BROWN TREESNAKE

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The brown treesnake, *Boiga irregularis,* was transported to Guam following World War II. A nocturnal, arboreal, and cryptic species, it initially escaped detection. Within a few decades, however, it reproduced, spread, and devastated the terrestrial vertebrate fauna of the island, causing economic damage and cultural disruption. The species is an excellent disperser; brown treesnakes originating from Guam have since been found as near as the island of Rota and as far away as Spain and Diego Garcia atoll. Research on control and interdiction methods has been extensive and productive, but eradication remains improbable, and the risk of further dispersal continues.

GUAM: GEOGRAPHIC AND HISTORICAL SETTING

Guam is a long way from everywhere. All islands within 1,500 km in every direction are even smaller than Guam's 550 km^2, and even these are few and far between. Despite this, humans first reached the island some 4,000 years ago. Although some nonnative species possibly arrived in pre-European times, many of those that have exacerbated the brown treesnake problem arrived with the Spanish colonialists, starting in the mid-1600s. Even more arrived with the Americans, who took possession of Guam after the Spanish-American War of the late 1800s. Invasive rodents, shrews, deer, feral hogs, Eurasian sparrows, and skinks either provide food for the snake (Fig. 1) or compound its negative impacts on the ecosystem, causing invasional meltdown.

THE BROWN TREESNAKE ARRIVES: GUAM, 1950–1980

In the wake of WWII, Guam served as a regional military base for the U.S. military. Movement of salvaged equipment resulted in the arrival of the snake around 1950. Details of this period are sketchy, and most of what little we know about spread of the snake on Guam emerged from the work of Julie Savidge, who reconstructed the process from interviews held in the early 1980s. As is the case with many invaders, the period between arrival and irruption ("lag period") was characterized by a slow buildup in brown treesnake numbers and effects. With abundant food, few predators, and no known diseases or parasites on Guam, snakes grew up to 3 m long. Early reports attached little importance to the snake's arrival, predicting that it would be beneficial by reducing rat populations.

FIGURE 1 A brown treesnake containing three introduced Eurasian sparrows (*Passer montanus*). Common introduced species thought to be benign, such as the sparrow and the curious skink (*Carlia ailanpalai,* formerly referred to as *C. fusca*), can subsidize snake populations and enhance their impact on native species. (Photograph courtesy of G. Perry.)

Lack of species on Guam that feed on or parasitize the snake, as well as abundance of naive prey, helped brown treesnake populations to explode. By the 1970s, brown treesnake numbers were high, their distribution included most of the island, and native birds were in clear decline. Initial thoughts on the cause of the bird decline, based on avian diseases in Hawai'i, turned out to be wrong; no explanation except that of the brown treesnake was supported. Nonetheless, Savidge faced considerable skepticism when she identified the brown treesnake as the culprit, since there was no previous example of a snake causing such ecosystem-wide impact.

BROWN TREESNAKE IMPACTS: 1980 ONWARD

Considerable work has focused on documenting brown treesnake impacts on Guam. Human impacts have taken three forms. Venomous snake bites to humans, and especially to infants, have not resulted in fatalities but have produced some cases of respiratory arrest. Economically, power outage caused by the brown treesnake is at the top of the list. Snakes climb into the transmission system, seeking food or simply moving along. Whenever they short the system, damage that ranges from purely local to islandwide can ensue, causing damaging power outages and requiring costly repairs. Lost tourist revenues resulting from bad publicity are also a concern. Culturally, the

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impact has been loss or massive decline of native species that were part of folktales and traditional lifestyles, such as the Mariana fruit bat (*Pteropus mariannus*, locally known as fanihi, and an important food source) and the Mariana fruit dove (*Ptilinopus roseicapilla*, tottot). Ecologically, the impacts have been some of the most extreme seen in any invasion, primarily as a result of direct predation. Native species had not evolved with a snake predator, and they had few defenses. Snake populations at the height of the irruption were higher than those for comparable snakes measured elsewhere, compounding the problem. Of the three native bat species, two are extinct and the third is barely holding on, despite considerable conservation effort. Practically all native forest birds—nine out of eleven, some of them species or subspecies unique to Guam—have become locally or globally extinct. Native reptiles have fared little better, with most species either gone or in decline. With most bird and mammal prey gone, large snakes are no longer common on Guam, and most adults are about 1.5 m in length.

Some of the extirpated species, such as the fantail (*Rhipidura rufifrons*, chichirika) were insectivorous, and their loss has resulted in changes in invertebrate populations. Other, perhaps more extensive if still unfolding, cascading effects resulted from the snake-caused extinction of important pollinators and seed dispersers such as the Mariana fruit dove and the Micronesian honeyeater (*Myzomela rubrata*, egigi). In an example of how invasive species can have synergistic effects, reduced pollination and seed dispersal are exacerbated by the invasive feral pig (*Sus scrofa*) and Philippine deer (*Cervus mariannus*) grazing on young plants. As a result, old-growth forest is not regenerating after natural or anthropogenic loss.

BROWN TREESNAKE DISPERSAL FROM GUAM

The fate of Guam is an alarming demonstration of the extensive damage that an invasive species can cause when conditions are right. Unfortunately, the same basic conditions exist on many Pacific islands, making them highly susceptible to invasion from a brown treesnake–like species. Even more unfortunately, high snake numbers, combined with the position of Guam as a civilian and military transportation hub, have allowed repeated human-aided dispersal of snakes to a remarkable diversity of locations (Fig. 2). Although some are relatively close (Fig. 2A), perhaps within the capacity of eventual natural dispersal for the brown treesnake, many are considerably further away (Fig. 2B), and a large number (Fig. 2C) would be considered long-distance dispersal by any standard.

BROWN TREESNAKE CONTROL EFFORTS ON AND OFF GUAM

More than anything else, it is the risk of further invasion that has prompted policymakers to fund brown treesnake interdiction efforts on Guam. These have focused on two primary goals. The first is to eliminate snakes from the transportation network. The second, discussed below, centers on understanding the biology of the snake on Guam, and on devising methods to control populations there. Guam's geographical isolation is an advantage in that snakes can leave the island only on aircraft or sea vessels. Indeed, brown treesnakes originating from

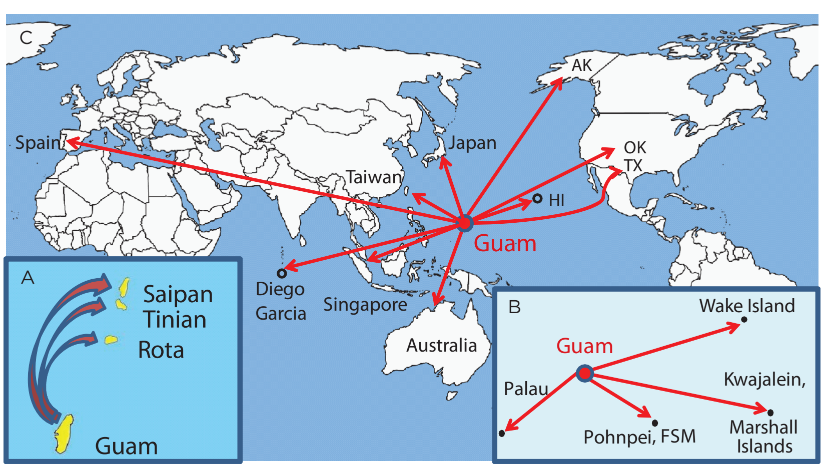

FIGURE 2 Documented brown treesnake dispersal from Guam. (A) Into the Commonwealth of the Northern Mariana Islands (CNMI; scale: tens of kilometers). (B) Within the region (hundreds of kilometers). (C) Globally (thousands of kilometers). Island locations and sizes are approximate. Some sites, such as the CNMI and Hawaii, received multiple snakes over the years, but most reported only one documented arrival.

Guam have been found on, or associated with, both. Although one might think that interdiction at two airports and two sea ports (one military and one civilian of each) would be easy, such has not been the case. Operational procedures, some local and others determined by agencies far away, limit operational access to sites and what may be done while there. Short-term and narrow economic interests also limit what can be done. Finally, much of the cargo shipped from Guam is prepared offsite, in a shifting number of privately owned facilities. Control staff have spent considerable effort identifying these facilities and gaining access to their operational areas so that snake education and inspections can be provided, with variable success.

Three primary operational tools are used on Guam. Snake traps are installed around the perimeters of ports and airports and trap hundreds of snakes annually as they approach the facility, but their success turns out to be surprisingly sensitive to details such as trap placement and the weight and material of the flap used to allow snakes in but prevent their exit. Both small and large snakes are relatively unlikely to be caught by such traps and require alternative methods to interdict. Barriers, either permanent or temporary, block snakes from entering specific areas. Although expensive in the short-term, they offer a savings over the long-run because they require relatively little maintenance. Detector dogs provide a last line of defense, inspecting both cargo that is ready to load and vessels. Research has focused on fine-tuning the efficacy of each of these methods to determine when they are most helpful and under what conditions they are ineffective.

Although brown treesnake interdiction operations on Guam have become increasingly more efficient as a result of lessons learned and research conducted, no system is perfect. Snakes are still occasionally sighted at other locations, especially those that have regular transportation links with Guam. Several locations, most notably Hawaiʻi and the Commonwealth of the Northern Mariana Islands, have established their own standing interdiction efforts, relying on one or more versions of the three tools described above. Because snake damage has not yet occurred at these locations, policy impediments tend to be greater than on Guam; budget levels fluctuate, and short-term economics are more likely to interfere with snake interdiction. In addition, a rapid-response team has been assembled, with trained members and at least some equipment available on multiple islands, which responds to new sightings and attempts to quickly capture and remove any snakes seen off of Guam.

ERADICATING THE BROWN TREESNAKE FROM GUAM

The argument has been made that brown treesnake damage on Guam is as bad as it is likely to get, and therefore interdiction should be the only concern. This view is short-sighted for two reasons. First, so long as the snake remains on Guam, expensive interdiction operations will be required and occasional escapes will occur. Since establishment of invasives is often tied with propagule pressure, the risk of eventual brown treesnake establishment elsewhere is unacceptably high. Second, with increasing success of island eradications and restoration efforts and the availability of some extirpated species in captive colonies, much can be done to improve things on Guam itself. Although Guam is larger than sites of most successful eradication efforts, the Oriental fruit fly (*Dacus dorsalis*) has been eradicated on Guam, showing that the process may be possible.

One of the most commonly asked questions about the brown treesnake is why the small Indian mongoose has not been released on Guam to control it. Unfortunately, this mongoose has caused more harm than good when introduced elsewhere, is not adept at climbing trees, and seems unlikely to be effective against an arboreal snake. Other biological control agents, such as diseases, currently also seem unlikely to be effective. However, research has identified a number of possible toxicants that are effective against the brown treesnake and suggests that aggressive application can drastically reduce, and with repeated coverage perhaps even eradicate, the snake from modest areas. Applying existing tools would be very difficult on Guam, most of which is privately owned and much of which is topographically rugged—but perhaps not impossible. However, the likely cost—perhaps several hundred million dollars—is likely to remain prohibitive for the foreseeable future.

SEE ALSO THE FOLLOWING ARTICLES

Biological Control, of Animals / Eradication / Invasion Biology / Islands / Lag Times / Reptiles and Amphibians / Restoration / Small Indian Mongoose

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BRYOPHYTES AND LICHENS

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Globally, invasions of bryophytes and lichens are strongly underrecorded; the best data exist for temperate regions with a strong tradition of floristic and taxonomic research. Compared to other taxonomic groups, numbers of alien bryophytes are rather low. In Europe, there are 45 bryophyte species that are considered to be alien in at least some parts of Europe. On this basis, only 1.8 percent of all European species are certainly alien; if cryptogenic species (i.e., species that are assumed, but not known with certainty, to be alien) are included, then the estimate rises to 2.5 percent. The cumulative number of alien bryophytes in Europe, and probably worldwide, has increased exponentially in recent decades. Countries and regions with humid climates are most heavily invaded. In comparison with other taxonomic groups, the contribution of distant regions (especially from the opposite hemisphere) to alien bryophyte floras is remarkable. The dominant pathway is unintentional introduction with ornamental plants. Alien bryophyte species display a strong affinity for human-made habitats. Within lichens, only a very few alien species have been recorded, and these are mainly restricted to human-made habitats in urban areas in the northern hemisphere.

GLOBAL PATTERNS

Invasions of bryophytes are strongly underrecorded, and the spatial distribution of data is very skewed toward temperate regions with a strong tradition of floristic and taxonomic research. Hence, for most (sub)tropical regions, even approximate numbers of alien bryopyhtes are currently impossible to estimate. However, one globally valid pattern is their low number of alien species. One explanation for the paucity of alien bryophytes is the lack of distribution data and historical knowledge, so some alien bryophytes (especially inconspicuous species) might well have been overlooked and therefore be wrongly considered to be indigenous. Spores of bryophytes are very efficient at long-distance dispersal, which means that human activities play a much less prominent role in overcoming geographic barriers than with vascular plants. In fact, many bryophytes appear to have colonized both hemispheres by natural means. Of those species considered to be native to the United Kingdom, 75 percent are also known from North and Central America, and 14 percent from Australia; 3 percent are even known from Antarctica. Although their biogeographic history remains largely unknown, many appear to be widespread and ecologically well integrated across their range, with little evidence to suggest recent arrival. Furthermore, bryophytes are only rarely transported for economic purposes; hence, intentional introduction—the prevailing pathway for vascular plants, for example—is of little importance.

The pattern of bryophyte invasions in the temperate regions of the northern hemisphere is best known for Europe due to the DAISIE project. Patterns emerging from this data set are presented below and supplemented by case studies from other continents. For alien lichens, the data situation is woefully incomplete, which limits analyses of invasion patterns. Checklists are available for only a few countries (e.g., Austria, Czech Republic, United Kingdom). However, this appears to genuinely reflect the rarity of alien lichens.

SPECIES NUMBERS AND INVASION HOTSPOTS

Globally, numbers of alien bryophytes are rather low. In Europe, there are 45 bryophyte species (excluding greenhouse species) that are considered to be alien at least in