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Ownership structure of protected areas influences the patterns of seed removal by mammals

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In Mexico, nature reserves vary greatly in the size of the property, administration, financial budget and measures to protect against land use change and illegal hunting. We compared two private and two public reserves and observed an influence between the ownership structure and the patterns of removal of large and small seeds from the forest floor by medium-sized mammals and rodents. We hypothesized that removal of all seeds, of large seeds only, and the removal of seeds by the medium-sized mammals would be higher in the private than in the public reserves as a consequence of better conserved populations in the private reserves. We also expected a direct effect of seed removal on seed germination. Medium-sized mammals removed more large-seeds in the private than in the public reserves, whereas removal of small seeds by rodents was lower in the private than in the public reserves, indicating an absence of larger-sized mammals in the latter. Seed germination was higher in control plots where seed removal was prevented by excluding all mammals. We conclude that patterns on seed removal by mammals in reserves can be strongly influenced by the type of ownership and hence the extent of their conservation.

Key words: Animal conservation, land-property, medium-sized mammals, protected areas, rodents, seed predation.

INTRODUCTION

Tropical rain forests continue to suffer from a heavy defaunation of fruit and seed mammal consumers due to habitat loss and illegal hunting (Ceballos et al., 2005; Sanchez-Cordero et al., 2005; Peres and Palacios, 2007). It is widely recognized that illegal hunting has severely depleted populations of large and medium-sized mammals in the tropics (Kinnard et al., 2003; Corlett, 2007; Topp-Jørgensen et al., 2009). Current mammalian populations in the humid tropics are highly devastated compared to 50 or 100 year ago (Corlett, 2007).

One of the main objectives of natural protected areas (NPA) is to avoid loss and damage to the ecosystem and its wildlife by preventing land use change and illegal hunting. Effectiveness of NPA had been particularly studied with respect to the prevention of land use change

(Figueroa and Sanchez-Cordero, 2008) since this trait directly effects other degradation processes, such as biodiversity loss (Sala et al., 2000; Kinnard et al., 2003; Sanchez-Cordero et al., 2005), land degradation (Riezebos and Loerts, 1998; Islam and Weil, 2000), local and regional climate change (Chase et al., 2000), global climate change (Houghton et al., 1999), and loss of ecosystem services (Vitousek et al., 1997). However, in Mexico and several other developing countries in the tropics, the full effectiveness of the NPA has not yet been attained. Notable factors that impede the NPA to meet their goals are the physical characteristics of the natural reserves, such as shape, size and connectivity, and operative factors, such as infrastructure, legislation, financial budget and human resources (that is, forest guards) which are vital (Dirzo and Miranda, 1991; Hernandez, 1994; James, 1999; Ervin 2003). Due to the relative low social return, investment in protected areas is, in general, below worldwide standards (Dixon and

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Sherman, 1991). Natural reserves in Mexico face important conservation and operative challenges, such as low financial resources, scarce personal, lack of management plans and low logistic resources, such that indicative species of large and well conserved areas, for example carnivores, have become absent (Hernandez, 1994). In Mexico, financial resources vary considerably depending on whether the NPA is a private, federal or state owned property and their budgets generally smaller in that order, as well. Vigilance, which is a direct consequence of financial budget, is also of great importance since it directly influences land use change and the presence of illegal hunting, which often occurs due to a significant social pressure from the human settlements within or close to the NPA (Chazdon et al., 2009).

Tropical rain forest defaunation has affected particularly the large-sized mammals and carnivores; this in turn has favored the increase of small mammalian populations such as rodents (Dirzo and Miranda, 1991; Sanchez-Cordero and Fleming, 1993; Dirzo et al., 2007), most likely owing to the high abundance of food resources and absence of predators. Populations of large mammals, such as the tapir (Tapirus bairdii), peccary (Tayassu tajacu and Tayassu pecari) and white-tailed deer (Odocoileus virginianus), which are consumers of large masses of fruits and seeds from the forest floor, have been depleted in Mexico (Ramirez-Pulido et al., 1986; Mendoza, 2005). Medium-sized mammals, such as the Mexican agouti (Dasyprocta mexicana), red brocket (Mazama americana) and lowland paca (Agouti paca) have been subjected to illegal hunting and have lost their habitat. However, due to their smaller body size and lower food requirements, they are able to occupy small habitats such that their distribution is less restricted to large fragments (Bodmer et al., 1997).

Distinct patterns of food resource partitioning have been observed among the various groups of seed consumers (Demattia et al., 2004; Beckman and Muller-Landau, 2007): Small mammals such as rodents tend to select small seeds (< 2.5 cm in diameter), while mammals over 30 g weights tend to consume larger seeds (> 2.5 cm). As a result of this differential seed predation, mammals exert an important role in the floristic composition of the seedlings, and possibly also in the composition of the tree community, by directly influencing germination and establishment (Dirzo, 2001; Wright, 2003; Wright et al., 2007).

Studies on how defaunation effects seed predation and, consequently, the seedling composition (Muller-Landau, 2007; Stoner et al., 2007a) have compared NPA to non-NPA. The results show that there is a significantly higher amount of predation of large seeds in the NPA without hunting, and thus there is also a larger population of medium-sized mammals, compared to the non-NPA without these mammals (Beckman and Muller-Landau, 2007; Dirzo et al., 2007; Wright et al., 2007).

In Mexico, three types of ownership structure of natural reserves can be distinguished: 'Federal reserves', which generally contain the national and most valuable archaeological and natural sites and which tend to be larger in size; 'state reserves', which protect sites of regional value; and 'private reserves', which generally protect small areas that have a rich biodiversity and that belong to non-government organizations or civil associations. In general, federal NPA receive a limited financial budget, state NPA receive even less (Bezaury-Creel, 2009; Greenpeace. Menos recursos para areas naturales protegidas. http://www.cimacnoticias.com/site/07101012-Menos-

recursos-para.30633.0.html), while private reserves commonly have a more efficient financial administration (James, 1999), and therefore, in most cases they are fenced and better protected.

The aim of the present work was to study the effect of different forms of ownership of NPA on the patterns of seed removal by mammals and their effect on seedling establishment. The following questions were raised. Does the pattern of seed removal by mammals of different size-categories change in natural reserves of different ownership category? Is the establishment of seedlings thereby effected?

Our working hypotheses anticipate (1) that seed removal by medium-sized mammals is higher in private NPA than in public NPA, and seed removal by rodents is higher in public NPA than in private NPA; (2) that removal of large seeds is higher in private NPA, and removal of small seeds is higher in public NPA; (3) in consequence, we expect a lower germination of large seeds in private NPA, and a lower germination of small seeds in public NPA.

MATERIALS AND METHODS

Study area

Four NPA were selected in Southern Mexico which are characterized by differences in ownership type, size and conservation status. All NPA were located in tropical forests with a warm humid climate. The Holcim-Apasco reserve (termed "Private-Small Hol" hereafter, 17°38' - 17°36'; 92°26' - 92°28') is a fenced 200 ha reserve and belongs to the concrete company Holcim-Apasco. The Estación de Biología Tropical, Los Tuxtlas ("Private-Small LT", 18º 34' - 18º 36'; 95º 04' - 95º 09') is a fenced 640 ha reserve and belongs to the Universidad Nacional Autonoma de Mexico. This reserve is connected to the Reserva Especial de la Biosfera Volcán de San Martín which has 5,730 ha (Comisión Protegidas, de Naturales Nacional Areas http://www.conanp.gob.mx/que_hacemos/reservas_biosfera.php). The National Park Zona Argueológica Palengue ("Federal-Medium Pal", 17º 27' 51" - 17º 30' 05"; 92º 01' 30" - 92º 04' 42") has 1.771 ha and is administrated by the Mexican federal government. The fourth study site is a forest fragment of the State Park Cañón del Usumacinta ("State-Large Usu", 17º 15' - 17° 20'; 91° 05' - 91º 15') which has 4,000 ha and is administrated by the government of the State of Tabasco (Areas Naturales Protegidas de Tabasco. Secretaría de Desarrollo Social y Protección al Ambiente. Gobierno

de Tabasco). This latter reserve was founded in 2005 and has an insufficient conservation conditions due to illegal and legal logging, as well as maize cultivation in the past years. The other three reserves were founded before 1985 and have good conservation conditions and the greatest amount of mature forest with small canopy gaps formed by natural and wind-blow branches and tree-falls.

Regarding the seed consumers of these NPA, no reports exist for the zone of the Holcim-Apasco reserve. However, according to local informants, the Mexican agouti and the nine-banded armadillo (*Dasypus novemcinctus*) are present in the area. In the Estación de Biología Los Tuxtlas, Estrada (1992) reported 47 species of birds and mammals per hectare of forest. Examples include rodents (*Tinamus major, Ortalis vetula, Orthogeomys hispidus, Heteromys desmarestianus, Oryzomys palustres*), Mexican agouti and paca (*A. paca*). Horvàlt et al. (2008) reported 20 species of rodents, lagomorphs and didelphimorphs in the National Park Zona Arqueológica Palenque, e.g., armadillo, squirrel (*Sciurus deppei*), paca, and racoon (*Procyon lotor*). In Parque Estatal Cañón del Usumacinta, eight species of non-flying mammals were registered (Guzmán, 2004) including the white-tailed deer and red brocket deer, paca, wild pig (*Pecari tajacu*) and kinkayou (*Potos flavus*).

Location of the experimental sites

In each NPA, three sites with mature tree vegetation and absence of canopy gaps were selected for the seed predation experiments. In the Private-Small Hol reserve, the first site was located 250 m from the forest edge, while in the Private-Small LT it was placed at 40 m, and in the Federal-Medium Pal and State-Large Usu at 600 m. The two remaining sites were located among 200 and 600 m along a tangent deeper into the forest. In each site, three seed predation experiments were set up within a distance of 3 to 10 m from each other, in which fruits and seeds were placed on the forest floor within a $1-m^2$ plot free from litterfall (nine plots in each reserve). In each plot the fruit and seeds of six species were placed inside six 25 × 25-cm subplots, to better record predation and to provide the bare ground with soil to register footprints of the visiting fauna.

Seed predation treatments

In the first treatment, the fruit and seeds were isolated completely with an iron cage (1 cm mesh) by the four lateral and topsides to prevent access of rodents and larger mammals. The top net was placed 20 cm from the floor. The second treatment used larger mesh (3.6 cm) to allow the access of rodents (< 15 g weight). In the third treatment, no iron net was placed around the seeds to permit visits of any kind of animal over 30 g weights (Dirzo and Miranda, 1991; Donoso et al., 2003).

To reflect the natural diversity of food resources, we selected both large and small seeds. The experiments were conducted during the rainy (July through November, 2005) and dry (May through June, 2006) seasons. Fruits and seeds from 24 tree species were used (Appendix a, b), six in each reserve. Particularly fleshy and sweet fruits that are attractive to the fauna and that can be collected in large quantities were selected. Some plant species used were not dominant in their location, nonetheless they were judged worthy for the experiment. Species composition was not the same in the four locations, therefore, few species coincided with those from the reserves for the rainy season experiment (Appendix a). In the dry season experiment, owing to the lower amount of fruiting species at the time, six identical fruit and seed species were used in the four reserves (Appendix b). Following Demattia (2004), the species were sorted according to their size resulting in 13 species with large seeds and 11 species with small seeds

(Appendix a and b). In the rainy season experiment, seeds were used along with the fruit flesh, however in the dry season experiment, only the seeds were used along with their dispersion structures but without their fruit body (exocarp).

Monitoring of the fruit and seed removal

Seed removal was recorded for 5 months in the rainy season experiment and 7 days in the dry season experiment. In both cases, a daily recording (twice a day, sunrise and sunset) was conducted during the first seven days at the beginning of the experiments. During this time, removed seeds were replaced at each count. Seeds bitten but not removed were left *in situ* and counted as removed. On the seventh day of the rainy season experiment, all removed seeds were replaced only once a month for the following five months without replacement. During this 5 month term, seed germination was also recorded.

In the rainy season experiment, 49 individual fruit or seed items per species and treatment were used, which gave a total of 441 items per species and 2,646 per reserve (10,548 in total). In the dry season experiment, 36 seed items per species and treatment were used, which gave a total of 216 per species and 1,944 per location (7,776 for the dry season and 18,324 for the whole study).

Faunal observation

No rodent traps were used during the study. Recording of fauna footprints was based on the footprints left on the bare ground within the 1 m² plots. Observations of the potential local faunal consumers were performed during the field walks. The total estimated time of observation was 10.1 h in Small-Private Hol, 38 h in Small-Private LT, and 19 h in Federal-Medium Pal and Large-State Usu.

Statistical analysis

Analysis was performed using the percentage values of seed predation recorded during the experiments. Prior to the variance analysis, which requires data homogeneity, the original data was arc sine transformed. Three-way ANOVA was used including their interactions. The first factor (NPA) consisted of four levels (Private–Small Hol, Private–Small LT, Federal-Medium Pal, and State-Large Usu), the second factor (treatment) consisted of three levels (all faunal seed predation, rodent and invertebrate seed predation, and invertebrate seed predation only), and the third factor (seed size) consisted of two factors (large seeds and small seeds) (n = 24). Each value of seed predation (n) was the mean value of the three plots of each treatment set up in each reserve. Mean comparison was performed with the Fishers' least significant difference test. All tests were carried out with Statgraphics Plus 4.0 at P < 0.05 level of significance.

RESULTS

Seed removal by the different size-category animals in the different NPA

Medium-sized mammals showed higher seed removal than rodents in the reserve Private-Small Hol (F = 4.67, P = 0.05), and a lower seed predation in the State-Large Usu (F = 5.19, P = 0.008) (Figure 1). In the Private-Small LT reserve, there was no significant difference (F = 3.04,



Figure 1. Seed predation by mammals and invertebrates in four natural protected areas of different ownership-category and size. Different letters are two means difference +1 SD at P < 0.05.

Table 1. ANOVA for seed removal and germination among the different ownership-categories of the reserves, animal size-categories and seed sizes.

Seed removal	df	F	Р
Ownership × Treatment	11	9.2	0.00001
Ownership × Seed size	7	6.1	0.00001
Seed germination			
Ownership × Treatment	11	16.5	0.003

P = 0.08) between seed removal by medium-sized mammals and rodents, though a tendency toward higher seed predation by rodents was observed. This significant higher seed predation by the medium-sized mammals in the Private-Small HoI and by rodents in the State-Large Usu is supported by the significant interaction between ownership-type of the reserves and size of the mammal consumers (F = 2.23, P = 0.05) (Table 1). Invertebrates, showed a significantly higher seed removal in the State-Large Usu reserve than in the other reserves (F = 4.14, P = 0.02) (Figure 1).

Removal of the two size-category seeds in the different NPA

Small and large seeds were differently removed among the different types of the reserves (Table 1). Seed removal of the large seeds was significantly higher in the Private-Small Hol and Private-Small LT than in the State-Large Usu (F = 4.23, P = 0.01) (Figure 2). Removal in the Federal-Medium Pal reserve was intermediate. The removal of small seeds was lower in the Private-Small Hol and Federal-Medium Pal reserves than in the Private-Small LT and State-Large Usu reserves (F = 3.21, P = 0.03).

Seed germination in the different NPA

Germination was higher in the Private-Small LT and Federal-Medium Pal reserves than in the state reserve (F = 16.47, P = 0.003) as a consequence of seed removal by invertebrates in the latter (Table 1 and Figure 3). Germination of small seeds was higher in the Private-Small LT reserve than in the Private-Small Hol and



Figure 2. Total predation of large and small seeds by mammals in four natural protected areas of different ownership-category and size Different letters are difference among treatment means +1 SD (F = 4.23, P = 0.01). (F = 3.21, P = 0.03).



Figure 3. Seed germination in four natural protected areas of different ownership-category and size. Different letters are different among treatment means +1 SD (F = 3.7, P = 0.022).



Figure 4. Seed germination in the various experimental treatments selectively allowing animal access to seed predation in four natural protected areas with different ownership-category and size. Different letters are two means difference +1 SD at P < 0.05.

State-Large Usu reserves (F = 3.7, P = 0.022). In the private and federal reserves, germination was lower in the experimental treatments open to mediumsized mammals and rodents than to invertebrates (F = 6.23, P = 0.001) (Figure 4).

Faunal observation

Faunal observation was limited to the field walks taken when visiting the experimental sets, since no faunal footprints were recorded in the bare ground small-plots. In the Private-Small Hol reserve, four faunal species were observed (nine observations), in the Private-Small LT seven species (21 observations), Federal-Medium Pal, four species (nine observations), State-Large Usu, four species (12 observations). A single deer observation in the Federal-Medium Pal was remarkable. In the State-Large Usu reserve the persistent presence of ants in the footpaths was remarkable.

DISCUSSION

One difficulty in studying natural reserves is the near impossibility to having suitable replicate reserves that are similar in size, form, connectivity, vegetation, etc. In spite of this, experimental studies lacking reserve replication have yielded positive results concerning biodiversity conservation (Beckman and Muller-Landau, 2007: Dirzo et al., 2007; Nuñez-Iturri and Howe, 2007). Since in the present study a correlation was found between the size of the reserve and type of ownership, these variables covary and cannot be separated. Despite this, we found relationships between reserve category and pattern of seed removal by mammals. The results tend to support the first hypothesis concerning a higher seed removal by medium-size mammals than by rodents in the private-small reserves and the opposite in the public reserves. The trend would have been more clear if the Private-Small LT reserve had shown the same response as the Private-Small Hol reserve; this did not occur probably owing to the high rodent populations there (Sanchez-Cordero and Fleming, 1993; Dirzo et al., 2007). The second hypothesis was also supported by the higher removal of large seeds observed in the private reserves, and a higher removal of small seeds in the public reserve, which suggests a higher presence of mediumsized mammals in the private NPA and more rodents in the public reserve.

In the State-Large Usu reserve, ppersonal comments from local inhabitants informed us of the considerable presence of poachers; evidence of this were three dead howler monkies, *Allouata palliata*, that had been killed by poachers during the period of the field work, as well as the presence of hunting shelters build by poachers inside the forest.

We observed a very low germination rate, which was not a direct consequence of high seed removal. Therefore, the third hypothesis concerning the effect of faunal seed removal on germination could not be supported. The outstanding role of ants as seed removers was observed. Further, they limited seed germination, at least, in-situ. Ants use seeds more to build up their nests than as a food resource. In the private NPA with a notably fewer ants, the highest germination rates were observed in the experimental treatment designed to allow access to invertebrates only, whereas seed germination was very low in the public reserve with a high occurrence of this group of invertebrates. These observations support the hypothesis that the secondary seed predators can exert a strong influence on the seedling community (Muller-Landau, 2007; Stoner et al., 2007b). When analyzing seed germination of each species, a clear effect of lower seed dermination was observed for the most often removed species. This was the case for the species Pseudolmedia oxyphyllaria and Ficus voponensis in the Private-Small LT reserve, and Celtis iguanaea, Pouteria sapota, and Ardisia paschalis in the Federal-Medium Pal reserve. In the latter reserve, the lower ant seed predation on Clarisia biflora was reflected by higher seed germination.

The results of the study suggest that private NPA may sustain higher populations of medium-size mammals than public reserves. Private reserves tend to have higher amounts of financial resources to enroll more personal for vigilance and to prevent illegal hunting in comparison with reserves with a smaller financial budget (public reserves) at their disposal. Although no formal method of sampling fauna was applied, medium-sized mammals were observed, e.g. wild pig, white-nosed coati (Nasua narica), Mexican agouti and armadillo in Private-Small LT, whitetailed deer and armadillo in Federal-Medium Pal, and lowland paca and Mexican agouti in Private-Small Hol and State-Large Usu reserves. Dirzo et al. (2007) has referred particularly to the Private-Small LT reserve as a location that had been defaunated of large-sized mammal removers of large seeds (currently recruited only from the south-eastern part of Mexico). However. most presumably due to its close vicinity to the nearby San Martin volcano, the presence of medium-sized mammals is favored. Also, the results confirm that medium-sized mammal elimination facilitates the increase of populations of small-sized mammals, such as rodents, as well as ants, both of which were remarkably notable in the Large-State Usu reserve. Their abundance was probably due to the greater availability of food resources. However, according to Wright and Duber (2001), invertebrates cannot easily compensate seed predation in the absence of mammals. Beetles are invertebrates that are negatively affected by the reduction of mammal populations by hunting (Andresen and Laurance, 2007). Both groups of insect seed removers deserve further mammal defaunation. Figueroa and study regarding

Sanchez-Cordero (2008) found that federal reserves based on local community management received the greatest financial support from the government and were more effective in preventing land use change than the other NPA categories. Furthermore, the effectiveness resulted largely from the fact that they act as effective forest protectors.

This fact emphasizes the relevance of financial support and patrolling in the effectiveness of the natural reserves which might also equally apply to the private reserves. In Africa and Latin America, current efforts for habitat protection based largely on public investment remain conductive to a significant loss in biodiversity. In this context, privately owned nature reserves represent an effective supplemented effort for conservation (Langholz, 1996), as may be the case in Argentina where more land reserves are in private ownership; public reserves occupy only 5.5% of the country (Projects in Argentina. Esteros del Ibera. Conservation Strategies. The Conservation Land Trust.

http://www.theconservationlandtrust.org/eng/pa_ibera_est rategias 03.htm#b).

Whether private or non-private natural reserves are better equipped for conservation purposes may depend on the location and on the country itself. One should be hesitant to make sweeping generalizations. For example, in South Africa, the reserves in private ownership are more adequate for conservation than state reserves (Ramutsindela, 2005). Lu (2001) emphasizes that communal management of resources cannot invariably lead to conservation; other factors need to be present. The common property regime was designed for conditions with plentiful resources, low population density, and clear membership.

Based on our observations, we conclude that seed removal by medium-sized mammals is lower in the investigated public reserves and removal by rodents and ants is higher. The results suggest that the type of ownership and, consequently, the management system exert strong effects on the patterns of seed removal by mammalian populations in tropical natural protected areas.

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APPENDIX

Size Size (length Species Family Natural protected area × width, cm) class C. biflora Ruiz and Pav. Moraceae 2.0 a 2.5 Large Guarea glabra Vahl Meliaceae 1.5 a 2.0 Large Spondias mombin L. Anacardiaceae 3.0×1.5 Large Private-Small Hol Quararibea funebris (La Llave) Vischer Bombacaceae 4.0 × 3.0 Large A. paschalis Donn. Sm. Myrsinaceae 1.0×1.5 Small Drendropanax arboreus (L.) Decne and Planch. (1854) Small Araliaceae 0.7×0.8 Dussia mexicana (Standl.) Harms. Fabaceae 5.0 a 6.0 Large Pseudolmedia oxiphillaria Donn. Smith Moraceae 1.5 a 2.0 Large G. glabra Vahl idem. idem. idem. Private-Small LT Brosimum alicastrum Sw. Moraceae 1.2 Small idem. C. biflora Ruiz and Pav. idem. idem. Ficus yoponensis Desv. Moraceae 1.6 Small B. alicastrum Sw. idem. 2.0 a 3.0 idem. Ouratea Ochnaceae 2.5×2.5 Large Celtis iguanaza Jack. Sarg. (1895) Cannabaceae 1.0 a 1.4 Small Federal-Med Pal Pouteria sapota (Jacq.) H.E. Moore and Stearn 20.0×12.0 Sapotaceae Large A. paschalis. Donn. Sm. idem. idem. idem. C. biflora Ruiz and Pav. idem. idem. idem. idem. idem. idem. Q. funebris (La Llave) Vischer Manilkara zapota L. (Royen) Sapotaceae 9.0 Large G. glabra Vahl idem. idem. idem. State-Large Usu Not determined 2.5×2.5 Large Ficus (not determined) Moraceae 0.2 ×0.3 Small Guarea Meliaceae 1.0×1.5 Small

Appendix a. Species used in the seed predation experiment during the rainy season in each location.

Appendix b. Species used in the seed predation experiment during the dry season in the four natural protected areas by equal.

Species	Family	Size (length × width, cm)	Size category
Cedrela odorata L.	Meliaceae	0.8 × 0.4	Small
Tabebuia rosea (Bertol) D.C.	Bignoniaceae	2.0 a 3.0 including the wing	Small
Glirisidia sepium (Jacq.) Standl	Fabaceae	0.8 a 1.8 × 1.2 a 1.5	Small
Albizia lebbeck (L). Bentn	Mimosaceae	1.0	Small
Leucaena esculenta (Moc. Et Sessé ex A.D.C.) Benth.	Leguminosae	0.8 a 0.9	Small
Not determined		1.0	Small