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Technical Report 169

Inventory of the reptiles of the War in the Pacific National Historical Park, Guam

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Executive summary – There are no native amphibians on Guam. Reptile species of offshore islets were reported in an earlier paper (Perry *et al*.1998). In February through April 2001 we intensively sampled the reptiles of the mainland portions of War in the Pacific National Historical Park (WAPA). Snake populations were sampled using a mark-recapture technique to estimate population size. Two trapping grids, each four ha, were placed in the Opop section of the Asan unit. Snakes were captured, marked, released, and recaptured for 33 days. Lizards in selected units were sampled using a total removal methodology. In our application of this technique, six 10 × 10 m patches of habitat were surrounded by a lizard-proof barrier (fence at ground level to contain terrestrial lizards and canopy separation to contain arboreal species), and all aboveground vegetation was minutely inspected for lizards as it was being removed. Three samples were collected in each of two types of habitat: grassland and tangantangan forest. These yielded the first absolute population density estimates for lizards in grassland habitat on Guam and on National Park Service land. Concurrently, we sampled the lizards of the same habitat types using adhesive trapping, a technique for estimating relative abundance that has been used extensively throughout the Pacific region. Adhesive trap samples can be compared to the densities discovered through absolute removals to assess the sampling biases of the more widely used but unvalidated relative-density technique. In addition, we conducted eleven spot adhesive-trapping samples of park units not otherwise sampled.

Only common species were found. Brown Treesnakes were found at low to moderate densities (7-20/ha compared to our Guam average of 29/ha). The lizard spot samples and removals indicated that several species, although fairly dense, do not generally attain densities in the sampled areas as high as in comparable tangantangan habitat elsewhere on Guam. For example, the Pacific Blue-tailed Skink (*Emoia caeruleocauda*) averaged 1933/ha and the Curious Skink (*Carlia fusca*) averaged 1800/ha compared to the Guam average of 2400/ha and 6000/ha respectively for tangantangan forest. Overall, about half of all lizard individuals were skinks (lizards in the family Scincidae, primarily day-active terrestrial species); the remainder were geckos (lizards in the family Gekkonidae, primarily nocturnal species found usually in trees).

Because this sampling yielded the first absolute density estimates for grassland habitat in Guam, these samples cannot be readily compared to other samples from Guam. Compared to the tangantangan habitat of WAPA, the total density of grassland lizards was less than half, with the gecko fraction accounting for most of the difference. All geckos averaged 467/ha in the grassland plot, significantly less than the 4500/ha average in tangantangan.

In addition to quantifying the lizard fauna of the WAPA in unprecedented detail, and providing data on the impact of the Brown Treesnake on Guam lizards, the data obtained from this work will be utilized for comparisons with tropical lizard assemblages throughout the world, for detailed evaluation of the role of forest structure in the habitat requirements of lizards, and for validating other techniques which may be used for sampling lizards. Representative analyses along these lines are presented.

Footnote

Carlia fusca. This taxon is now known as *Carlia ailanpalai*, as a result of a taxonomic revision (Zug, G.R., and Allison, A., 2006, New *Carlia fusca* complex lizards (Reptilia: Squamata: Scincidae) from New Guinea, Papua-Indonesia: *Zootaxa*, v. **1237**: 27-44.).

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INTRODUCTION

There are no native amphibians (salamanders, caecilians, or frogs), turtles, tuataras, or crocodilians (except birds) in the Mariana Islands. Within the squamates (lizards and snakes), the only unquestionably native species are two endemic lizards: *Perochirus ateles*, the Micronesian Gecko, and *Emoia slevini*, the Mariana Skink (Pregill 1998). Because both species are endemic (found nowhere else), it is presumed that they evolved in Micronesia (as opposed to having evolved elsewhere and subsequently migrated here and disappeared from their original range). These species are morphologically unlike any other species and therefore it is probable that their evolutionary divergence took place over a substantial period of evolutionary time (they did not arise recently). Because humans have been present in the Mariana Islands for only about 3500 years (an evolutionarily short period of time), and because fossils or sub-fossils of those two lizard species are present in pre-human deposits, it is believed that the lizards colonized the Marianas without human intervention. Many gecko eggs are tolerant of submersion in salt water (Brown and Alcala 1957); thus their eggs may have arrived here on floating or submerged debris. Skink eggs are generally less resistant, but no tests have been conducted on Mariana Skink eggs and in any event, they may have arrived amid debris that held the eggs or adults out of water. The southern Mariana Islands emerged from the ocean about 42 million years ago (Farrell 1991); the unaided colonization since then of only two species of lizards attests to the improbability of natural colonization occurring. Unfortunately, both of these native species have tended to disappear from areas colonized by introduced species, and neither has been found on Guam in recent years. The Mariana Skink was last seen on Guam immediately after World War II (Brown and Falanruw 1972), and the Micronesian Gecko has not been seen on Guam since 1978 (McCoid and Hensley 1994).

It is possible that additional species are native, but fossil evidence is sparse and no fossils from Guam have been inspected (the above assessment was based on fossil deposits on Rota, Agiguan, and Tinian: Pregill 1998). The two most likely candidates for additional native species are the Brahminy Blindsnake, *Ramphotyphlops braminus*, and the Pacific Blue-tailed Skink, *Emoia caeruleocauda*. The all-female blindsnake species is a good candidate for natural colonization in that all individuals are parthenogenetic and capable of starting a population by cloning themselves. Through human transport the blindsnake has become the world's most widespread snake, found throughout the globe in warm areas. Because it is a burrower, it might die underground in a place that a later paleontologist might interpret as a soil layer from an earlier time period. Thus the occurrence of this species in a pre-human bone deposit is not unequivocal evidence that it arrived in the Mariana Islands without help from man.

The Pacific Blue-tailed Skink is found in the earliest human-era deposits and it may be native. Both of these species have such wide distributions (e.g., the Pacific Blue-tailed Skink is found on most islands from Borneo and Sulawesi to the Marshalls, the eastern Solomon Islands, and Fiji) that they are not considered to be species of special conservation concern. Both are common throughout WAPA.

Many of the other herpetofauna species now found in the Mariana Islands are recent introductions, most notoriously the Marine Toad, *Bufo marinus,* Brown Treesnake, *Boiga irregularis*, and Curious Skink, *Carlia fusca.* These species were introduced to Guam around 1937, 1949, and 1968, respectively. Their presence has resulted in the demise of numerous native birds, mammals, and reptiles, not to mention damages to human pets, domestic livestock, human health, and electrical power systems (Savidge 1987, Rodda *et al*. 1999). In many cases it would be appropriate to manage WAPA to discourage these interlopers.

A second tier of introduced reptiles consists of less-damaging turtles and lizards. The adverse impacts of these introductions are less well known, perhaps because they have not been studied. All of the introduced turtles are recent introductions and most are limited to wetland areas, which we did not inventory. The lizard introductions vary in time from recent (the Green Anole, *Anolis carolinensis*, was introduced to Guam around 1955), to early western contact (the Mutilating Gecko, *Gehyra mutilata*, and the Oceanic Gecko, *Gehyra oceanica* about 400 years ago), to prehistoric (the Indo-Pacific House Gecko, *Hemidactylus frenatus*). The Mangrove Monitor, *Varanus indicus*, has not been found in pre-Western deposits on Rota, Agiguan, or Tinian (Pregill 1998), but Guam archeologists (pers. comm.) report it to have been present on Guam since prehistoric times. Four of these five lizard species have each been directly associated with loss of native wildlife; the fifth, the Green Anole, provides sustenance to the Brown Treesnake. Because they are non-native and harmful, WAPA management should discourage these species.

Guam's remaining reptile species are lizards whose origins are uncertain (Oceanic Snake-eyed Skink, *Cryptoblepharus poecilopleurus*; Littoral Skink, *Emoia atrocostata*; Azure-tailed Skink, *Emoia cyanura*; Blue-tailed Copper-striped Skink, *Emoia impar*; Mourning Gecko, *Lepidodactylus lugubris*; Moth Skink, *Lipinia noctua*; and Pacific Slender-toed Gecko, *Nactus pelagicus*). Until the conditions of their arrival are firmly established, they should be conserved. With the exception of the Mourning Gecko, all are rare or extirpated on Guam; of these species only the Mourning Gecko was found on WAPA.

What Is Known about the Abundance of Guam's Lizards

Although some published information is available on the relative abundances of the various species (see References), inferences from those sources should be done with some skepticism. Several species are not readily distinguishable on the basis of sightings, the relative visibility or detectability of each species is not known, nor is it known if the detectability is constant among habitats. Finally, the precision of relative measures of abundance is not known for any technique used in this area. Thus, it has been possible to make only general statements about the abundances of lizards, and clear inferences about the influence of habitat and predator assemblages have not been possible.

Although no absolute population density estimates have been published for lizards in the Marianas, we have collected some statistics for Saipan (Rodda and Fritts 1997), Rota (Rodda and Dean Bradley 2000), and Guam (Rodda and Fritts 1996, 1998), some of which have been noted in Campbell (1996). These support the general impression of many herpetologists that lizards are relatively abundant on remote islands such as Guam, which are depauperate (species poor) compared to mainland faunas. However, the Guam data cannot be considered representative of Pacific Islands, as Guam is home to an extraordinary abundance of Brown Treesnakes (*Boiga irregularis*), a well-known lizard predator (Rodda and Fritts 1992, Rodda et al. 1997). Although there is no island that is exactly like Guam while lacking snakes, the large snake-free southern Mariana islands are the most similar in terms of their lizard faunas. However, of these, Rota differs from Guam in that it experienced much less loss of native habitat due to warfare and agriculture, whereas Tinian has suffered more. In addition, Rota has not yet experienced the major disruptions caused by the introductions of *Suncus murinus*, a shrew, and *Carlia fusca*, an exotic skink that has seemingly replaced the native skinks in many sites in the Marianas. Saipan, like Guam, has both the shrew and *Carlia*; unlike Guam, Saipan has no resident population of Brown Treesnakes.

Although Guam has not had its vegetation mapped, as best we can tell, the proportion of native forest on Guam is surely greater than that of Saipan, which was documented to be about 4% native forest by Falanruw *et al*. (1989). Engbring and Ramsey (1984) judged that 23% of northern Guam was "primary limestone forest" based on aerial photos of unspecified date. Although Saipan forests were more extensively converted to agricultural land uses prior to WWII, Saipan is probably as similar to Guam as an island can be found in terms of lizard community ecology.

What this Study Adds to Knowledge of Mariana Lizards

Details of Guam's grassland herpetofauna. – This is the first lizard density study to provide absolute population densities of lizards in grassland on Guam. While it is premature to generalize about all Guam grasslands on the basis of three samples, the samples are high validity samples, and may well represent WAPA grasslands.

Details of tangantangan forest surrounded by disturbed habitats. – The tangantangan forests that we sampled at WAPA differed from the tangantangan forests we have sampled elsewhere on Guam in their geographic location (the others have been on northern Guam) and in their relative isolation (the others have been part of continuous forest, not patches amidst grassland). Because these two factors are confounded, it will not be possible to draw firm conclusions as to the cause of differences, if any, but the samples will contribute to a larger understanding of lizard ecology as additional samples are obtained. The samples were chosen to be representative of isolated tangantangan patches in WAPA.

Tools for evaluating other survey techniques. - Absolute population density estimates can be compared to the relative estimates we collected (lizards on sticky traps), but also to those made by others previously and subsequently. We can thereby determine the relative detectability of different species and begin to collect needed data on the precision and stability of these detectability estimates.

MATERIALS AND METHODS

Snake Population Estimates

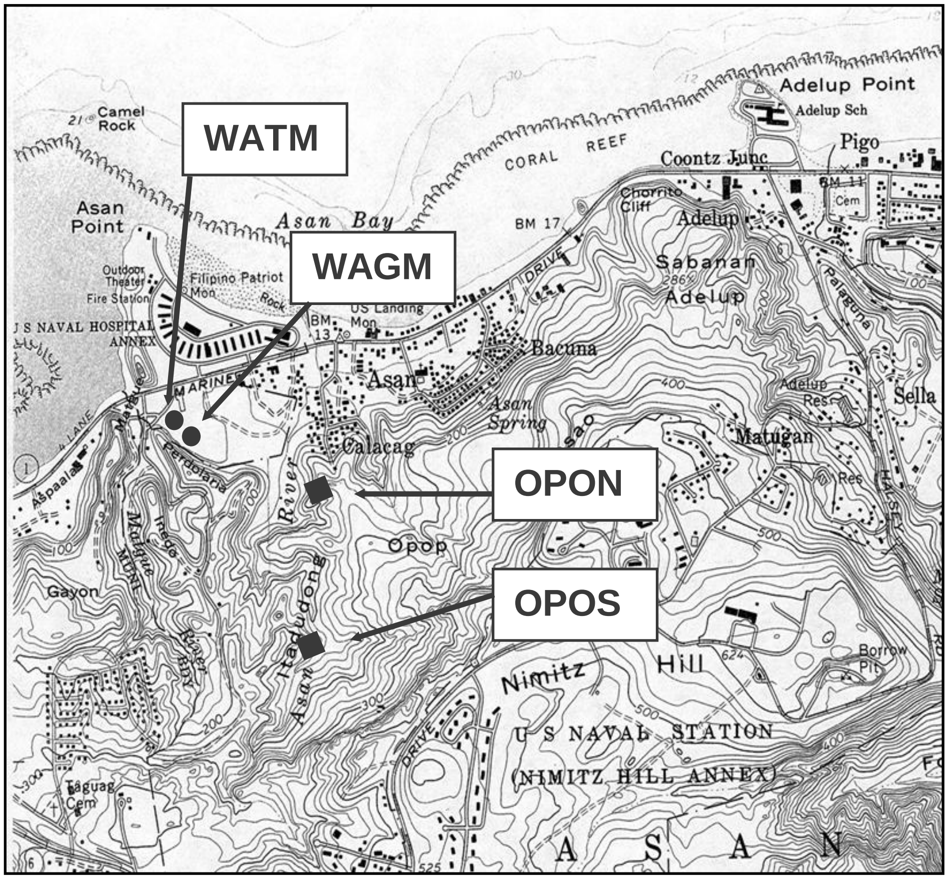
Two four-ha trapping grids were constructed in the Opop area of the Asan Unit (Table 1). Each grid was an array of 8 × 8 traps (128 traps total) with 25 m spacing between each trap. We used our standard modified commercial minnow traps (6 mm galvanized steel mesh) fitted with a live mouse lure enclosed within a snake-proof chamber. The funnel at each end of the trap was fitted with a one-way entrance flap made of 6 mm galvanized steel mesh. A plastic cover shaded the top ½ of the traps to keep snakes and mice from overheating. Traps were hung about 1 m high from trees, vegetation, or rebar buried into the ground.

Table 1. Outer boundaries of the trapping grids. Coordinates are decimal degrees.

Site				
North Grid (OPON)	N 13.46672 E 144.71106	N 13.46768 E 144.71234	N 13.46644 E 144.71332	N 13.46548 E 144.71205
South Grid (OPOS)	N 13.46229 E 144.71162	N 13.46133 E 144.71034	N 13.46008 E 144.71132	N 13.46104 E 144.71260

Traps were baited 12 Mar 01 and were monitored daily until 14 Apr 01. Each trap was checked daily for snake captures. Upon capture, a snake was weighed (g), measured (snout-vent length and total length, mm) and probed to determine gender. The first time a snake was captured it was given an individual scale clip and implanted with a passive integrated transponder (PIT) tag. Snakes were then released on the ground at the site of capture.

Capture histories of snakes were analyzed using program MARK (White and Burnham 1999). The Cormack-Jolly-Seber open population model was used to estimate capture probability (*p*-hat) and survivorship and emigration (φ-hat). In this case, where capture history matrices reflect only 33 days of trapping, φ-hat estimates mainly emigration and not survivorship. Population abundances, N,

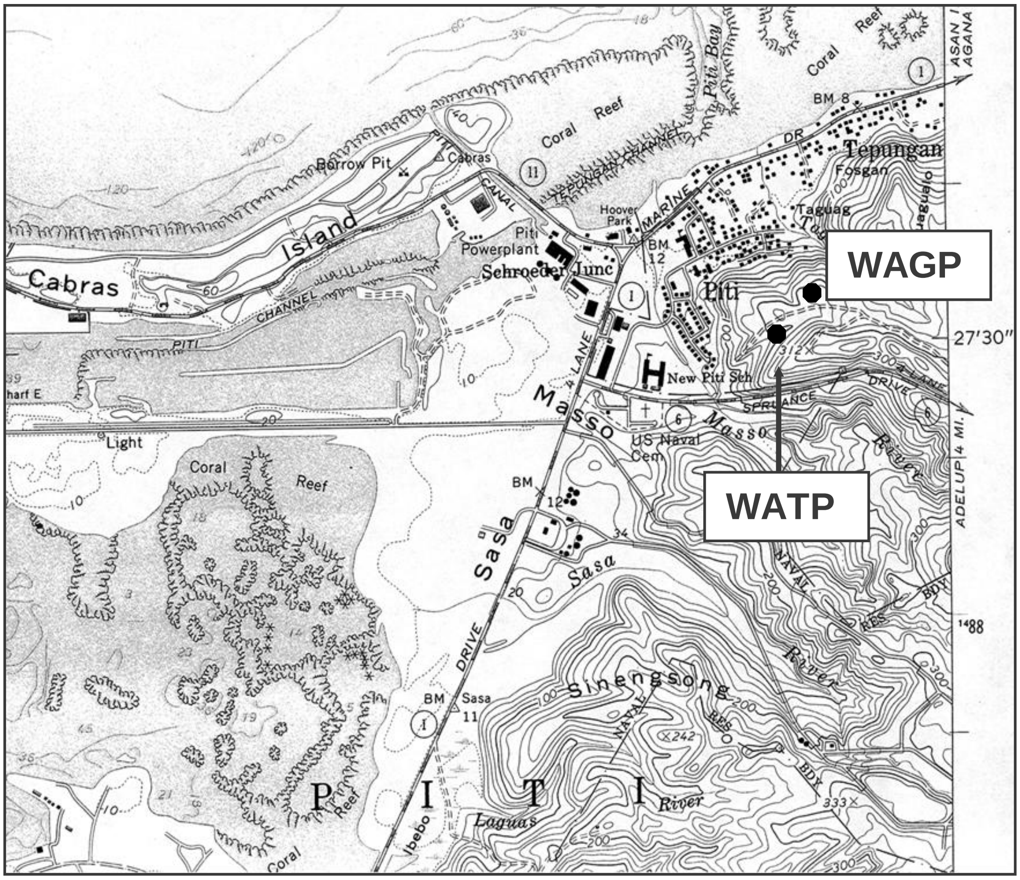


Map 1. Location of snake trapping grids OPON and OPOS. Also shown, location of two lizard removal plots, WATM and WAGM.

were calculated by dividing the average number captured per day, n-bar, by capture probability, N=*n*-bar/*p*-hat. Population densities, D, were calculated by dividing N by the area sampled (A), D=N/A. Populations were analyzed separately for OPON and OPOS, although, due to low recapture success in the OPON grid, we pooled the data from the two grids and obtained a more accurate population estimate for the whole trapping area, designated OPOP.

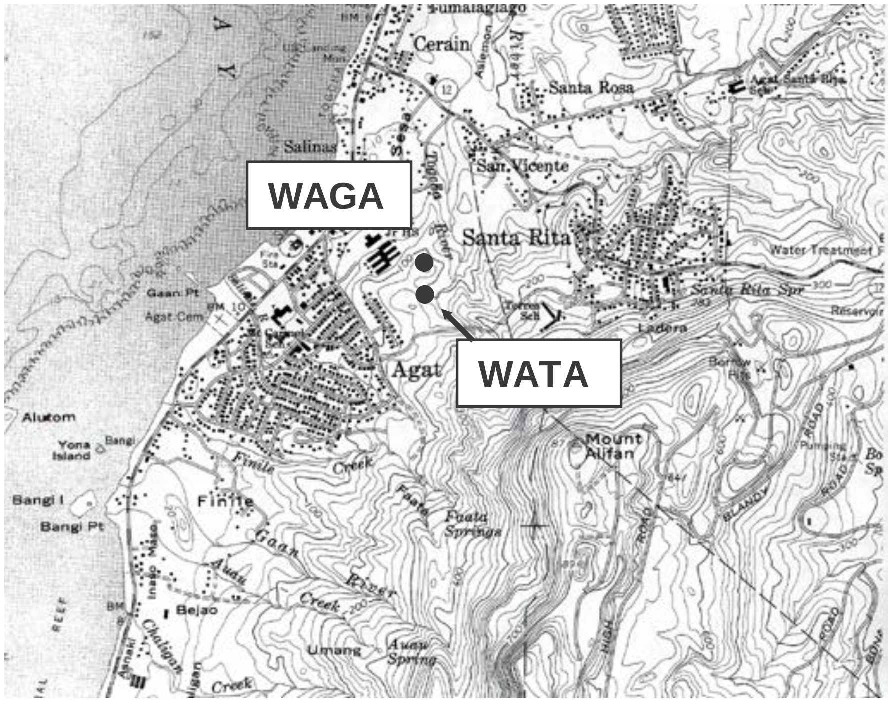
Lizard Abundances

We used a total removal methodology to obtain our absolute population density estimates. This technique has recently been published (Rodda et al. 2001), but we will describe it here in slightly greater detail so that those conducting any follow-up surveys of WAPA can use exactly the same protocol. Our use of this method differed from some previous uses in that we not only



Map 2. Location of two lizard removal plots, WAGP and WATP.

progressively removed all animals from the study plots, but we also removed all aboveground vegetation, which greatly facilitated the detection of animals. However, in order for this method to give an unbiased estimate of the population density, we had to insure that the animals were taken from a precisely known amount of forest. To accomplish this, we first isolated the patch of forest, insuring that no animals could enter or leave during the removal. Thus, there were two major components to this work: isolation of the forest plot, and removal of all animals and plants. In addition, we obtained relative lizard population density estimates for the area surrounding each of the plots following removal. These four steps are described in greater detail below.



Map 3. Location of two lizard removal plots, WAGA and WATA.

Isolation of the Forest Plot

Equipment used. - A wide variety of forestry tools are useful for this work (see appendix). A crew of 3-4 persons is desirable for the various phases of plot isolation (see below), but a larger crew is preferred for the removal phase, as this can require considerable effort. In principle, it should be possible to leave the barrier in place for whatever time is required to inspect all vegetation thoroughly. However, in practice, one wishes to minimize the time span, as the longer the barrier is relied upon, the greater is the risk of immigration or emigration. Using

Table 2. Characteristics of the WAPA lizard removal plots. Note that latitude and longitude are given in decimal degrees. Dates are for 2001. Vegetation mass is kg.

Site	Latitude (N)	Longitude (E)	Barrier Date	First Day	Last Day	Pers Hrs	Veg Mass
Grassland							
Agat (WAGA)	13.384	144.662	01-Apr	02-Apr	03-Apr	15	335
Asan (WAGM)	13.469	144.707	19-Mar	20-Mar	21-Mar	35	803
Piti (WAGP)	13.460	144.696	26-Feb	27-Feb	28-Feb	8	153
Tangantangan							
Agat (WATA)	13.383	144.662	29-Mar	30-Mar	31-Mar	56	1,702
Asan (WATM)	13.470	144.706	13-Mar	14-Mar	15-Mar	54	1,702
Piti (WATP)	13.460	144.694	21-Mar	22-Mar	23-Mar	50	2,011

the first sixteen removal plots sampled, the number of person-h required for removal is correlated with the wet mass of vegetation removed ($r^2 = 0.68$; est. removal effort = 0.0178*(veg. mass) + 36.4 person-h).

Site selection. - Site selection was constrained by the availability of suitable habitat, and the requirement that forest patches be more or less level and composed of soils that were deep enough to allow the emplacement of aluminum flashing fencing buried to a depth sufficient to preclude the passage of lizards.

While we endeavored to locate 10 × 10 m plots in each case, the occasional intervention of a large boulder or inappropriate soil caused us in some cases to choose alternate layouts that nonetheless constituted an area of 100 m^2, for example 8.3 × 12 m. In addition, we sometimes deviated from straight-line boundaries in order to minimize the amount of vegetation that would have to be removed to achieve canopy separation. However, we insured that deviations to the inside of the nominal boundary were exactly balanced by equivalent deviations to the exterior of the straight-line perimeter.

Vegetation sampling. - We characterized the vegetation of each forested plot in six ways: ground cover by percent cover of major structural types (e.g., graminoids v. vines, etc.); tree cover by number of stems, tree basal area, canopy height, and canopy coverage; and total fresh biomass of removed vegetation. Ground cover was sampled at 20 equidistantly placed points covering the entire 10 × 10 m plot. At each sampling point, a 20 × 50 cm Daubenmire frame [a 20 x 50 cm frame conspicuously marked to denote patches of 1, 5, 10, 20, 40, 50, and 60% of the total area] was placed (oriented parallel to the nearest boundary) and the percent cover estimated within the frame for each of ten major vegetation types. The average coverage by each of the ten types was the basis for the values reported here: litter coverage, grass coverage, herb coverage, and ground cover diversity (Shannon-Weiner Index; Pielou 1970).

Trees were defined as those with woody stems exceeding 1.0 cm diam. at breast height; large trees were those exceeding 10.0 cm diam. at breast height. For these, we report: number of stems, cross sectional area at breast height (estimated by measuring dbh with calipers and assuming that stems are circular in cross section), typical canopy height (i.e., excluding rare emergents), and canopy cover (estimated visually and with a spherical densiometer).

Ground separation/trenching. - It would be preferable to instantly emplace the barriers that preclude lizard immigration and emigration from a plot. However, it is inevitable that some lizards will leave a plot in response to the disturbance required to establish the barrier. Also, it is possible that the vegetation removed to provide canopy separation might inadvertently constitute a valued refugium and thereby concentrate lizards in the brush piles created. We attempted to avert these possibilities through a combination of carefully timed actions.

The first step was to remove enough low-lying vegetation to insure that lizards could not use the vegetation to bridge across the ground level barrier when it was later emplaced. The ground-level barrier was made from a fence of 508 mm wide (sold as "20 inch wide") aluminum flashing that was buried 50-100 mm into the ground. The lizards on Guam have only limited ability to leap upwards, but they can span distances of about 0.5 m when leaping downward. Thus to effect an unequivocal separation, we cleared a swath about 1 m wide to a height of about 2 m along the course in which the flashing fence would later be placed. In addition, in order to expedite the subsequent emplacement of the flashing, we used the occasion of ground clearing to excavate a furrow into which the flashing would later be inserted. Furrow excavation inevitably revealed the presence of root obstacles. Such roots were severed to allow the later burial of the bottom of the flashing. In addition, we placed rebar supports at places where the flashing would bend sharply. Flashing would have to bend in a horizontal plane at the corners of the enclosure, and flashing would have to bend in a vertical plane at especially high and low places. Generally we used 2-3 supports per 10 m side. Additional rebar supports were later positioned where each roll of flashing ended or began, but these spots were not easily ascertained in advance. We used rebar for the supports, but any sharpened metal post would do. The preferred length of the bar depends on the hardness of the soil or substrate; the diameter is not critical. We used rebar pieces that were mostly about 0.9 m long. The bottom end of the rebar should be sharpened symmetrically, so that it does not tend to veer as it is being driven. The rebar was pounded vertically into the ground at the bottom of the trench such that the top of the bar was level or below the height of the flashing whenever possible. As a safety measure, it was sometimes desirable to place gaudy flagging on isolated rebar posts; this was not needed once the flashing connected and covered the rebar posts.

Five rules were followed to minimize the influence of this trenching/clearing activity on the lizards: 1) activity occurred during the day to minimize disturbance of nocturnal geckos, 2) no motorized tools were used (in our experience, chainsaws in particular induce flight in lizards), 3) brush removed at this stage was dispersed rather than being piled, so that lizards would not be attracted to potential brush pile refugia, 4) half of the removed vegetation was placed within the plot and the other half was place outside, to limit any bias this vegetation might have on lizard movements, and 5) this activity was scheduled to occur 24 h prior to initiation of vegetation removal, so that any terrestrial lizards disturbed by the activity would have plenty of time to regain their normal home range prior to isolation. On the other hand, heliophilic (sun-loving) lizards may be attracted to the light gap created by vegetation removal, so it is best to otherwise minimize the time that might permit heliophilic lizards to move into the area.

Canopy separation. - Canopy separation inevitably has an adverse effect on arboreal species. Most arboreal species on Guam are also nocturnal. Generally, unless physically disturbed, nocturnal species will not move away from an area of disturbance until nightfall following the disturbance. However, the terrestrial species disturbed by canopy separation are likely to move away immediately, but normally return to their home ranges if given sufficient daylight hours without a disturbance. Therefore, we always separated the canopy as early as possible in the day on which the barrier would be placed after nightfall. In this way, nocturnal species would have no opportunity to vacate the plot if they were disturbed by canopy separation, and diurnal species would have at least half a day to return to their terrestrial haunts after we had left the area.

Canopy separation is straightforward in principle; a gap of at least 1 m must be achieved between all aboveground vegetation. This measurement must accommodate tree movements induced by wind. If possible, it is desirable to create the gap in the foliage directly over the line on which the ground level barrier will later be placed (to minimize the ability of lizards to immigrate or emigrate by jumping from a leaning tree to the other side of the barrier), and in forests composed of trees with vertical trunks this can be achieved. However,

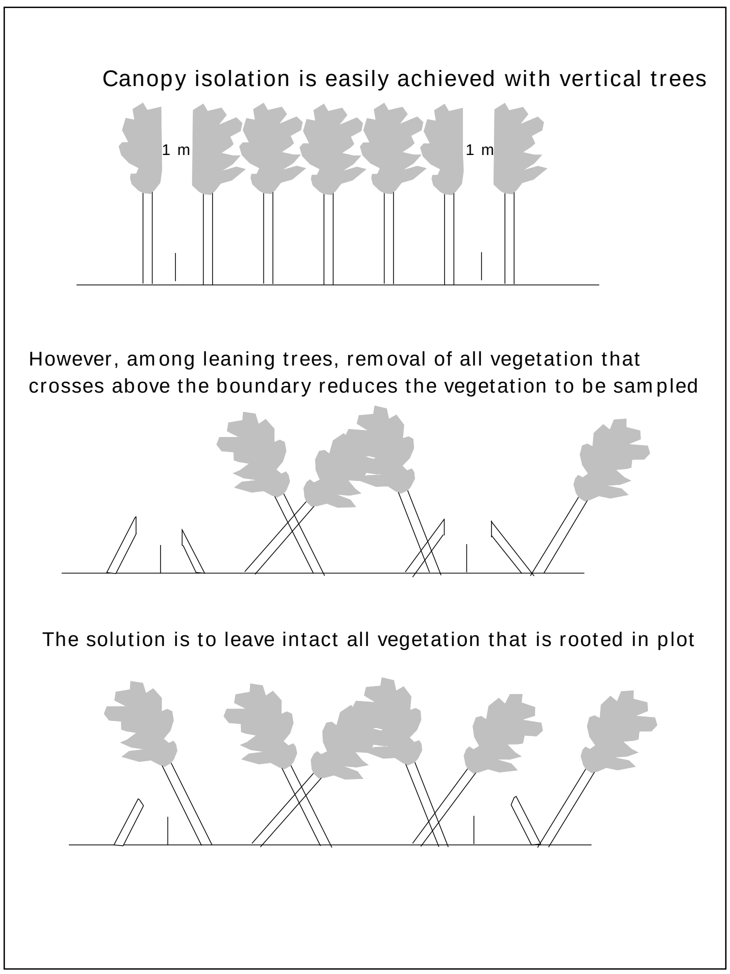


Fig. 1. In general, trees rooted in a plot should be left undamaged by canopy separation, to insure sampling of a full measure of forest volume (equivalent to 10 × 10 × 10 m, though not usually in a cubic shape).

forests of the Marianas often have trees that have partially fallen in response to typhoon winds. We attempted to minimize inclusion of such trees when choosing a site, but not all could be avoided. The problem is illustrated in Fig. 1.

Wherever a cut is made in a tree, all limbs, branches, and leaves distal to the cut fall to the ground. If all stems that pass above the perimeter line are cut, the total amount of aboveground vegetation formerly within the plot will be reduced by the amount of leaning vegetation that entered the plots "airspace" from trunks rooted outside of the plot (Fig. 1). Furthermore, strict boundary cutting creates excessively large light gaps (altering the lizard habitat). The solution is to generally leave intact all stems that arise from trees rooted within the plot, regardless of whether they pass to the outside of the barrier above ground level. This insures that the aboveground vegetation that is sampled is quantitatively representative of what would be found in the airspace of an arbitrary 10 x 10 m column of forest.

Installation of barrier. - We installed the aluminum flashing barrier in the first hours of darkness on the night immediately preceding removal of lizards. This insured that nocturnal species would be trapped within the sampled plot (because they are loath to crawl out of the trees while humans are disturbing the area). The diurnal species were also trapped because they had already cloistered themselves in their nighttime refugia by the time we began barrier installation. Given that the trench to receive the barrier had already been cleared, it took only 1-2 h to install the fence.

Rebar supports were added as needed during the installation of the fence. All supports can be placed during fence erection, but the pounding needed for their emplacement may create additional disturbance, which we reduced by preplacing rebar supports at all of the predictable locations (the rebar needed for finishing or beginning a roll of flashing cannot easily be predicted). The rebar was connected to the aluminum flashing with two short pieces of tie wire, which were twisted together on the outside of the barrier and were themselves covered with smooth tape. The rebar and the upper half of the fence were thoroughly sprayed with lithium automotive grease to present a chemical and mechanical barrier to climbing geckos (none of the lizards could climb clean and unblemished aluminum flashing, but geckos are capable of climbing soiled flashing and even skinks can climb irregularities created by poorly placed or damaged tape). Finally, the edges of any limbs or branches that passed near the barrier and might have inspired a lizard to jump were protected with a sticky trap. Details of all these procedures follow.

There are eight steps, that were done in the following order: 1) insert flashing in ground, 2) emplace any needed rebar supports, 3) tamp earth to hold bottom of flashing, 4) tie rebar to flashing, 5) tape all seams and rugosities, 6) spray lithium grease on completed fence, 7) if necessary wet soil at base of fence and retamp for better seal, and 8) place sticky traps.1) The aluminum flashing was rolled out by one or two persons while one or two more forced it into the trench and backfilled soil. We found that it was vastly preferable to have the fence follow a subtly sinuous path rather than run in a straight line. Sinuosity in the fence line enables it to conform to the inevitable irregularities in the ground's

Fig. 2. Sinuosity in the line of the barrier fence made it easier for the flashing to conform to the inevitable irregularities in the height of the ground. At places where the ground is concave, the top edge of the flashing becomes more sinuous (side-to-side) than does the bottom, which exhibits little side-to-side sinuosity in the concavity; above convexities, the converse occurs.

height without the necessity for seaming the flashing or creating sharp curves which lizards could climb (Fig. 2).

2) Sharpened rebar was driven into the ground on the outside of the fence as needed. Rebar supports were not strictly necessary, but were of considerable help in protecting the fence from being uprooted by people who accidentally tripped over the fence while entering or leaving.

3) The tamping of soil can be difficult if the soil is dry. We have found that wetting the soil helps, but it is important not to wet the soil on the first tamping, because it is very difficult to wet the soil right next to the flashing without getting the flashing wet, and wet flashing cannot be greased. Also, we found it best to finalize tamping only after the fence was in its final position.

4) To tie the flashing to the rebar it was necessary to punch two small holes (about 1 cm apart, pushing from the inside to the outside of the enclosure), one on either side of the rebar. Holes punched from the outside to the inside of the enclosure tended to create a rough spot on the inside, potentially enabling a climbing lizard to gain purchase and escape; therefore, this was avoided. One pair of holes was punched 5-10 cm below the top of the rebar, the other at the

base of the flashing. The 20 cm long tie wire was doubled into a U shape and pushed through the flashing from the inside. After twisting the two ends tightly together, the excess was cut off, and the protruding remainder folded down against the rebar.

5) After smoothing the tie wire against the inside, a 5 × 5 cm patch of aluminum tape (such as is sold at hardware stores for patching holey car bodies or mufflers) was placed over the inside ties. When carefully rubbed down, this tape presented an extremely smooth surface. Aluminum tape was also used to close the seam at the ends of flashing pieces. However, aluminum tape is expensive and it does not accommodate irregular surfaces. Therefore, for the outside we used duct tape, which covered the ties, rebar, and the ends of flashing rolls.

6) We sprayed white lithium grease on all tape and rough surfaces, as well as the top 15 cm of the fence (both inside and out).

7) As mentioned above, we poured water along the base of the fence (inside and out) if the soil was too dry to pack well, and gave a final tamping.

8) To minimize immigration/emigration by jumping lizards, we put sticky traps on all surfaces near enough to the barrier to tempt a lizard. These were attached to trees using a stapling gun. They were placed at vulnerable points both inside and outside of the plot.

Relative Density Sampling

Adhesive trapping. - Although the above sticky traps were used simply to capture any potential emigrants/immigrants, we also set adhesive traps in the forest nearby to independently measure the relative abundance of lizard species in the area. This can be done at any time when lizards would not be disturbed by removal plot activities. Adhesive trapping was normally conducted well after vegetation disturbance. The traps were positioned as close to the plot as possible in similar habitat to the plot itself. Typically we placed the traps at least 5 m away from the plot boundary, in a concentric ring around the plot. We placed 12 traps on the ground and 12 in nearby trees (at roughly breast height). These were checked more or less hourly during daylight hours and maintained for a total of about 24 h. Captured lizards were released once the adhesive trapping had concluded.

Removal

General strategy and inspection notes. - Live lizards are extremely easy to detect; dead lizards are easily lost in the debris. Therefore, it was our first priority to keep all the lizards in the plot alive. As the barrier was secure, there was little opportunity for a lizard to escape. Therefore, it was not necessary to catch each lizard on first sighting. Instead, we inspected the vegetation systematically and captured the lizards when it was made easy by their being "trapped" against the fence or out in the open. Desperate lunges for lizards running into the vegetation tend to result in non-target lizards being crushed unseen beneath fallen vegetation. Therefore, we avoided such chases and attempted to minimize the amount of vegetation that had been cut down but not yet inspected. Inspected vegetation was placed in trashcans greased on the outside to repel climbing lizards. Cans were initially filled outside of the plot, and later placed in open areas of the plot (i.e., containing no vegetation that could be used as an avenue for a lizard to climb into the trash can). Once a trashcan was full, it was taken out of the plot for weighing and disposal of the brush.

For practical reasons we weighed fresh vegetation rather than dried mass. Others have found that vegetation dry mass is very close to 50% of the fresh mass for mixed tropical samples of this sort (Rodin and Basilevic 1968, Odum *et al*. 1970, Art and Marks 1971, Lieberman and Lieberman 1994). Fittkau and Klinge (1973) weighed each component of the forest separately and found that only 2.2% of the fresh mass was leaves (84% stems and trunks, 7.5% litter, and the remainder vines and lianas). Vogt (pers. comm.) weighed three components, live plant material (including leaves, branches, limbs, and trunks), coarse woody debris, and fine woody debris, from a tangantangan forest in northeastern Saipan, and found that these constituted 60.7, 14.7, and 24.8% of fresh mass respectively. Thus we presume that our biomass measurements reflect primarily the amount of woody mass in a study plot.

The general strategy was to work from the outside in, first by dropping into the plot any trees that leaned out over the fence. Usually, such leaners were pulled to the inside by ropes as they were being dropped. Although lizards jumping from trees have been very rare in our experience, almost all jumping has occurred at the moment when treetops are felled. Therefore, for such moments we assigned one person to do nothing other than watch for possible escapes. Fewer than three such attempts were detected, and most of these were captured on the ground. The others were visually identifiable, allowing inclusion in the reported totals.

Lizards can hide in remarkably small cavities. A 3 mm gap in wood grain may conceal a small gecko. Therefore, it was necessary to inspect every item with great care. All vegetation was cut up into modest-sized pieces before being inspected. Solid woody pieces were generally less than 1 m long and carefully inspected. Wood with crevices was chopped apart completely. Leafy branches are harder to inspect and often needed to be chopped into hand-sized pieces for complete inspection prior to placement in the trash cans. We found that lizards were often concealed: within dead or live leaves that had curled, within holes in rocks (all porous surface rocks were broken apart), under rocks and roots (all were excavated to solid undisturbed soil), within tree cavities (all were split open), and under bark (all removable bark was removed). While following these rules, lizards were eventually exposed, causing them to flee and become extremely conspicuous. They usually ran to the edge of the plot where they were trapped against the fence. In a few cases, however, unseen lizards were unintentionally trod under foot. We believe that most of these were found, either by visual detection of the carcass, or by paying attention to aggregations of flies or ants, which generally indicated the presence of a dead animal. However, we found it vastly preferable to keep the ground clear, so that lizards were not rendered inconspicuous through death.

We have found that lizards react with extreme distress to the sound of a chain saw. They may run frantically and leap off branches. Therefore, we attempted to cut all trees leaning to the outside of the barrier with a hand saw (to minimize jumpers), and we avoided using a chainsaw until all upright vegetation was well within the perimeter of the plot. We also maintained sticky traps against the fence, to capture fleeing lizards that might not otherwise have been seen. It was necessary to closely monitor any such traps left in sunny places, as the solar-heated glue becomes hot and will quickly kill trapped lizards. We made a special attempt to hand capture lizards fleeing into open areas when the chainsaw was first started.

We found that the sawdust created by the chainsaw could cover the grease on the flashing and make it possible for lizards to climb the flashing. Therefore, we endeavored to face towards the flashing when using the chainsaw. This insured that the resultant debris sprayed towards the center of the enclosure and did not coat the flashing grease and render it inoperable.

Felling trees. - There is a temptation to cut trees at an angle to the ground to influence the direction they will fall. This can often produce counterintuitive results, with the base sliding in the intended direction, but the crown going in the opposite direction (Fig. 3). Furthermore, angled cuts almost always result in binding of the saw within the cut. The preferred alternative is to make all cuts horizontal to the ground, with the first cut being made on the side of the tree in the direction of the intended drop, and the second cut being made on the opposite side of the tree, but higher. The optimal height of the second cut is determined by the brittleness of the wood, the amount of lean that must be overcome (trees that have been partially toppled by the wind may be unbalanced), and the speed with which one wishes it to fall (greater vertical separation between the cuts slows the abruptness with which a tree falls, though it also reduces assurance in the direction Fig. 3). In addition, relief cuts that extend to the full depth of the first cut can improve the accuracy of the direction of fall, particularly in trees that flex before breaking. Trees that flex a lot will pinch the first cut completely closed before breaking, thereby creating a second pivot point (in addition to the break line) which may cause the falling tree to tip unpredictably (and undesirably) off to the side. A relief cut that goes to the full depth of the first cut will insure that a flexing tree hinges along the line established by the deepest edge of the first cut.

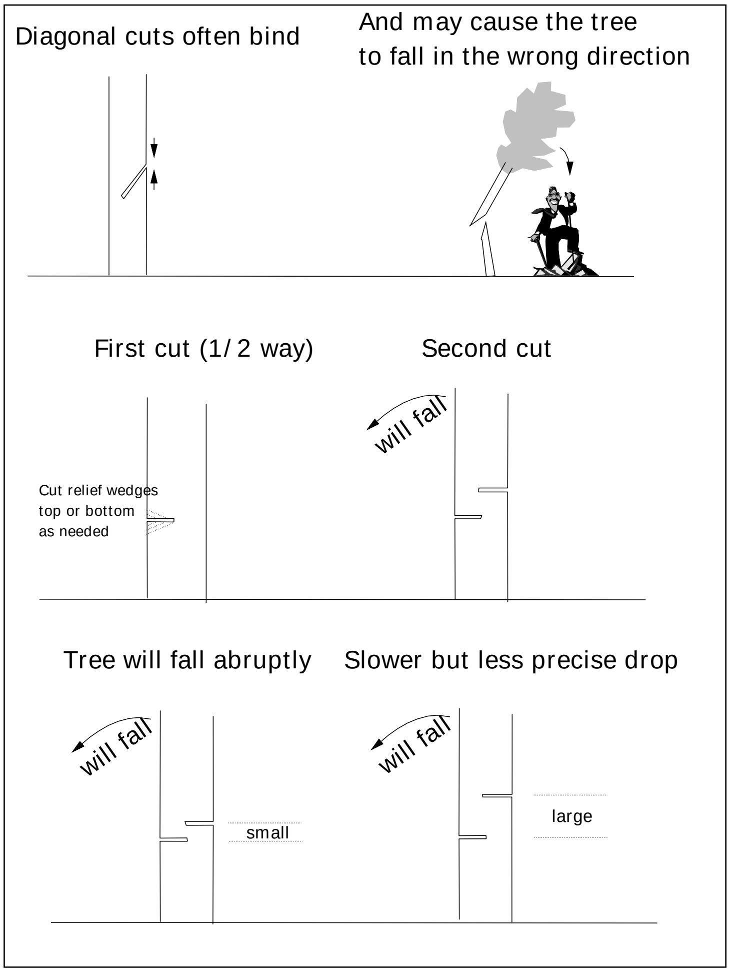


Fig. 3. Principles for the felling of trees in the appropriate direction (away from the fence and people).

Ground clearance. - As indicated, we found it useful to keep the ground as clear as possible. However, raking did not work well, as it tended to bury lizards in small mounds of tiny debris. It was found to be better to pick up all pieces of debris one handful at a time. We did not exert any effort to quantify the abundance of subterranean reptile species (e.g. *Ramphotyphlops*) by excavation. Fortunately, there are no subterranean lizards on Guam.

Follow-up check. - After the plot had been cleaned down to mineral soil, we set a new array of sticky traps within the plot and left the area. These traps were checked throughout the day and for the last time on the following morning. Occasionally, a lizard was buried during vegetation clearing and undetectable in the duff until we left the area or night fell and the lizard ventured forth, only to be snared by the traps. We judged the removal complete following the morning-after trap check.

Disposition of specimens. - Any lizards that were dead or moribund at the conclusion of a removal session were preserved as soon as possible. Live specimens were generally maintained in plastic bags until vegetation removal was complete. As unbiased samples of all of the lizards in an area are extremely rare, it was essential that all specimens be retained. All were weighed and measured when freshly sacrificed and all were deposited in the U.S. National Museum (Smithsonian) (see appendix for collection numbers).

Site Restoration

Site restoration included removal of the fence, but future work is facilitated if the fence is partially cleaned prior to its removal from the ground. Field cleaning includes wiping the bulk of the grease off the flashing (first with rubber squeegees, then will paper towels, and finally – in the lab - with grease solvent) and smoothing the flashing for future use. It was necessary to remove all grease so that tape would adhere to the flashing during subsequent installations. Casual site visits to the removal plots in August 2001 indicated more or less complete regrowth of the grass plots and tree regrowth reaching to about 2 m. Thus it is expected that tree regrowth will make the sample plots indistinguishable from surrounding forest within 1-2 years.

RESULTS - VALIDATION OF REMOVAL METHOD

Although we did not conduct any validation studies as part of the WAPA removals, it is worth noting that prior to the first Guam removals we created several very small enclosures on Guam, removed all resident lizards, stocked the enclosures with a known number of skinks and geckos, left them for 24 h to give them opportunities to escape, and then recaptured all lizards within the enclosure to assess its permeability to lizards. We found that spray cooking lubricants such as Pam® and hand applied grease did not maintain as good a barrier as did the spray lithium grease. Within both greased test enclosures on Guam we experienced no escapes, although we prefer to use the spray grease for its ease of application and more consistent coverage.

RESULTS - SITE CHARACTERISTICS

Vegetation Composition

The plots we sampled were composed of tangantangan trees or grasses. The tangantangan plots differed among themselves in that the Agat site had fewer but larger tangantangan and the Piti site had a higher diversity of trees, with *Morinda* constituting 14% of the cross-sectional area (Table 4). The grassland sites varied among themselves slightly in the density and height of grasses (Table 3). Grassland sites contrasted strongly with tangantangan forest sites by having different species composition, no large trees, less tree diversity, lower canopy height, much less vegetative biomass, less light at ground level, and higher herb coverage and diversity).

Table 3. Vegetation characteristics of the grassland study plots.

	Agat (WAGA)	Asan (WAGM)	Piti (WAGP)	Grassland plots ($\bar{x}$)
Ground layer				
Med. basking light (%)	100	100	100	100
Total fresh vegetation biomass (kg)	335	803	153	430

Table 4. Vegetation characteristics of the tangantangan study plots.
The diversity measures are for the Shannon-Weiner index.

	Agat (WATA)	Asan (WATM)	Piti (WATP)	Tangantangan plots ($\bar{x}$)
Ground layer				
Grass cover (%)	31	33	2	22
Litter cover (%)	53	43	34	43
Herb cover (%)	42	37	57	45
Herb diversity	1.08	0.53	0.49	0.7
Large trees (> 10 cm dbh)				
Number of stems	1	1	0	1
Basal area (cm^2)	816	949	0	588
All trees (>1 cm dbh)				
Number of stems	25	153	274	151
Basal area (cm^2)	28,265	18,872	20,774	22,637
Canopy height (m)	6.0	6.5	5.5	6.0
Canopy cover (%)	94.1	97.5	97.0	96.2
Med. basking light (%)	10.4	11.4	6.4	9.4
% tangantangan (basal)	96	98	81	92
Tree diversity	0.64	0.51	1.06	0.74
Total fresh vegetation biomass (kg)	1,702	1,702	2,011	1,805

RESULTS – BROWN TREESNAKE POPULATIONS

The model selected by program MARK as the most parsimonious, based on AICc, included no heterogeneity in phi, and heterogeneity in p associated with the size of the snake captured. However, for our purposes here, we will report the second best model selected, with only a slightly higher AICc, that did not allow for any heterogeneity in p or phi (model p., phi.). The results of the two models are nearly identical and the reporting of the more simplistic model (p., phi.) allows for easier interpretation.

Snake population density on the northern trapping grid (OPON) at 20 snakes/ha was slightly lower than the all-Guam average of 29 snakes/ha while density on the southern trapping grid (OPOS) was exceptionally low at 7 snakes/ha (Table 5).

Table 5. Population characteristics of the snake trapping grids. OPOP is the pooled data from both OPON and OPOS. The pooled data allowed for better parameter estimates in program MARK. Nightly movement is expressed as a proportion, 1-phi.

	OPON	OPOS	OPOP
# captures	27	41	68
# recaptures	4	16	26
Abundance (#)	79	26	62
Density (#/ha)	20	7	8
Recapture probability (***p***-hat)	0.01	0.05	0.03
Nightly movement	0.015	0.032	n/a

RESULTS-LIZARD ASSEMBLAGE COMPOSITION

Our lizard density estimates can be expressed either as number/ha (Tables 6 and 7) or biomass/ha (Tables 8 and 9). As each plot was exactly 0.01 ha in size, actual numbers captured in each plot can be deduced by dividing the reported densities by 100/ha. Because different sites have different mixes of large and small species, we prefer to use biomass (kg/ha) rather than density (individuals/ha) when comparing sites or species. For comparison to other sites, the average aggregate biomass of lizards at WAPA (10.9 kg/ha) was next to lowest of the averages we have recorded using removal techniques in the Mariana had the lowest average to date (7.4 kg/ha), and tangantangan (14.5 kg/ha in the WAPA plots). The WAPA tangantangan average was more than the Rota tangantangan (snakes absent), in line with Saipan tangantangan (snakes absent), but less than the NW Field tangantangan, with or without snakes. Comparison of the composition of WAPA tangantangan lizard assemblages (Fig. 4) to other tangantangan sites in the Marianas (no comparison possible for grassland sites) indicates that WAPA sites had a greater abundance of *Gehyra mutilata* than most other sites, but an unexceptional abundance of the other species.

Table 6. Observed densities of lizards per hectare in grassland plots.

	Agat (WAGA)	Asan (WAGM)	Piti (WAGP)	Grassland plots ($\bar{x}$)
Geckos				
Gehyra mutilata	0	600	0	200
Hemidactylus frenatus	0	300	0	100
Lepidodactylus lugubris	200	100	200	167
Skinks				
Carlia fusca	1400	5000	1700	2700
Emoia caeruleocauda	0	1100	0	367
Anoles				
Anolis carolinensis	100	0	0	33
All lizards	**1700**	**7100**	**1900**	**3567**

Table 7. Observed densities of lizards per hectare in tangantangan plots.

	Agat (WATA)	Asan (WATM)	Piti (WATP)	Tangantangan plots ($\bar{x}$)
Geckos				
Gehyra mutilata	1600	400	900	967
Hemidactylus frenatus	600	2300	800	1233
Lepidodactylus lugubris	2600	600	3700	2300
Skinks				
Carlia fusca	1900	2000	1500	1800
Emoia caeruleocauda	1400	3200	1200	1933
Anoles				
Anolis carolinensis	100	0	0	33
All lizards	**8200**	**8500**	**8100**	**8267**

Table 8. Observed biomasses of lizards (kg) per hectare in grassland plots.

	Agat (WAGA)	Asan (WAGM)	Piti (WAGP)	Grassland plots ($\bar{x}$)
Geckos	**0.02**	**1.87**	**0.29**	**0.73**
Gehyra mutilata	0	1.06	0	0.35
Hemidactylus frenatus	0	0.72	0	0.24
Lepidodactylus lugubris	0.02	0.09	0.29	0.13
Skinks	**3.72**	**12.12**	**3.52**	**6.45**
Carlia fusca	3.72	10.70	3.52	5.98
Emoia caeruleocauda	0	1.42	0	0.47
Anoles	**0.55**	**0**	**0**	**0.18**
Anolis carolinensis	0.55	0	0	0.18
All lizards	**4.29**	**13.99**	**3.81**	**7.36**

Table 9. Observed biomasses of lizards (kg) per hectare in tangantangan plots.

	Agat (WATA)	Asan (WATM)	Piti (WATP)	Tangantangan plots ($\bar{x}$)
Geckos	**5.79**	**6.46**	**5.75**	**6.00**
Gehyra mutilata	2.30	0.62	1.07	1.33
Hemidactylus frenatus	1.09	4.92	1.75	2.59
Lepidodactylus lugubris	2.39	0.92	2.92	2.08
Skinks	**7.81**	**10.66**	**6.60**	**8.36**
Carlia fusca	5.51	5.96	4.79	5.42
Emoia caeruleocauda	2.30	4.70	1.81	2.94
Anoles	**0.30**	**0**	**0**	**0.10**
Anolis carolinensis	0.30	0	0	0.10
All lizards	**13.89**	**17.12**	**12.34**	**14.45**

Gecko fraction. - As would be expected of the arboreal geckos, these were far less abundant (though not absent) from the grassland plots. On average they constituted 10% of the grassland lizard biomass, whereas in the tangantangan plots they made up nearly half (42%) of the lizard biomass. The fraction of the lizard biomass in various plots in the Mariana Islands is related to the structure of

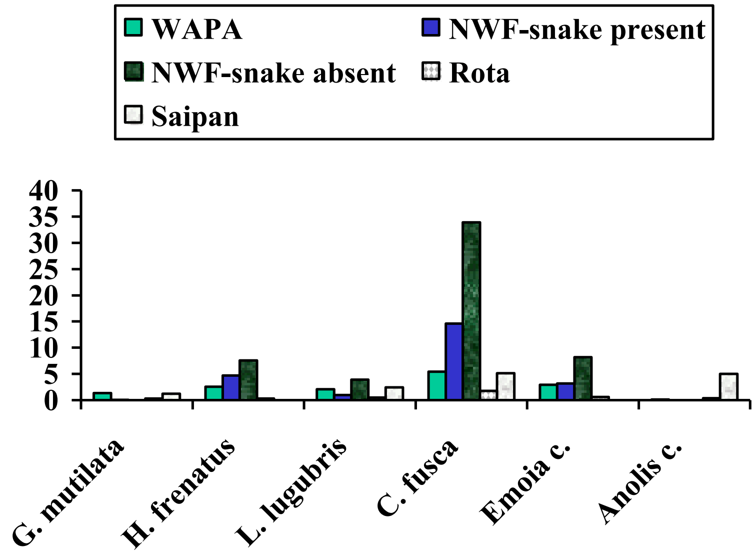


Fig. 4. Average lizard biomasses present in WAPA tangantangan forest in comparison to other tangantangan sites in the Marianas

the forest (Rodda and Dean-Bradley 2000); more geckos tend to be found in denser, older forest. Thus it is not surprising that young tangantangan stands on WAPA would tend toward the low end of that spectrum (10-94% for all forest types in the Marianas; 19-65% for tangantangan).

Introduced v. native species. – In general introduced species tend to do best in disturbed habitats. Recently-introduced species (in this case *Carlia fusca* and *Anolis carolinensis*) made up 84% of the grassland lizard biomass, the highest average we have recorded in the Mariana Islands. The representation of these species in the tangantangan plots was substantially less (38%), and less than has been observed for other tangantangan forests on Guam (56-65%).

Adhesive trap yields. - We captured only four of the six resident species on our adhesive traps set at removal plots (Tables 10-11). These data are to be used primarily in combination with similar data from other removal plots for developing estimators for the detectability of each species, but they can also be viewed in comparison to spot sample detection rates and the absolute densities reported above (see below). In comparison to the absolute population densities revealed through removals, the adhesive trap yields were not very good predictors of overall abundances. For example, *Lepidodactylus lugubris* was undetectably rare based on adhesive trapping in trees, but in actuality it was the most common arboreal species. In time it should be possible to develop species-specific correction factors to adjust for the relative trappability of each species. With that information it will be possible to make crude density estimates based solely on the adhesive trap samples, such as the spot samples

The spot sample adhesive trap results can also be used directly in comparison to any adhesive trap samples made in the same habitat with the same sampling protocol (time of day, length of trapping period, positioning, etc.). The raw capture rates are presented in Table 12.

Table 10. Observed capture rates (captures/trap-h) for skinks from 12 adhesive traps set on the ground for three morning hours around total removal sites.

Habitat	Site	*Carlia fusca*	*E. caeruleocauda*
Grassland			
	Agat (WAGA)	0.389	0
	Asan (WAGM)	0.781	0
	Piti (WAGP)	0.269	0
	MEAN	**0.36**	**0.00**
Tangantangan			
	Agat (WATA)	0.917	0
	Asan (WATM)	1.056	0
	Piti (WATP)	0.444	0.056
	MEAN	**0.60**	**0.01**

Table 11. Observed capture rates (captures/trap-h) for geckos from 12 adhesive traps positioned in trees for 24 h. No geckos were captured in the grassland sites.

Habitat	Site	*L. lugubris*	*H. frenatus*	*G. mutilata*
Tangantangan				
	Agat (WATA)	0	0.014	0
	Asan (WATM)	0	0.021	0.010
	Piti (WATP)	0	0	0
	MEAN	**0.00**	**0.01**	**0.00**

Table 12. Observed capture rates for skinks (captures over a 3 h period) and geckos (captures over a 24 h period) from adhesive trapping sites other than from the total removal plots. *indicates 24 h ground traps. Coordinates are decimal degrees.

Unit	Habitat	*C. fusca*	*Emoia c.*	*L. lugubris*	*H. frenatus*	*G. mutilata*
AGAT						
	Rocky Shore ($\bar{x}$)	**0.153**	**0.0**	**0.001***	**0.003***	**0**
	Apaca Pt N 13.4011, E 144.6603	0.139	0	0	0.003*	0
	Ga'an Pt N 13.3858, E 144.6552	0.167	0	0.002*	0.002*	0
ASAN						
	Beach (Asan) N 13.4714, E 144.7053	**0.234**	**0.009**	**0.001***	**0.005***	**0.007**
	Burn (Opop N) N 13.4667, E 144.7111	**0.167**	**0**	**0**	**0**	**0**
	Grass, short ($\bar{x}$)	**0.139**	**0.0**	**0**	**0**	**0**
	Opop North N 13.4667, E 144.7111	0.111	0	0	0	0
	Opop South N 13.4623, E 144.7116	0.167	0	0	0	0
	Grass, tall ($\bar{x}$)	**0.111**	**0.0**	**0**	**0**	**0**
	Opop North N 13.4667, E 144.7111	0.167	0	0	0	0
	Opop South N 13.4623, E 144.7116	0.054	0	0	0	0
	Ravine (Opop S) N 13.4623, E 144.7116	**0.287**	**0.115**	**0.007**	**0.003**	**0.000**
	Second Growth (Fonte Plateau) N 13.4600, E 144.7270	**0.328**	**0.260**	**0**	**0.003**	**0.014**
PITI						
	Grass (Mt. Tenjo) N 13.4322, E 144.7039	**0.222**	**0**	**0**	**0**	**0**

Discussion by species

Brown Treesnake

The most notable attribute of our Brown Treesnake sample was that it was obtained during an irruption of mice and other rodents. On the first day we captured nearly 40 rodents in our snake traps, whereas prior trapping on Guam has yielded no more than two on a single day. Thus we had an opportunity to assess the density and trappability of snakes in a high-rodent environment. However, the density of rodents was not the same on the two trapping grids. From post-snake-trapping snap trapping of rodents (Rodda, unpub. data), we obtained an average capture rate of 0.084/trap-n on the northern plot (OPON), but only 0.052/trap-n at OPOS. Previous snap-trapping associated with snake trapping grids on Guam had produced no more than 0.02/trap-n, thus the OPOP trapping greatly extended the range of rodent densities that had been observed in relation to snake trapping.

One might expect that higher densities of rats would increase snake densities. This may be true, but too few data are available from grassland sites to evaluate this hypothesis in the absence of a confound with habitat type. Much higher Brown Treesnake densities (up to 60/ha) have been observed in tangantangan forest on Guam, but it would not be surprising if a treesnake would do better in forested areas than in grassland. Within grassland habitat we can compare only the two OPOP sites: the site with a higher rodent density (OPON) also had a higher snake density (20 v. 9/ha).

Any analysis of the trappability of snakes in relation to rodent density suffers from the same logical confound with habitat type mentioned above. However, we would think that a snake ought to be much easier to capture in the two-dimensional space of a grassland in comparison to the three-dimensional complexity of a forest. In a forest, one would expect many snakes to be crawling through the trees at a height at which they would bypass a trap. In a grassland, on the other hand, one would expect all snakes crawling past a certain location to detect a snake-trap in front of them. Thus one might expect greater capture success in grassland than in trees, but we observed the lowest values we have obtained at venues where rodent density was monitored. Furthermore, the higher rodent density site had a much lower average capture probability (OPON was about $1/5^{th}$ that of OPOS). In combination with other data on capture success in relation to rodent density, this observation has convinced us that the presence of many wild food items limits the effectiveness of food-based snake traps. The overall r^2 relating snake capture success to rodent density is 0.90. That is, the higher the rodent density, the harder it is to capture a snake. This is a vital finding for control efforts of the snakes in places like Saipan, where rodents tend to be exceptionally dense, and it places similar constraints on snake control efforts that might be considered for WAPA.

Geckos

Gehyra mutilata (Mutilating Gecko). – The Mutilating Gecko is a very early historical introduction to Guam (Pregill 1998), though no record of its arrival has survived. It has been associated with the disappearance of the endemic Micronesian Gecko, though direct evidence of this interaction has not yet been sought. The habitat preferences of *Gehyra mutilata* are complex, with the species being absent from two of three grassland sites, but reasonably abundant at the third (Asan 1.06 kg/ha). Among spot samples it was detected at one coastal site (Table 12), but none of the others; it was also detected at Fonte Plateau, but none of the other inland sites. It is generally spotty in distribution on Guam (Rodda and Fritts 1996, 1998). The mean biomass density observed at WAPA in tangantangan (1.33 kg/ha) exceeds that of all other tangantangan sites studied (range 0-1.23 on Saipan, but only up to 0.13 on Guam). The particularly large discrepancy between WAPA and other tangantangan sites on Guam may have a geographic component, as the highest biomass density for this species among all habitats on Guam was 3.25 kg/ha at nearby Ordnance Annex. Thus the density in WAPA tangantangan appears low in relation to the neighborhood but high in relation to similar habitat further north on Guam. The average value for Ordnance Annex conceals some important variability; within Ordnance Annex it was extremely abundant at a site with much *Pandanus* (5.4 kg/ha), but much less so in an adjacent area lacking *Pandanus* (1.1 kg/ha). Even higher densities occurred in Rota *Pandanus,* where an average density of 6.7 kg/ha was observed. Perhaps the wetter environment provided by *Pandanus* is favorable to the Mutilating Gecko, as it appears to be for most geckos.

Our analyses of the abundance of *Gehyra mutilata* (Rodda in prep.) have indicated an adverse interaction between it and the similar-sized gecko *Hemidactylus frenatus*, which seems to prefer more open habitats. Neither habitat type nor the presence of *Hemidactylus* adequately predicts the abundance of *Gehyra mutilata* in all localities, however. A mathematical model incorporating the density of *Hemidactylus* (partial r^2=0.494), and the densities of all other lizards combined (a surrogate for insect abundance and other features that were not measured directly but indicate habitat suitability for all species; partial r^2=0.490) produced a model R^2 of 0.57.

The hypothesized negative interaction between the Mutilating Gecko and the House Gecko may have been present in WAPA sites, as the lowest density of the Mutilating Gecko in tangantangan sites was the site of the highest House Gecko density in WAPA tangantangan and vice versa, though both species were absent from two of the three grassland sites and present at the Asan plot. Thus no unequivocal pattern was evident at all WAPA sites.

Hemidactylus frenatus (House Gecko). – The House Gecko is arguably native on Guam (see introduction), though no prehuman remains have been documented. Because it has been associated with displacement of native geckos in other parts of the Pacific (Frogner 1967), it is generally considered to be an undesirable introduced species.

Among Guam forest sites, the House Gecko appears to be most at home in tangantangan. In WAPA tangantangan the biomass density achieved (2.6 kg/ha) was lower than that associated with tangantangan on northern Guam, but higher than that for any other sites sampled on Guam, Rota, or Saipan. The reasons for these differences are not immediately evident. The House Gecko consistently does better on Guam than on the neighboring islands, perhaps because it is more resistant to Brown Treesnake predation. Campbell (1996) found that House Geckos were more likely to escape from a human predator than were the other Mariana geckos. If there is a negative interaction between the House Gecko and the Mutilating Gecko, snake predation on the Mutilating Gecko may release habitat for the more snake-resistant House Gecko. The greater success of the House Gecko in tangantangan may also be due to actual or "apparent" competition with other geckos ("apparent" competition occurs when a predator is more effective at excluding one species than another, causing the more predator-resistant species to appear to be a better competitor).

A mathematical model offered all of the vegetative characters we measured for the removal plots (8 variables) as well as the density of *G. mutilata* and all other lizard species in aggregate (as before, a surrogate for general habitat suitability) yielded a very good model (R^2=0.91) using just three variables: small tree basal area (partial r^2=0.47), *G. mutilata* density (partial r^2=0.57), and density of other lizards (partial r^2=0.89). The positive contribution of small tree basal area and general lizard abundance indicates that these features are positively correlated with *H. frenatus* abundance, whereas there is a negative demographic interaction between the two similarly-sized geckos (whereas the mean mass difference between most-similar lizards is > 1 g for all other species pairs in the Marianas, the mean masses for *H. frenatus* and *G. mutilata* are nearly identical: 1.97 g v. 1.92 g). It is interesting that only small tree basal area was associated with the abundance of *H. frenatus*; there was no association with large trees or other measures of vegetation. Apparently *H. frenatus* thrives in areas with dense stands of small trees.

Lepidodactylus lugubris (Mourning Gecko). - The Mourning Gecko is endemic to Pacific Islands (Radtkey *et al*. 1995 proposed that this widespread species arose in Micronesia) and could easily have arrived here naturally, though direct evidence is lacking (Pregill 1998). In our samples it was a moderately common gecko at all tangantangan sites, and it was the only gecko present at all grassland sites. It is most often found on leaves or very small branches, perhaps to stay out of the way of the larger and more carnivorous species. Although the most numerous gecko in four of six sites, it is also consistently overlooked by other sampling methods (see Tables 11,12 for adhesive trap results). Indeed, it was not detected at all by adhesive traps set at the forest removal plots (Table 11).

Skinks

Carlia fusca (Curious Skink). - *Carlia fusca* was introduced to Guam around 1968. It is associated with disturbed habitats and reaches very high densities in some areas (in snake-free tangantangan plots on Guam, this species attains 33.9 kg/ha, making it one of the world's most dense insectivorous lizards (of 885 insectivorous lizard venues for which absolute population density data are available, only 7 exceed this value for *Carlia fusca* on Guam)). On WAPA it occurred at a biomass density of around 5 kg/ha in both grassland and tangantangan forest, the same as has been observed in tangantangan forest on Saipan. However, it attains much higher densities even in snake-occupied tangantangan forest of northern Guam (14-15.1 kg/ha). The reasons for its relative lack of success in WAPA are unknown. We speculate that the dense herb layer in the WAPA tangantangan sites may limit its density, but direct tests of this hypothesis must await collection of additional samples from central Guam.

During the day, *Carlia* are conspicuously active on the forest floor. Presumably this is the reason that this species is so readily trapped (Table 10 and 12). Although very common, this species tends to be less common than adhesive trapping would suggest.

Emoia caeruleocauda (Pacific Blue-tailed Skink). - This species may be native. Due to its bright blue tail (at least among juveniles) and daytime activity, it has been the most conspicuous lizard of the Marianas historically. However, it is now rare or inconspicuous in many places. It was moderately abundant at all tangantangan sites and the Asan grassland site (WAGM), but absent from the other two grassland sites. Based on recent studies on Rota (Rodda and Dean-Bradley 2000), it appears to avoid very bright/dry sites even if those sites are not occupied by the larger and aggressive Curious Skink. Perhaps the dense grass at the Asan site (denser than the other two grassland sites) provides adequate moisture or protection for this species. Overall there was little support for the notion that it is displaced by the Curious Skink, as the grassland site that was best for the Curious Skink (Asan) was also the site at which the Pacific Blue-tailed Skink was most dense. Similarly, the tangantangan site with the highest density of Curious Skinks (Asan) also housed the densest population of Pacific Blue-tailed Skinks.

Other reptiles

Anolis carolinensis (Green Anole). – This recently introduced species is no longer abundant on Guam, probably due to Brown Treesnake predation (sleeping anoles are extremely vulnerable to the stealthy approach of the arboreal snake). This may account for its relative rarity in our samples from Guam (absent from 16 of 18 total removal plots on Guam). However it was present in low numbers at Agat (both grassland and tangantangan). This may suggest that

Brown Treesnake densities are unusually low at Agat, but direct evidence on this point is not yet available.

Ramphotyphlops braminus (Brahminy Blindsnake) . – One individual of this species was detected in WAPA. Our failure to find more of this subterranean species probably reflects the hot dry weather that occurred during our samples. Our techniques did not target this species and its appearance seems to depend on favorable weather. Based on long-term sampling throughout Guam, it is probably present in reasonable numbers throughout the Park.

Other species. - We did not find any introduced turtles in the removal plots, presumably due to the absence of nearby water sources. Toads were seen at several sites in WAPA, and can be expected to appear near water bodies or after rains. We found moderate densities in both grassland ($\bar{x}$ = 267/ha) and tangantangan sites ($\bar{x}$ = 300/ha). Because these toads are heavy, these corresponded to appreciable biomasses (grassland $\bar{x}$ = 23.3 kg/ha; tangantangan $\bar{x}$ = 15.6 kg/ha). We did not find the rare species of lizards (e.g., *Nactus pelagicus* and *Lipinia noctua* are present in Ordnance Annex), either because they are absent from the area (e.g., the Oceanic Gecko, *Gehyra oceanica*, and the Micronesian Gecko, *Perochirus ateles*), because the habitat is unsuitable (*Nactus* in particular seems limited to undisturbed forest), or because our sampling effort focused on especially disturbed habitat types (grassland and tangantangan).

It is extremely difficult to disprove the presence of a rare species. Efforts to establish their presence or absence from WAPA should focus on the least disturbed forest types.

GENERAL DISCUSSION

What this Study Adds to Population Biology of Reptiles in the Mariana Islands

Brown Treesnakes are difficult to catch in areas with high rodent densities. – Trapping Brown Treesnakes at WAPA was much more difficult than expected based on prior work on Guam, apparently due to high densities of rodents in the area at the time of trapping. A strong negative correlation was observed between rodent density and capture success, which is an important discovery that will guide future Brown Treesnake control efforts. This phenomenon also draws attention to the exceptional rat and mouse density present on the Asan upland unit of WAPA, and suggests that it will be exceptionally difficult to control snakes there under the conditions observed.

What this Study Adds to Knowledge of Mariana Lizards

Details of WAPA populations. - Perhaps the most important value of this work will be in providing population density estimates that can be compared with any future collections from WAPA. Habitat needs of each species can be crudely inferred from the relative densities observed (see above).

Understanding the role of grasslands. - Because these data are based on absolute densities, it is possible to identify habitat (rather than difficulty of sighting) as the reason for differences between sites in measures of abundance. Conservation biologists emphasize the importance of native species, because these are the species that tend to become globally imperiled by habitat destruction and species introductions. Guam's native habitat seems consistent with this generalization. There are few native species present on WAPA; the bulk of the reptile biomass is due to a single recently introduced species (the Curious Skink) that dominates grassland habitats and constitutes over a third of the biomass in tangantangan forest on WAPA.

Tools for evaluating other survey techniques. - Although the present work is only part of a larger work dealing with the validity of various sampling techniques, it is apparent from casual comparison of Tables 6-9 and 10-12 that adhesive trap sampling protocols present a very different portrait of lizard assemblages than does removal sampling. In the absence of validation studies, it may be inappropriate to make inferences about species' relative abundance (among species or habitats) based on the relative population abundance measuring techniques now in use (adhesive trapping is the tool most widely used for relative abundances of lizards in the Marianas). Their use for quantifying population trends within a single species and habitat is also suspect, although additional data are needed to measure their precision for this application.

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APPENDIX - SPECIMENS DEPOSITED AT THE US NATIONAL MUSEUM

SPECIES	SITE	FIELD TAG
Carlia fusca		
	Asan tangantangan	BSFS8905-8921, BSFS8931-8933
	Asan grassland	BSFS8942-8973, BSFS8989-8994 BSFS9006-9015
	Piti tangantangan	BSFS9019, BSFS9021-9025 BSFS9027-9034, BSFS9097
	Piti grassland	BSFS9107-9119, BSFS9123, BSFS9125-9127
	Agat tangantangan	BSFS9129-9144, BSFS9204-9205
	Agat grassland	BSFS9212-9223, BSFS9225-9226
Emoia caeruleocauda		
	Asan tangantangan	BSFS23956-23982, BSFS8934-8936, BSFS8940
	Asan grassland	BSFS8982-8987, BSFS8996-8998 BSFS9016-9017
	Piti tangantangan	BSFS9026, BSFS9044-9053, BSFS9098
	Agat tangantangan	BSFS9150-9161, BSFS9207-9208
Gehyra mutilata		
	Asan tangantangan	BSFS8922-8925
	Asan grassland	BSFS8974-8979
	Piti tangantangan	BSFS9041, BSFS9054-9058 BSFS9060, BSFS9100-9101
	Agat tangantangan	BSFS9162-9175, BSFS9202-9203
Lepidodactylus lugubris		
	Asan tangantangan	BSFS8926-8930, BSFS8941
	Asan grassland	BSFS8988

Piti tangantangan	BSFS9061-9092, BSFS9102-9106
Piti grassland	BSFS9121, BSFS9124
Agat tangantangan	BSFS9176-9199, BSFS9209-9210
Agat grassland	BSFS9224
Hemidactylus frenatus	
Asan tangantangan	BSFS23983-24000 BSFS8901-8904, BSFS8937
Asan grassland	BSFS8980-8981, BSFS8995
Piti tangantangan	BSFS9035-9040, BSFS9099
Agat tangantangan	BSFS9145-9149, BSFS9206

APPENDIX - EQUIPMENT USEFUL FOR REMOVAL SAMPLING

prepared by Stan Kot

PLOT DELINEATION
compass
machetes x 2
yellow string
hand clippers x 2
orange flagging
gloves x 2 pair
hip chain
rebar x 4

VEGETATION SAMPLING
Daubenmire frame
data sheets
caliper
covered clipboard
tape measure
pencils x 2
yellow string
wide felt-tipped marker
orange flagging

PERIMETER CLEARING AND TRENCHING
machetes x 4
32 inch beveled rebar x 24
large saw
sledge hammers x 2
folding saws x 3
flip top container
limb loppers x 4
gloves x 7 pair
hand clippers x 4
spf 45 sunblock
pick axes x 2
hats x 5
shovels x 2
drinking water
trowels x 4
1st aid kit

CANOPY SEPARATION
folding saws x 3
braided nylon rope, 50ft x 3
large saw
flip top container
pole saw/clipper
gloves x 7 pair
hedge shears x 2
spf 45 sunblock
hand clippers x 4
hats x 5
limb loppers x 4
drinking water
stepladder
1st aid kit

BARRIER SETUP
flashing, 50 meters
sticky traps x 1 box
tin snips x 2
staple gun
wire ties x 2 rolls
staples
wire cutters x 2
paper towels x 1 roll
duct tape x 2 rolls
trash bags x 3
metallic tape x 2 rolls
flip top container
white lithium grease x 6
charged head lamps x 7
trowels x 4
gloves x 7 pair
dirt pail
mosquito repellant x 2 cans
trench water x 5 gal jug
drinking water
limb lopper for stray roots
1st aid kit

FOREST REMOVAL
machetes x 4
sticky traps x 1 box
hedge shears x 2
stapler
hand clippers x 4
staples
limb loppers x 4
vegetable oil twist bottle x 2
folding saws x 3
lizard bags x 6
large saw
rubber bands
pole saw/clipper
covered clipboard
stepladder
Rite in Rain fieldbook
braided nylon rope, 50 ft x 3
pencils x 2
hatchets x 2
white lithium grease x 2 cans
sledge hammers x 2
paper towels x 1 roll
wedges x 2
trash bags x 3
rakes x 2
flip top container
shovels x 2
gloves x 7 pair
dirt pail
spf 45 sunblock
32 gal trash buckets x 6
hats x 5
bathroom scale
lotsa soda on ice in cooler
plywood base
1st aid kit
tuned chain saw
chain saw tool kit (ammo box): fresh 40:1 gasoline/oil mix x 1 gallon, bar & chain guard, bar & chain oil x 1 quart, wrench with flat head screwdriver, spark plug, spark plug wrench, pull cord, allen wrench, round file, hearing protectors, bump hat, goggles, gloves

SPECIMEN PRESERVATION
specimen catalog
preserving trays x 5
extra heavy pages
handiwipes
permanent ink pen
widemouth screwtop 500ml
preserving jars
electronic balance
masking tape
stainless steel caliper
marker
formalin x 1 gal
preservation kit: 100ml formalin jar, 30cc syringe w/ 16ga needle, 10cc syringe w/ 23ga needle, 3cc syringe w/ 23ga needle, 1cc syringe w/ 27ga needle, spare 16, 23, 27ga needles, scalpel w/ #10 blade, spare #10 blade, 10% pentobarbital x 2 vacutainers, small curved scissors, small straight scissors, large scissors, tied BSFS tags x 500, extra ties, round-bodied needle in cork, clear 15mm ruler, 150mm tape

FLASHING REMOVAL
grease squeegees x 4
flip top container
vegetable oil degreaser
gloves x 3 pair
paper towels x 3 rolls
spf 45 sunblock
rakes x 2
hats x 3
wire cutters
drinking water
wire ties x 1 roll
1st aid kit
garbage bags x 3