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Demography and Recruitment of Selected Trees in the Limestone Forest of Guam in Relation to Introduced Ungulates

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Abstract—The island of Guam had no ungulates until after European contact, when several species such as deer and pigs were introduced. Both deer and feral pigs have become numerous within the forests of Guam, and may be damaging the forest through over-browsing and rooting. This study was initiated to determine whether introduced ungulates might be affecting recruitment of several species of native trees.

The study showed that, within the Northern Guam area, high populations of deer were largely confined to the Air Force Base, but feral pigs were abundant at almost all study sites.

Four tree species were studied. *Tristiropsis obtusangula* Radlk. (faia) did not appear to be affected by ungulates. Young trees and seedlings were common at all sites and little evidence of deer browsing was seen on seedlings monitored for several years. Very few young trees of *Eleaocarpus joga* Merr. (yoga) were found at any of the sites sampled. Only four seedlings were found, of which two were browsed and one disappeared within two years. For *Macaranga thompsonii* Merr. (pengua), young trees tended to be sparse where deer were abundant. Seedlings suffered high mortality from browsing in a location where deer were abundant, but little evidence of browsing was seen on seedlings in an area with low deer density. In a location with high deer density, uncaged *Intsia bijuga* (Colebr.) Ktze. (ifit) seedlings suffered high mortality. However, small trees were common in at least one site where deer are currently numerous. Little sign of browsing was seen when seedlings were grown in a location where deer sign were not observed.

Introduction

Guam has several types of native forest, of which one of the most important is limestone forest. The limestone forests grow on the northern plateau of Guam on an upraised fossil reef, as well as on limestone outcroppings and benches on other

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parts of the island. Although much of this forest has been cleared for housing, agriculture and military activities, significant remnants remain. The limestone forest grows on karst or on a thin soil over limestone. It is a mixed mesophytic forest with no one species universally dominant or even characteristic of the forest (Fosberg 1960). The canopy is about 10–15 meters high with several species such as seeded breadfruits and banyan figs emergent. Nearly 40% the tree species in this forest are endemic to the Mariana Islands or Micronesia, as are many understory shrubs and herbs (Lee 1974). The rest of the forest is composed of widespread Indomalayan or paleotropical species.

The Mariana Islands had no ungulate herbivores until the arrival of Europeans in the 1600s. Philippine sambar deer were introduced by the Spanish from the Philippines in the 1700s (Safford 1905). The precontact indigenous population also apparently lacked pigs, as current feral pigs all appear to have descended from domestic stock brought to the islands in the 1600s (Intoh 1986). Because of a lack of selection pressure by ungulates, many plant species in the Guam forests may be highly susceptible to browsing damage. One tree, *Serianthes nelsonii* Merr., is classified as endangered, and although a number of factors are implicated in its great rarity, death of seedlings caused by ungulates appears to be a major cause (Wiles et al. 1996). Other more common trees may also be affected by ungulate herbivores.

On other islands, introduced ungulates have often been implicated in the destruction of certain tree species. Several *Auracaria* species are becoming rare in New Guinea because of pig predation of seeds and rooting under trees (FAO 1986). In Mauritius, monkeys and deer have destroyed most of the populations of several *Diospyros* species, and *Pinus radiata* D. Don has almost disappeared from the California channel islands due to goat predation (FAO 1986). In Hawai'i, assorted ungulate species have degraded whole ecosystems (Cuddihy & Stone 1990). Goats and sheep are known to limit the reproduction of *Sophora chrysophylla* (Salisb.) Seem, *Acacia koa* A. Gray and other species in Hawai'i (Spatz & Mueller-Dombois 1973, Loope & Snowcroft 1985). Pigs have been shown to dig up as much as one third of the diggable area in mountain forests in Hawai'i every year (Cooray & Mueller-Dumbois 1981). In the process they consume many seeds and seedlings of endemic species, as well as providing a fertile seed bed for invading exotic plants (Cuddihy & Stone 1990).

Observation on Guam suggested that at least on Andersen Air Force Base, seedlings of some trees are rare, and that the forest might be slowly degrading. The current study was initiated to determine whether ungulate herbivores could be associated with a lack of recruitment of selected forest trees. *Intsia bijuga* (Colebr.) Ktze. was chosen because it is Guam's most valuable timber species. *Eleaocarpus joga* Merr. is a canopy emergent, frequently used for nesting by the endangered Marianas crow. The tree is endemic to the Mariana Islands and Palau. *Macaranga thompsonii* Merr. is endemic to the Mariana islands. *Tristiropsis obtusangula* occurs in the Marianas and in Melanesia. It is also occasionally used as nest tree by the Marianas crow.

Materials and Methods

DEMOGRAPHY OF SELECTED TREE SPECIES

The species surveyed were *M. thompsonii, T. obtusangula, E. joga,* and *I. bijuga.* Locations where each of these trees was reasonably abundant were selected. Surveys of tree diameter were done by measuring the diameter at breast height of the first 50 trees found within each sample site. Sample sites are marked on Figure 1. In order to determine whether young trees were being missed by this method, two 100 m^2 quadrats in the same area were also measured out, and all trees within

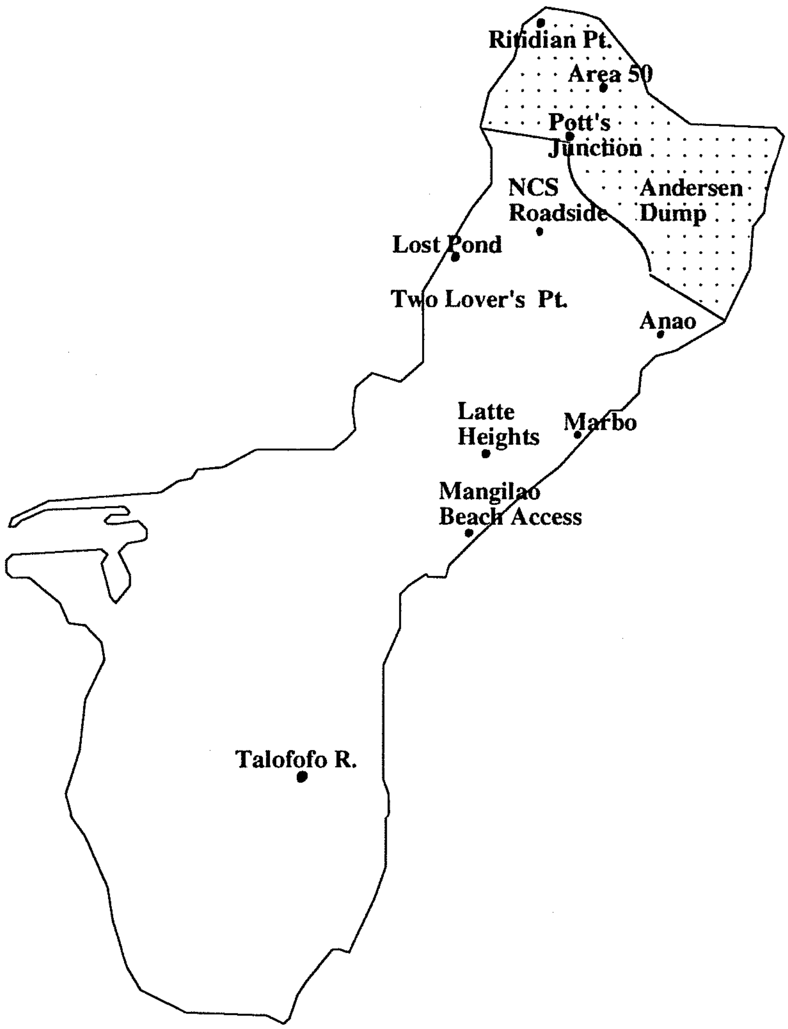

Figure 1. Location of sample sites. Shaded area is Air Force Base.

the quadrat were sampled. The average size of trees in the large sample and the combined data from the two quadrats was compared by a Student's t test. Surveys took place June through August, 1993 and 1994. For *T. obtusangula,* one of the sites used was in a ravine forest (Talofofo River). All other samples were taken in the northern limestone forest.

DENSITY OF FERAL UNGULATES

For each site where tree diameters were measured, an estimate of the relative density of ungulates was made. For each site, 1 transect of 225 m was done. The width of the transects was approximately 2 meters. All sign of ungulates encountered on this transect were recorded, and an attempt was made to distinguish between deer and pig sign. Sign recorded included droppings of both species, footprints, trails and damage to plants. An attempt was made to distinguish between deer and pig footprints. Pig footprints were more splayed. Deer and pig dens and trails were distinguished principally by how muddy they appeared. Various types of plant damage which appeared to have been caused by animals was also recorded. Only the droppings were considered a reliable index to distinguish between deer and pigs, and analysis of variance performed to compare sites on the island was done only using this variable. All transects were done in July 1995 except at the Talofofo River site where the access was too muddy, and that transect was done January 1996.

To compare the density of animals to previously collected data on pigs (Conry 1989), the data were re-examined by dividing the transects to make 23 10 m $\times$ 2 m quadrats for each transect. For each quadrat the presence or absence of animal sign was recorded and a percent of quadrats with sign was calculated.

A correlation was performed relating the incidence of deer droppings along a transect from each site and the percentage of young trees at that site. Young trees were defined as those with a DBH $<$ 10 cm.

SEEDLING SURVIVAL

Patches of tree seedlings of various species were found at several locations. Whenever a patch of seedlings was located, seedlings were tagged and monitored periodically to determine survival and, where possible, causes of mortality. Mortality was determined after one year, but seedlings continued to be monitored until the end of the study in March 1996. The seedlings followed included two patches of *M. thompsonii* seedlings, one at Ritidian Point (60 seedlings tagged March 1993) and one at Mangilao Beach access (50 seedlings tagged March 1995). Three patches of 40 of *T. obtusangula* seedlings were tagged: at Anao (in July 1993), within an animal exclusion fenced area (Area 50) at Northwest airfield (in December 1993), and at the Talofofo River (in February 1994). Only four seedlings of *E. joga* were found, all within the animal exclusion area. These were tagged in December 1993 and followed.

I. bijuga seeds were collected from pods on trees. One set of 40 seeds was planted out at Anderson AFB in October 1994. Seeds were planted in sets of 10 near large *I. bijuga* trees. Five seeds were placed each inside a small cylinder of wire construction mesh, and five were not caged, but the site was marked with a plastic utensil so they could be found again. Some of the seeds were found to be immature, so sites were checked after two months and rotten seeds were replaced. Sites were checked once a month, and a record made of whether the seed had germinated, the number of leaves on the seedling, whether the plants had sustained damage from large herbivores and when the seedlings died. Plants were checked until March 1996, at which time the height of the surviving seedlings was also recorded. A second set of seeds was germinated in the laboratory, and seedlings were planted out at the Mangilao beach access in September 1995. These were tagged and checked monthly until May 1996.

Results

DEMOGRAPHY OF SELECTED LIMESTONE FOREST TREES

The size distribution of *M. thompsonii* trees is shown in Table 1. Except at Marbo, the proportion of small trees (DBH < 10 cm), was always less than that in the next size class. At two sites, just outside Area 50 and at Ritidian Point, there were no small trees. At Marbo, however, there were no old trees and many young trees. Seedlings were found at Marbo, Ritidian Point and the Mangilao beach access site.

The size distribution of *E. joga* trees is shown in Table 2. Small trees were absent in two of the four locations, and only small numbers were found in the other two locations. At Anao, notes were kept indicating that of the three trees with a diameter less than 10 cm, at least two were root suckers of larger trees. Two trees with a diameter less than 10 cm were found at the Ritidian Point site but it was not

Table 1. Percent of *M. thompsonii* trees in each size class at sample locations and comparison with trees in sample quadrats at same locations.

	Percent of trees							
Diameter of trees (cm)	Two Lovers	Lost Pond	Mangilao Beach ac.	Marbo	Pott's Junct.	Ritidian Pt.	Outside Area 50	Area 50
1 to 10	6	5	14	60	39	0	0	16
11 to 20	44	28	46	40	49	24	70	52
21 to 30	38	35	23	0	6	62	24	29
31 to 40	8	25	14	0	6	14	6	0
40+	4	7	3	0	0	0	0	3
Average diameter of 50 tree sample								
$\mu \pm$ SD	21 ± 9	26 ± 10	18 ± 9	10 ± 5	13 ± 8	24 ± 5	18 ± 5	16 ± 8
n	50	40	35	50	52	50	50	31
Average diameter of trees in quadrat samples								
$\mu \pm$ SD	22 ± 6	n.a.	31 ± 8	12 ± 6	10 ± 3	19 ± 7	12 ± 7	26 ± 13
n	2	0	2	21	3	8	3	4
Students *t*	0.006		1.95	1.51	0.47	2.33	1.95	2.16
	0.99		0.058	0.1	0.6	0.02	0.056	0.03

Table 2. Percent of *E. joga* trees in each size class at sample locations and comparison with trees in sample quadrats at same locations.

Diameter of trees (cm)	Percent of trees: Anao	Area 50	Ritidian Point	NCS Road
1 to 10	8	0	4	0
11 to 20	26	8	2	0
21 to 30	24	11	12	18
31 to 40	14	36	25	30
41 to 50	14	14	23	30
51 to 60	12	17	10	21
61 to 70	2	8	8	0
71 to 80	0	3	12	0
81 to 90	0	3	2	0
91 to 100	0	0	2	0
100+	0	0	2	2
Average diameter of 50 tree sample				
$\mu \pm$ SD	30 ± 16	44 ± 18	48 ± 22	41 ± 12
n	50	36	52	57
Average diameter of trees in quadrat samples				
$\mu \pm$ SD	23 ± 22	32 ± 10	29 ± 20	84 ± 2
n	4	2	5	2
Students t	0.83	0.94	1.80	4.85
p	0.4	0.4	0.08	0.0001

recorded whether they were root suckers or new trees. Almost no seedlings were found, except for four inside the fence at Area 50.

The size distribution of *T. obtusangula* trees is shown in Table 3. At all four sites small trees represented at least 10 percent of the trees found, ranging up to nearly 30 percent at the Talofofo site. Seedling were found at three of the four sites.

The size distribution of *I. bijuga* trees is shown in Table 4. Small trees represented a substantial fraction of the population at five of the seven sites, but were only a very small fraction of the Andersen AFB dump site and at Latte Heights. Except for the two sites on base, large trees were mostly absent. Seedlings were found at the Marbo site.

Comparison of the quadrat and large samples suggested that the method of walking through the forest and measuring the first fifty trees seen did not discriminate against small trees (Tables 1–4). Although for each species there were some quadrats where the average size of the trees differed significantly from that of the 50 tree sample, there were about as many samples where the average was larger as there were where it was smaller.

DENSITY OF INTRODUCED UNGULATES

A record of all sign seen on the transects is in Table 5. Pig and deer footprints and trails are recorded separately as the technicians doing the count were certain

Table 3. Percent of *T. obtusangula* trees in each size class at sample locations and comparison with trees in sample quadrats at same locations.

	Percent of trees			
Diameter of trees (cm)	Area 50	Outside Area 50	Anao	Talofofo River
1 to 10	12	8	17	28
11 to 20	18	32	34	37
21–30	29	34	21	13
31–40	29	12	21	15
41–50	8	4	8	4
50+	4	10	0	4
Average diameter of 50 tree sample				
$\mu \pm SD$	26 ± 12	24 ± 13	21 ± 12	21 ± 16
n	49	50	53	54
Average diameter of trees in quadrat samples				
$\mu \pm SD$	35 ± 24	23 ± 16	19 ± 19	7 ± 12
n	6	11	10	34
Students t	1.46	0.32	0.54	4.33
p	0.15	0.7	0.6	0.0001

Table 4. Percent of *I. bijuga* trees in each size class at sample locations and comparison with trees in sample quadrats at same locations.

	Percent of trees				
Diameter of trees (cm)	Andersen Dump	Latte Heights	Marbo	Pott's Junction	Ritidian Point
1 to 10	4	2	86	22	42
11 to 20	50	46	10	41	7
21 to 30	30	36	2	29	2
31 to 40	2	10	0	6	12
41 to 50	4	6	0	2	7
51 to 60	0	0	0	0	12
61 to 70	0	0	0	0	9
71 to 80	0	0	0	0	5
81 to 90	2	0	0	0	2
91 to 100	4	0	0	0	0
100 to 110	0	0	0	0	0
110+	4	0	2	0	2
Average diameter of 50 tree sample					
$\mu \pm SD$	27 ± 26	22 ± 9	6 ± 15	18 ± 9	10 ± 9
n	51	51	50	51	44
Average diameter of trees in quadrat samples					
$\mu \pm SD$	19 ± 9	13 ± 7	14 ± 21	27 ± 9	33 ± 3
n	15	8	9	4	2
Students t	1.22	2.89	1.31	1.88	3.22
p	0.2	0.005	0.2	0.06	0.002

Table 5. Incidence of animal signs per 750 ft. (225 m) at locations where tree diameters were surveyed.

Location	Droppings Deer	Droppings Pig	Footprints Deer	Footprints Pig	Animal trail	Den Deer	Den Pig	Plant chewed	Rooting	Bark scraping
Anderson Dump	19	5	8	1	11	1		6		7
Area 50	9	7		9	6		3	5	1	3
NW of Area 50	30	10	10	9	14		1	19	2	9
S of Area 50	15	4	9	5	9	1		12	2	6
Pott's Junction	5	2	3	2	10		1	4		16
Ritidian Pt.	22	16	9	3	5			21	5	8
Road at NCS	15	2	16	11	10	3	3	13	2	11
Anao	5		2	1	6	1	2	2	5	8
Latte Heights		31		16	5			3	16	27
Marbro		8		10	11			20	2	
Two Lover's Pt.		5		5	7		1	6	1	
Lost Pond								1		4
Mangilao Beach Ac.				2			2		4	2
Talofofo R.		20	21	12		12		3	6	

they could distinguish the two. Nevertheless, it is probable that these were often mistaken for the wrong species. Droppings, however, were unmistakable. Transects on the Air Force base averaged 17 instances where droppings were sighted. Locations near the base averaged 10 instances, but away from the base there were no deer droppings ($F = 10.03$, $p = 0.003$, d.f. $= 2, 11$). Pig droppings were distributed much more evenly, averaging about 7 instances per transect both on the base and away from the base. There was however, variation in pig sign which ranged from 100% of quadrats at Latte Heights down to 0% at Lost Pond (Table 6).

Table 6. Percent of quadrats with animal sign at each location.

Location	Percent of quadrats with: Plant damage	Deer sign	Pig sign
Anderson Dump	39	65	26
Area 50	13	13	83
NW of Area 50	39	78	70
S of Area 50	61	83	39
Pott's Junction	4	78	57
Ritidian Pt.	57	70	52
Road at NCS	57	83	57
Anao	17	39	43
Latte Heights	13	0	100
Marbro	48	9	74
Two Lover's Pt.	26	0	57
Lost Pond	22	0	0
Mangilao Beach Ac.	9	0	35
Talofofo R.	0	61	65

Area 50 is an area of about 60 acres enclosed in 1992 with an 8 foot fence for animal exclusion. Several drives to kill animals within the enclosure have taken place. Deer, however were still present in the enclosure at the time of sampling, although the incidence of droppings was lower than for sites outside the fence and more similar to those seen near the base. Pig density inside Area 50 did not appear any different from the areas around it. The Potts' Junction area also had a relatively lower incidence of deer droppings. While this is technically inside the base, it is unfenced and easily reached from the main road. The one ravine forest site, on the Talofofo River, was different from other sites. It could not be sampled in July along with the other sites due to impassable mud and flooding. In January 1996, when the sample was done, there was still some flooding in the sample area. Although there was much evidence of deer at the site, no deer droppings were recorded in the sample, possibly as a result of the very different conditions at this site compared to the other drier limestone forest sites. Over 60% of quadrats had other deer sign (Table 6).

The correlation between the percentage of young trees and the incidence of deer droppings at that site in shown in Figure 2 and Table 7. There was a suggestion of an inverse correlation between deer density and the size of trees for *M. thompsonii,* but it was not significant. No hint of any relationship was observed for *E. joga* or *I. bijuga.* Because the Talofofo site was anomalous in having many deer sign, but no deer droppings in the animal sample, no correlation between proportion of small *T. obtusangula* and deer droppings was run.

SEEDLING SURVIVAL

Sixty *M. thompsonii* seedling were marked at Ritidian. Only five seedlings were alive after 12 months, three of which had lost their top to herbivores (Table 8).

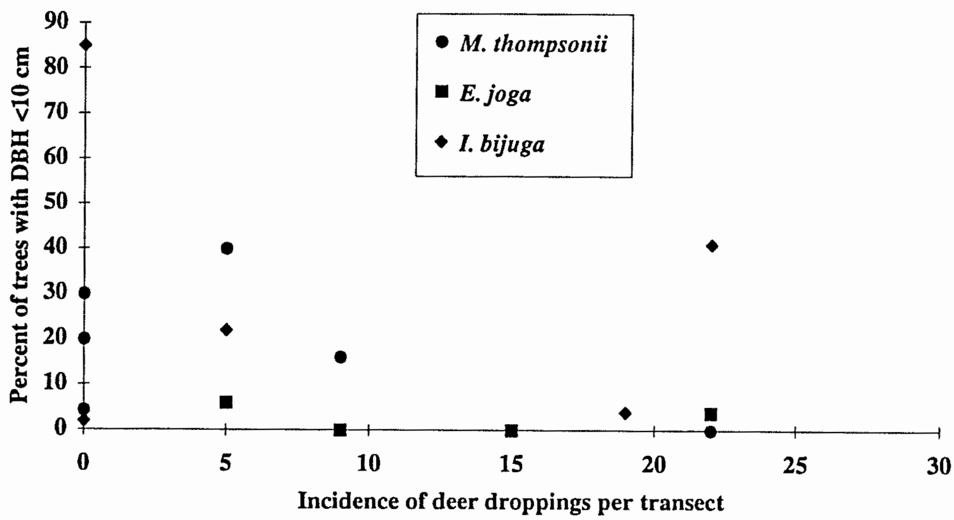

Figure 2. Percent of trees in smallest size class (DBH < 10 cm) in relation to incidence of deer droppings at sampling sites.

Table 7. Correlation between proportion of trees in the youngest age class, and the incidence of deer droppings at that location. (Spearman's Correlation coefficient)

Tree species	N	Z corrected for ties	
M. thompsonii	7	−1.51	0.13
E. joga	4	−0.48	0.58
I. bijuga	5	0.20	0.83

Another year later, two of the five live trees were missing, and the remaining three had all been chewed, in some cases repeatedly. At the Mangilao beach access site where fifty seedling were marked, few plants were damaged by animals. Although survival was poor, most of the plants (36 of the 39 which died) appeared to have died of drought stress during the first dry season. Ritidian Point was a location with high deer sign incidence, and the Mangilao beach access site had no recorded deer sign (Table 6).

Only four *E. joga* seedlings were found (Table 8). Within one year, 1 died, 1 disappeared, and two were chewed off, but had still not died at the time of the last sample 27 months after tagging. These seedlings were found within Area 50 (the animal exclusion area).

The *T. obtusangula* seedlings had a much higher survival rate. After one year of monitoring 40 plants at each of three sites, 17 to 19 plants were still alive at each site (Table 8). After another year of monitoring, 14 seedlings were still alive at Anao (until the whole area was bulldozed for housing). At Area 50, the 19 plants alive after one year were still alive two years after they were tagged. At Talofofo

Table 8. Survival of seedlings of forest trees 12 months after tagging.

			Fate of seedlings				
Species	Location	Number tagged	Alive (browsed)	Browsed and died	Uprooted	Disappeared	Dead other cause
M. thompsonii	Ritidian	60	5(3)	14	3	24	14
M. thompsonii	Mangilao	50	6	1	0	4	39
E. joga	Area 50	4	2(2)	0	0	1	1
T. obtusangula	Anao	40	17	2	1	8	12
T. obtusangula	Area 50	40	19	1	1	13	6
T. obtusangula	Talofofo	40	18	0	0	14	8
I. bijuga[1]	Anderson (uncaged)	17	2(2)	8	0	0	5
I. bijuga	Anderson (caged)	20	14(7)	0	0	0	7
I. bijuga[2]	Mangilao	20	10	0	1	8	1

[1]*I. bijuga* planted from seed and followed for 17 months. Most of seeds germinated within 2–5 months.

[2]*I. bijuga* seedlings transplanted and followed for 7 months.

River, after two years all the plants were dead, but no evidence of chewing was seen. These seedlings were growing in a heavily shaded site, and likely this caused their death. Area 50 and Anao were sites with relatively lower deer populations. The deer population at Talofofo River appeared to be high, although no deer droppings were found in the transect.

For the *I. bijuga* seeds planted near the Anderson dump, all 20 of the sufficiently mature seeds planted in cages germinated, but only 17 of the uncaged seeds did (one seed in three of the four replicates failed to germinate). The data was analyzed by analysis of variance, with each site representing a replicate. The difference was significant ($F = 9.00$, $p = 0.024$ d.f. = 1,6.). One of the uncaged sites where no seed germinated had signs of pig rooting. The small cages were not entirely successful at preventing the tips of the plants from being chewed. Overall 11 of the uncaged plants and 7 of the caged plants had their tips chewed off at least once. However none of the caged plants immediately died as a result of being chewed, whereas many of the uncaged plants did. At the time the last record was taken, 17 months after planting, 14 of the caged plants (3.5 ± 0.4 ($\mu \pm$ S.E) per replicate), but only 2 of the uncaged plants, were still alive. This difference was significant ($F = 27.00$, $p = 0.002$, d.f. 1,6). The caged plants had more than twice as many leaves (5.3 ± 1.4 vs. 2.0 ± 1.4 for the uncaged plants), although due to high variance the difference only approached statistical significance ($F = 3.72$, $p = 0.06$, d.f. = 1,21). Caged plants were taller (44 ± 5 cm vs. 25 ± 13 cm), but again the difference was not statistically significant due to high variance. The Andersen dump site was a location with relatively high deer sign incidence. After 8 months at the Mangilao site, which had no deer sign, out of 20 seedlings, 10 were still alive, and none showed signs of browsing. One of the dead seedlings had been uprooted.

Conclusions

Animal sign were abundant in the Guam forests. Although the transects done were not very intensive, results were comparable to that seen in Conry (1989). In that study, he found that 79% of plots (out of 1167 sampled) had pig sign at Northwest Field. In the current study, 64% of 69 plots sampled at Northwest Field had pig sign. Based on harvest data, Conry estimated that pig density in that area was between 34 and 86 pigs per km^2 in the year preceding his survey of pig sign. Deer density has not been estimated in any of the areas sampled in the current study, but the incidence of deer sign was comparable to that of the pigs on the Air force Base. Off the base, deer were absent or present only at low levels.

One tree species, *T. obtusangula,* did not appear to be affected by feral ungulates. At all locations, there was a high proportion of trees with a DBH less than 10 cm, and seedlings were seen at three of the four sites. Seedlings did not appear to be heavily consumed by deer or pigs.

The recruitment of two species appeared to be affected by feral ungulates in at least some situations. Young *M. thompsonii* trees were missing at two sites where deer populations were high, but present at other sites. There was a suggestion of an inverse relationship between the proportion of small trees at a site and the incidence of deer droppings. Although the relationship was not statistically significant, given the number of years which trees require to reach even the smallest size class and the one time nature of the herbivore sample, it is surprising there should be any hint of a relationship at all. Most seedlings at a site with a high incidence of deer sign were killed by herbivores. At a site with low deer incidence, few seedlings were damaged by mammals.

I. bijuga was less clearly affected by deer populations. Young trees were present at one site with high levels of deer sign, and absent from a site with no deer sign. However, seedlings placed out in a location with high deer populations were significantly more likely to be killed by herbivores if they were not protected from browsing. At a site with low deer incidence, there was no sign of browsing, although one seedling was uprooted, probably by pigs. Large trees were missing from sites away from the Air Force Base. Although local legislation prohibits cutting live *I. bijuga* trees, it is known that considerable poaching of this valued timber occurs.

E. joga seemed to be suffering from more problems than deer predation. There were almost no small trees found in any of the four samples. Only four seedlings were found in the whole study. We were unable to successfully germinate seeds in the laboratory despite various treatments such as decortication and seed nicking which often increase germination. Although there was a difference in the incidence of deer droppings among various locations, there was little difference in the incidence of pig droppings, which were abundant at all sites where *E. joga* trees were measured. If pigs are consuming fruit, this might explain the small numbers of seedlings and young trees. In this case, it should be possible to find *E. joga* seedlings on Guam on very dissected karst landscapes where adult trees occur, but pigs cannot easily obtain passage. Alternatively, perhaps *E. joga* seeds require passage through a bird gut to germinate with a higher frequency. Many tropical seeds require complete removal of the fruit to germinate successfully and normally only germinate after passage through an animal gut, and at least in Mauritius, extinction of much of the native fauna may have thus have caused the great rarity of several tree species (Jackson et al. 1988, Witmer 1991). If this is the case, the extinction native forest birds caused by snake predation (Savidge 1987), may have impacted the reproduction of the tree. If bird dispersal is important, one should be able to find *E. joga* seedlings more frequently in Rota and Saipan where the forest birds are still present. When germination does occasionally occur on Guam, herbivore browsing is clearly significant, since out of four seedlings found, two were browsed, one disappeared, possibly because the whole plant was consumed, and one died of other causes.

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