

declined greatly owing to loss of habitat and hunting (Bellis *et al.* 2004a, 2004b; Martella and Navarro 2006; Giordano *et al.* 2008). As a consequence, this species has been listed as Near Threatened globally (IUCN, see <http://www.iucnredlist.org>, accessed 5 December 2009) and placed in appendix 2 of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora; see <http://www.cites.org/eng/app/appendices.shtml>, accessed 17 March 2010). To the best of our knowledge, the only study to date on the effect on seeds of passage through the gut of the Greater Rhea is that of Pratolongo *et al.* (2003) on the seeds of the leguminous tree *Prosopis nigra* from eastern Argentina. If Greater Rheas are effective dispersers of seeds they could be a keystone species in forest regeneration and restoration, which is especially important in central Argentina where less than 5% of the original forest cover remains and soil loss is common (Kopta 1999; Gavier and Bucher 2004; Zak and Cabido 2004; Cingolani *et al.* 2008b; Renison *et al.* 2009).

Assuming that the Greater Rhea could play a major role as a disperser of tree seeds, our objective was to determine whether passage of seeds through the digestive tract of the Greater Rhea affects germination of six species of native tree. We postulate that if at least a small proportion of the seeds passing through the gut of the Greater Rhea are viable, the Greater Rhea could be classified as a potential disperser and that if germination of seeds is enhanced by passage through the gut the dispersal role of Greater Rheas will be greater.

## Materials and methods

The Greater Rhea is a large ratite (height 1.4 m, mass 20–25 kg) that inhabits grasslands, shrublands and open woodlands in Bolivia, Paraguay, Brazil, Uruguay and Argentina, extending south as far as the Río Negro River (Bruning 1974). The species is mainly herbivorous, and when tree seeds are available they are abundant in scats of wild Greater Rheas (Pereira *et al.* 2003). The average home-range of the Greater Rhea is 2.6 km<sup>2</sup> and birds move about to forage in forest fragments, grasslands and agricultural lands, with the maximum recorded distance travelled 7.8 km in a 2-month period (Martella *et al.* 1995; Bazzano *et al.* 2002; Bellis *et al.* 2004a, 2004b).

From December 2006 to March 2007 we collected ripe fruits of six species of tree from three localities situated in the Province of Córdoba, central Argentina: the Botanical Garden of Córdoba city (31°23'11"S, 64°14'58"W), Cuesta Blanca (31°28'57"S, 64°34'59"W) and San Marcos Sierras (30°48'36"S, 64°39'05"W). Mean monthly temperatures in this area range from 26°C in summer to 8°C in winter and annual rainfall is ~800 mm (Cabrera 1976).

The species of tree were selected based on the availability of fruit and a range of fruit types: two tree species with large fleshy fruits (*Geoffroea decorticans* (commonly known as Chañar) and *Ziziphus mistol* (Mistol)), two legumes with medium-sized fruit (*Prosopis nigra* (Algarrobo negro) and *Prosopis alba* (Algarrobo blanco)), and two species with small fleshy fruits, which are usually dispersed by small birds (*Celtis erherbergiana* (Tala) and *Condalia microphylla* (Piquillín)); summary descriptions of the trees and their fruits are in Table 1. Wild Greater Rheas are known to consume fruits of *Prosopis nigra* (Pereira *et al.* 2003; Pratolongo *et al.* 2003) and *Geoffroea decorticans* (M. Martella, pers. obs.). We are not aware of any studies or observations of Great Rheas eating the seeds of the other species, but the geographical distributions of the trees overlap the distribution of the Greater Rhea, and these trees have abundant fruits that occur on low branches or become accessible when they have fallen to the ground. It is therefore possible they are eaten by Greater Rheas. All selected trees are fairly abundant in remnant forest fragments of central Argentina and are good colonisers of disturbed sites, and are abundant near forest edges (Arturi 1997).

The gut-passage assays were performed on six captive Greater Rheas (two adult females, one adult male and three juveniles of unknown sex) from the Córdoba Zoo, which were individually identified with coloured Velcro leg-bands. Between May and July 2006, individual Greater Rheas were offered a combination of fruits of the six tree species that provided 100 seeds or more of each species. To determine the number of seeds in fruits, we

assumed there was a single seed in each lobule of the fruits of the two *Prosopis* species (15–20 seeds for *P. nigra* and 22–28 seeds for *P. alba*) and that there was one seed per fruit for the other species of tree. As suggested by Traveset and Verdú (2002), fruits of the six tree species were thoroughly mixed before use. Droppings were collected 36 h after feeding, which is the maximum retention period for ratite birds like the Greater Rhea (Stewart 1994). Seeds were manually collected from faeces and then identified by comparison with a reference collection. The retrieved seeds were stored in paper bags at room temperature.

The germination success of the six tree species was evaluated in: (1) control seeds remaining inside fruits, as found under trees when not consumed by animals; (2) seeds obtained after passage through the digestive tract of a Greater Rhea, washed and stored in paper bags until tests of seed germination; (3) seeds manually extracted from fruit and treated with the pre-germination treatments recommended for each species by Haene and Aparicio (2001; see below); and (4) seeds treated with the pre-germination treatments recommended by Kopta *et al.* (1996; see below). Following Samuels and Levey (2005) we used complete fruits for the control treatments – rather than seed removed from fruits, as is more usual – to better mimic the natural situation of fruits that are not eaten. We also included pre-germination treatments recommended by others because we assumed they mimic the natural processes that break seed dormancy and thus considered them a better comparison. The pre-germination treatments recommended by Haene and Aparicio (2001) and by Kopta *et al.* (1996) are based on experience in production of seedlings of these species but differed between the authors for the six species. Optimum germination treatments according to Haene and Aparicio (2001) were: for *G. decorticans*, *Z. mistol* and *Condalia microphylla* we removed exocarp and mesocarp; for *P. alba* and *P. nigra* we removed endocarp with sand paper and submerged the seed in water at 80°C until the water cooled to room temperature; and for *Celtis erherbergiana* we removed exocarp and mesocarp and soaked the endocarp in water at room temperature for 48 h. The germination treatments of Kopta *et al.* (1996) were: for *G. decorticans*, *Z. mistol* and *Condalia microphylla* we removed exocarp and mesocarp and immersed seeds in water at 22–26°C for 48 h; for *P. nigra* and *P. alba* we removed the endocarp and immersed the seeds in water at 22–26°C for 48 h; and for *Celtis erherbergiana* we removed exocarp and mesocarp.

Germination of seeds was tested in Petri dishes held at 30°C for 16 h of light and 20°C for 8 h of darkness in a climate

**Table 1. Brief description of the six species of tree and their fruits fed to Greater Rheas. Descriptions based on Haene and Aparicio (2001) and Demaio *et al.* (2002)**

Species (and vernacular name)	Family	Tree height	Fruit characteristics
<i>Geoffroea decorticans</i> (Chañar)	Fabaceae	6–10 m	Drupe, 2–3 cm in diameter, orange-red skin, a dry fleshy pulp and one hard thick seed
<i>Ziziphus mistol</i> (Mistol)	Ramnaceae	4–10 m	Drupe, 1.5 cm in diameter, dark red skin, a fleshy pulp and one hard thick seed
<i>Prosopis nigra</i> (Algarrobo negro)	Mimosaceae	3–8 m	Long fleshy pod 10–20 cm, yellow with purple stripes, very sweet taste
<i>Prosopis alba</i> (Algarrobo blanco)	Mimosaceae	Up to 18 m	Long fleshy pod 12–25 cm, yellowish in colour, sweet taste
<i>Celtis erherbergiana</i> (Tala)	Celtidaceae	4–12 m	Drupe, 0.4–0.6 cm in diameter, yellow-orange skin, sweet thin fleshy pulp and one hard seed
<i>Condalia microphylla</i> (Piquillín)	Ramnaceae	2–5 m	Drupe, ~0.7 cm in diameter, dark purple skin, sweet fleshy pulp and one hard seed

chamber with a warm-white light source, resembling favourable germination conditions for many native trees of central Argentina (Aráoz 2006). Seeds were watered with distilled water as necessary and seedling emergence checked every 5 days. The experiments finished after 80 days, when emergence was zero for all species. Sample sizes varied according to the number of seeds from each species of tree that we were able to retrieve after passage through the gut (see 'Results'). As we wanted to compare differences between individual Greater Rheas, seeds of each tree species and individual Greater Rhea were kept in separate Petri dishes for the germination tests (e.g. for the gut passage treatment of *G. decorticans* we had six Petri dishes with 10, 6, 8, 11, 5 and 16 seeds, see Table 2). In order to keep the rest of the experimental design as balanced as possible given the above caveat, for the other three treatments of the same tree species we used the same sample sizes for each Petri dish (e.g. for the control treatment of *G. decorticans* we set up six Petri dishes with 10, 6, 8, 11, 5 and 16 fruits). In the case of the two *Prosopis* species of tree the control treatments consisted of six entire pods per species, with 15–25 seeds each. Distance between seeds and fruits within a dish varied according to sample size, but was always greater than 1 cm.

#### Analysis of data

To establish differences in germination of seeds among control, gut, and the two pre-germination treatments we performed a Kruskal–Wallis test for each tree species. For simplicity we used non-parametric statistics because conditions for parametric statistics were not met for some of the tree species, and if met, parametric and non-parametric statistics yielded similar results.

To determine if the percentage of seeds that germinate after passage through the gut could vary among individual Rheas, we performed a Chi-square test for each tree species, comparing the number of germinated and non-germinated seeds among individuals.

## Results

### Passage through the gut and germination

The number of seeds retrieved from the six Greater Rhea droppings was low and varied. From the total of 600 seeds of each tree species fed to the six Rheas we were able to retrieve 56 seeds of *G. decorticans*, 161 of *Z. mistol*, 21 of *P. nigra*, 57 of *P. alba*, 50 seeds of *Celtis erherbergiana* and 30 of *Condalia microphylla*. All retrieved seeds were macroscopically intact. A visual inspection of seeds revealed that the membranes joining the two testa capsules of *G. decorticans* seeds and the operculum

stopping the micropyle pore of *Z. mistol* seeds had disappeared during passage through the gut, allowing water to enter the embryo. We did not detect any visible modifications to the seeds of the other species.

The rate of germination of seeds of *G. decorticans*, *Z. mistol* and *P. nigra* were significantly greater after passage through the gut compared with the control seeds (Fig. 1). The seeds of *G. decorticans* only germinated (with few exceptions) after passage through the gut, whereas rates of germination of the control seeds and of the seeds from the two pre-germination treatments was significantly lower (Kruskal–Wallis analysis of variance (ANOVA):  $H=13.14$ , d.f.=3,  $P<0.001$ ; Fig. 1a). Germination of seeds of *Z. mistol* and *P. nigra* was similar for seeds that passed through the gut and those of the two pre-germination treatments, but always significantly greater than rates of germination of the control seeds (Kruskal–Wallis ANOVA for *Z. mistol*:  $H=11.50$ , d.f.=3,  $P=0.007$ ; for *P. nigra*:  $H=11.05$ , d.f.=3,  $P=0.008$ ; Fig. 1b, c). Germination of seeds of the legume *P. alba* and of *Condalia microphylla* (with small fleshy fruits) was not significantly affected by passage through the gut of Greater Rheas, with rates of germination for passage through the gut similar to those of the control treatment and lower than the optimum treatments (Kruskal–Wallis ANOVA for *P. alba*:  $H=17.78$ , d.f.=3,  $P<0.001$ ; for *Condalia microphylla*:  $H=8.58$ , d.f.=3,  $P=0.007$ ; Fig. 1d, e). Germination of seeds of the small fleshy fruits of *Celtis erherbergiana* was negatively affected by passage through the gut, because the highest germination rates were recorded in the control group (Kruskal–Wallis ANOVA:  $H=7.90$ , d.f.=3,  $P=0.039$ ; Fig. 1f).

### Differences among Greater Rheas

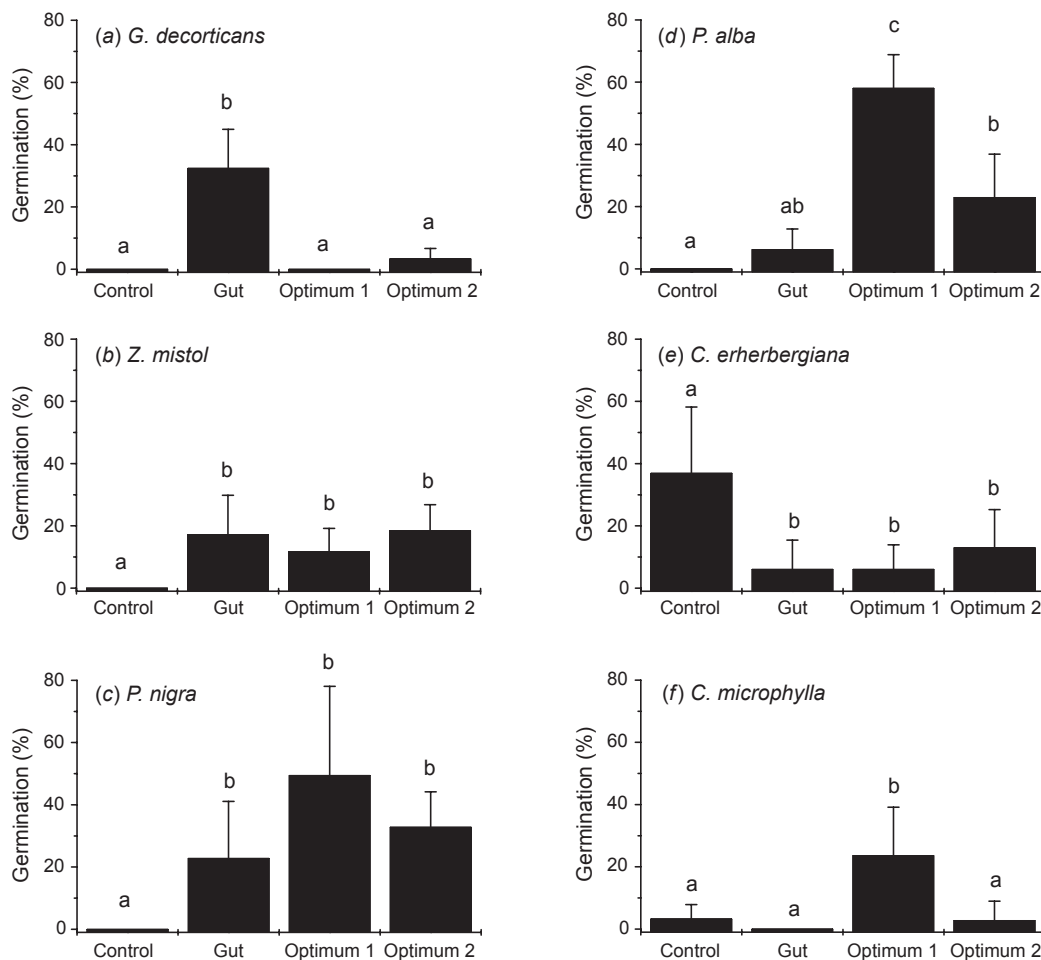
Differences in rates of germination of seeds among Greater Rheas were significant for *Z. mistol* ( $P=0.007$ ), whereas there were no significant differences for *G. decorticans*, *P. alba* or *Celtis erherbergiana*. Coincidentally, sample sizes were also smaller for these species (Table 2). We did not analyse differences for *P. nigra* or *Condalia microphylla* because few or no seeds germinated after passage through the gut.

## Discussion

Our results suggest that the Greater Rhea is a disperser of tree seeds in central Argentina, especially of leguminous trees and trees with large fleshy fruits, and Greater Rheas may be one of the few extant, large-bodied, native dispersers of such seeds. Additionally, Greater Rheas may also be dispersers of some species of trees with small seeds, and that the effect on seed

**Table 2. Rate of germination (%) for seeds evaluated after passage through the digestive tract of six Greater Rhea individuals**  
The number of retrieved seeds for each species of tree is given in parentheses; sex of juveniles not known

Tree species	Greater Rhea						Total number of retrieved seeds	$\chi^2$	P
	Female 1	Female 2	Male	Juvenile 1	Juvenile 2	Juvenile 3			
<i>Geoffroea decorticans</i>	10 (10)	33 (6)	25 (8)	36 (11)	40 (5)	50 (16)	56	4.79	0.441
<i>Ziziphus mistol</i>	0 (20)	7 (27)	27 (22)	38 (26)	13 (30)	17 (36)	161	15.97	0.007
<i>Prosopis nigra</i>	20 (5)	50 (4)	33 (3)	0 (4)	0 (2)	33 (3)	21	–	–
<i>Prosopis alba</i>	14 (22)	15 (13)	8 (12)	0 (3)	0 (6)	0 (1)	57	0.31	0.858
<i>Celtis erherbergiana</i>	0 (12)	11 (18)	25 (16)	0 (1)	0 (2)	0 (1)	50	0.388	0.144
<i>Condalia microphylla</i>	0 (3)	0 (7)	0 (8)	0 (4)	0 (4)	0 (4)	30	–	–



**Fig. 1.** Rate of germination (%) for fruits of six species of trees under different pre-germination treatments: a control, passage through the gut of a Rhea, and two optimum pre-germination treatments for maximising seedling production (see text for details). (a) *Geoffroea decorticans*; (b) *Ziziphus mistol*; (c) *Prosopis nigra*; (d) *Prosopis alba*; (e) *Celtis erherbergiana*; and (f) *Condalia microphylla*. Different letters indicate significant differences within each species of tree ( $P < 0.05$ ).

germination may vary between individual Greater Rheas. The seeds retrieved after passage through the Rhea's gut were all macroscopically intact and their low recovery rates did not seem to be related to deterioration, because no seeds were broken; rather, we incidentally observed that retrieved seeds were consumed again by the same or other Greater Rheas (the ingestion of scats is a behaviour often observed in captive Greater Rheas), and also that on several occasions the Zoo personnel threw away Rhea faeces while cleaning the enclosure, thus causing additional loss of seeds.

Of the tree species studied, the fruits of *G. decorticans* and *Z. mistol* are greater than 1 cm in diameter, their seeds are protected with a hard endocarp, and their fleshy fruits accumulate on the ground when ripe. It has been suggested that mammals or reptiles are likely to eat them (Varela 2004). As the Greater Rhea is a large bird, it can easily swallow and disperse these fruits. Many retrieved seeds of *G. decorticans* were scraped, possibly in the Rheas' gizzard, and the rate of germination of these seeds was clearly increased by passage through the gut of the Rhea. Interestingly, even optimum pre-

germination treatments, consisting of removing physical barriers, did not perform as well as passage through the gut for this species, suggesting that Greater Rheas could have an important role in the dispersal of *G. decorticans*, but also suggesting that further research is needed to enhance pre-germination treatments of this species for silvicultural purposes.

Seeds of the large fleshy fruits of *Z. mistol* trees have physical dormancy because of their hard protective endocarp (Aráoz 2006). Our results indicate that passage through the gut of the Greater Rhea provides the necessary abrasion to break down this type of physical dormancy. The physical barrier that produces dormancy in the seeds of *Z. mistol* is given by a whitish membrane that forms a plug on an endocarp perforation (Aráoz 2006). When *Z. mistol* seeds were retrieved from Greater Rhea droppings, in many cases we observed abrasion or complete elimination of the plug, which left the perforation free for exchange of air and water.

The *Prosopis* species we selected for this experiment produce a pod that contains seeds with physical dormancy induced by a hard tegument (physical coat-imposed dormancy; Haene and Aparicio 2001). As a consequence, the germination of control



treatments was zero and any treatment or scarification will increase rates of germination. Accordingly, passage through the gut improved rates of germination in both species. For *P. alba*, the passage of seeds through the gut was insufficient to reach rates of germination similar to those of the pre-germination treatments, whereas for *P. nigra* there was no significant difference in rates of germination between passage through the gut and the pre-germination treatments, though we cannot state if this is a real pattern or a result of lack of statistical power. Pratolongo *et al.* (2003) found that germination of *P. nigra* seeds retrieved from wild Greater Rhea droppings was similar to the percentages we found (~10%) but in their study control seeds without the pod and no pre-germination treatment had germination percentages about three times more than seeds retrieved from the droppings. The difference between the study of Pratolongo *et al.* (2003) and our study could be a result of differences in the control treatments (they removed seeds from the pod whereas we did not), or differences between tree ecotypes.

The fairly small fleshy fruits of *Celtis erherbergiana* had non-dormant seeds (Verzino *et al.* 1998). Because passage through the gut of the Greater Rhea reduced rates of germination of seeds compared to control seeds, Rheas that eat these fruits could act only as dispersers of seeds without increasing rates of germination and these seeds are probably better adapted to dispersal by small birds, in which gut passage is more rapid. As for the small-fruited tree *Condalia microphylla*, our results suggest that this species would not be effectively dispersed by Greater Rheas, because germination for seeds subjected to the gut passage was zero.

Other species of tree from central Argentina have fruits similar to the ones we selected, and further studies are needed to determine the potential role of the Greater Rhea in their dispersal. Examples include several other species of *Prosopis* (commonly known as Algarrobos), *Acacia aroma* (Espinillo), *Ximena americana* (Albaricoque), *Triptrinax campestris* (Caranday), *Condalia buxifolia* (Piquillín grande) and *Castela coccinea* (Mistol del zorro) (Demaio *et al.* 2002). Studies would also be necessary to determine the dispersal of seeds by the Greater Rhea in the wild; to date, there has been only one study that has quantified rates of consumption of tree seeds by wild Greater Rheas (Pereira *et al.* 2003) and no study has compared gut and control treatments in the field, as suggested by Traveset (1998). The results of *in vitro* studies, such as this one, also need to be supported by field trials (Rodríguez-Pérez *et al.* 2005; Robertson *et al.* 2006). Lastly, the results of this study show that the effects of passage of seeds through the gut of the Greater Rhea differ between individual Rheas for at least one of the tree species. These differences, previously reported in other animal species (e.g. Razanamandranto *et al.* 2004), could be a result of differences in gizzard content or passage time through the gut, two aspects that are poorly known in wild Greater Rheas.

Our finding that germination rates of tree seeds are generally increased by passage through the gut agrees with Traveset (1998) and Traveset and Verdú (2002), who showed that seeds of trees benefit by passage through the gut, in comparison to seeds of other plant forms, such as grasses and herbs. A similar example of seed dispersal by large birds can be found in Australasia, where Southern Cassowaries (*Casuaris casuaris*), Dwarf Cassowaries (*Casuaris bennetti*) and Emus (*Dromaius*

*novae-hollandiae*) appear to be the only extant frugivores large enough to effectively disperse some of the plant species with big fruits (Stocker and Irvine 1983; Clifford and Monteith 1989; Mack 1995; Bradford *et al.* 2008; Bradford and Westcott *in press*).

Plant species with large fruits will be particularly affected if populations of Greater Rheas continue to decline, because animals that have large mouths or bills suitable for ingestion of large fruits and effective dispersal of their seeds are scarce (Cramer *et al.* 2007). If seeds from these species are eaten by smaller animals, such as native lizards, rodents, turtles and tortoises and foxes (e.g. Campos and Ojeda 1997; Varela and Bucher 2002a, 2002b; Varela *et al.* 2008), they are unlikely to be transported more than 100 m because the consumers have fairly small home-ranges (e.g. Lindstedt *et al.* 1986; Wang *et al.* 2007). The home-range of Greater Rheas is large, and the gut-retention time should be sufficient for the faeces to be deposited several kilometres away from the parent plant. Domestic livestock may at least partly supplement populations of Greater Rheas in the dispersal of seeds (e.g. Campos and Ojeda 1997) but these animals often have, or appear to have, a negative effect on biodiversity conservation of South American ecosystems (Cingolani *et al.* 2008a, 2008b; Renison *et al.* 2009) and it would be prudent to promote other alternatives.

We conclude that Greater Rheas may play a key role in maintaining seed-dispersal services for a variety of tree species, and may promote greater gene flow among forest patches and regeneration of disturbed sites by doing so. Thus, the dispersal services that the Greater Rhea may offer should be taken into account when considering management for conservation of this species and for forest conservation and restoration.

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