Human–Wildlife Interactions 6(2):181–203, Fall 2012

Brown treesnakes: a potential invasive species for the United States

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Abstract: Brown treesnakes (*Boiga irregularis*) are mildly venomous, exotic snakes that have the potential to become an invasive species in North America, Hawaii, and the Commonwealth of the Northern Mariana Islands. The snake is native to northern and eastern Australia, New Guinea, and other islands of northern and western Melanesia. The snakes were first found outside their native range on Guam in 1953. The exact date they reached the island is uncertain, but they are believed to have arrived on military cargo transport vessels some time during or just after World War II. During the years that followed, the population of brown treesnakes increased considerably on Guam. The snakes have extirpated or endangered many native animal populations, attacked pets and poultry, bitten humans, and caused power outages resulting in millions of dollars in damage. This snake species has been found on ships and aircraft, which have transported it to other islands in the Indo-Pacific, as well as Hawaii and the continental United States (i.e., Texas, Oklahoma, and Alaska) in military cargo. Because the U.S. military is expanding its bases on Guam, resulting in increased shipments and military movements from Guam to the United States, there is an increasing risk for brown treesnake invasion into the United States, as well as other islands in the Pacific. Two-thirds of the literature concerning brown treesnakes is in gray area publication outlets that can be difficult to ascertain. A literature review is offered to provide a background of past research on brown treesnakes. This review of literature elaborates on the native range, morphology, behavior, biology, ecology, venom, diet, reproduction, habitat, mortality, and control of the brown treesnakes.

Key words: biology, *Boiga irregularis*, brown treesnake, control, diet, ecology, Guam, human–wildlife conflicts, invasive species, reproduction

Invasive species are a serious threat to ecosystems and are rated second after habitat loss as the greatest threat to endangered species (Wilcove et al. 1998, Simberloff et al. 2005). The history of invasive species is a long-recognized, international problem that can be linked to people's movement around the globe (Westerkov 1952, Craighead and Dasmann 1966). The Invasive Species Specialist Group (ISSG; 2001) began the Global Invasive Species Database (GISD) by providing a brief overview of the most damaging invasive species around the world, highlighting which species are the most problematic global invaders. Brown treesnakes (*Boiga irregularis*) were among them.

The Office of Technology Assessment (OTA) report (1993) identified ≥50,000 invasive species in the United States, and this number may be underestimated (Pimental et al. 2005). The rate of invasion is expanding with increased global trade and tourism (Pimental et al. 2005, Simberloff et al. 2005), and the potential for more species arriving in new ecosystems is a significant problem.

Already a devastating invader on the island of Guam, the brown treesnake is considered by the U.S. government as a potential threat to other ecosystems, particularly Hawaii (OTA 1993). It is believed that the brown treesnake arrived on Guam with returning military equipment during or just after World War II from the Admiralty Islands, north of New Guinea (Rodda 1991, Rodda et al. 1992*b*, Whittier et al. 2000). It did not achieve an island-wide distribution on Guam, whose area is 540 sq km, until the early 1980s when the species became a widespread and recognized problem (Savidge 1987*a*, Rodda et al. 1992*b*, Fritts and Rodda 1998). Savidge (1987*a*) first identified the brown treesnake as a major factor in the disappearance of Guam's avifauna. Species that cause the removal or loss of an entire taxon can have cascading effects throughout an entire community (Simberloff 1990). A review of literature pertaining to the brown treesnake regularly cites problems typical of most invasive species: it is a major threat to native wildlife; it causes economic damage; it poses a threat to human health; and it has the potential to move to new localities and the ecosystems therein, with the help of humans (Elton 1958, Cox 1999). It has also been noted that damage caused by brown treesnakes on Guam could occur elsewhere (McCoid 1993).

We conducted a literature search that yielded >300 citations about brown treesnakes. With this wealth of information, we have provided a detailed summary of brown treesnake information. We found that nearly half (47%) of the citations were in gray literature, including: 15% in government bulletins, reports, and conference proceedings; 13% in foreign-based journals (i.e., Japan, Philippines, Australia, Micronesia); 15% in books or chapters within books; 3% in theses and dissertations; and 1% in state journals. The remaining publications were located in medical-based journals and internationally distributed journals. Because much of the literature concerning brown treesnakes is difficult to acquire and because so many references exist, we conducted a literature review to assist researchers to gain an understanding of this species without having to recreate such an extensive list of references.

Geography and morphology

Brown treesnake are a native to Indonesia and northern and eastern Australia (Rodda et al. 1999*b*, Savarie et al. 2001). Analysis of mitochondrial DNA showed founding individuals for Guam's population came from the Admiralty Islands (Rodda et al. 1992*b*, Rawlings 1995, Whittier et al. 2000, Rodda and Savidge 2007). They are a member of the family Colubridae, sub-family Boiginae whose members are found throughout tropical Africa to eastern Asia (Rodda et al. 1999*b*). Brown treesnakes are one of 9 species of colubrids that occur in Australia (the primary location where specimens have been collected within the native range) and one of only 3 arboreal colubrids there (Shine 1991*a*). Members of the Boiginae sub-family often are referred to as cat-eyed snakes due to their large protruding eyes and vertical pupils, which dilate in darkness (Reinhard and Vogel 1975). These snakes are nocturnal, oviparous, and have the long, slender body shape typical of arboreal snakes. All members of the Boiginae sub-family are arboreal or semi-arboreal, with 1 exception, *Boiga trigonata* (Rodda et al. 1999*b*).

Brown treesnake coloration varies throughout the species' geographic range. Individual patterns vary greatly from indistinct markings to striking banding patterns in parts of Australia (Shine 1991*a*, Qualls and Fritts 2000). Even with this wide range of coloration in the native range, local populations on Guam tend to have uniform color morphology (Rodda et al. 1999*b*). This uniformity is likely a result of substantial changes in the morphological characteristics of the snake between the native and introduced populations (Whittier et al. 2000). Within the native range, banded forms of *Boiga irregularis* are commonly referred to as banded cat snakes or night tigers and may be recognized as subspecies *B. irregularis ornate* (Whittier et al. 2000).

All arboreal snakes, including brown treesnakes, have distinct morphological adaptations that enable them to be successful in their habitat. These include a slim body (i.e., low body mass:body length ratio), which facilitates movement on thin branches in the forest canopy and enables a snake to bridge wide gaps between branches. The body of the brown treesnake is dorso-ventrally flattened, and the long, slender tail often is used as an anchor (Pough et al. 1998, Rodda et al. 1999*b*). Brown treesnakes are large for an arboreal species (Rodda et al. 1999*b*). At the peak of population expansion, specimens from the native range reach >2 m in snout-to-vent-length (SVL); specimens on Guam historically attain similar lengths and in rare cases >3 m (Fritts 1988, Fritts and McCoid 1991, Rodda et al. 1999*b*). Whittier et al. (2000) attribute the larger sizes on Guam to ecological release, where wider habitat use and freedom from competition enable the snakes to develop unhindered. Brown treesnake have the typical narrow neck and wide head of an arboreal species, allowing them to take a wide-ranging size of prey; the throat region is highly elastic to allow passage of larger prey items (Rodda et al. 1999*a*).

Venom

The venom is produced by Duvernoy's gland, a modified salivary gland located in the temporal region. The gland has a smaller storage capacity than the venom glands of viperids (Zalisko and Kardong 1992). Brown treesnakes deliver venom to prey in a drip form that runs down the channel present in the 2 posterior maxillary teeth; venom is not injected via a hollow fang as in viperids (Hayes et al. 1993). Kardong and Lavin-Murcio (1993) described the differences between the 2 delivery systems as low-pressure (colubrids) and high-pressure (viperids). Delivery of venom by a constant drip is inefficient in comparison to injection, and in brown treesnakes, it can take several minutes to deliver approximately 50% of its stored venom to the prey (Hayes et al. 1993, Kardong and Lavin-Murcio 1993). This has led to speculation that the venom serves some other purpose than just a killing agent for capturing prey. Vest et al. (1991) reported that a LD_{50} (dose that kills half the victims) of the venom was 80mg/kg body weight for mice. However, the snake delivers approximately 174 mg/kg of venom over a period of minutes, which is considerably more than necessary to kill (Hayes et al. 1993).

Venom in brown treesnakes aids in prey capture and quiescence (Lumsden et al. 2004) and promotes digestion (Hayes et al. 1993, Hill and Mackessy 2000). Some of the properties found within the venom indicate digestive capabilities; Hayes et al. (1993) speculated that components of the venom may act upon a prey's integument to degenerate it around the puncture wounds and allow easier entry of the digestive enzymes. Weinstein et al. (1991) showed that the venom is less effective on mammalian tissue than on bird tissue. In general, larger brown treesnakes deliver larger volumes of venom than do smaller individuals (Weinstein et al. 1993).

Biology

Habitat. Brown treesnakes are associated with humid climates and occupy a variety of habitats from sea level to >1000 m, with a preference for dense arboreal foliage (Fritts 1988, Shine 1991*b*, Rodda et al. 1999*b*). Overall, habitat preference is for dense arboreal foliage, although the snake can be found using most habitat types (Fritts 1988, Shine 1991*a*, Tobin et al. 1999, Rodda et al. 1999*b*). On Guam, they use all habitat types available, including native forest, secondary growth forests comprised mostly of invasive plant species, grasslands, and urban areas (Savidge 1991, Santana-Bendix 1994, Shivik and Clark 1999*a*). Preferred daytime resting places seem to be dark, cool, narrow areas that afford protection from the sun and predators. Brown treesnakes have been observed resting in a variety of microhabitats during the day, including treetops, under rocks, and on the crowns of Pandanus plants (Santana-Bendix 1994, Rodda et al. 1999*b*, Tobin et al. 1999, Hetherington et al. 2008). Tobin et al. (1999) found juveniles more frequently above ground (>2.5 m high) and adults more frequently on the ground while resting in daytime refugia. The species will readily travel on the ground, particularly if ground cover is dense, and will also move across open areas, such as lawns and roads (Savidge 1987*b*). While brown treesnakes have prodigious climbing abilities, they have difficulty negotiating the sheer vertical surfaces of buildings (Rodda et al. 1999*a*). They will readily enter homes and other urban structures (Fritts 1988, Fritts et al. 1990, Rodda et al. 1997, Campbell et al. 1999).

Foraging and diet. Brown treesnakes use both sight and odor to detect prey items during nocturnal foraging. They may use ambush tactics with some prey (Shine 1991*a*, Rodda 1992, Rodda et al. 1999*b*). In their search for prey, brown treesnakes seemingly will attack movement, which appears to have led to attacks on infants and pets, although researchers are unsure whether or not snakes view the object of their attack as a prey item (Fritts 1988; Fritts et al. 1990, 1994). Small prey items are swallowed whole, and large prey are subdued by constriction (Rochelle and Kardong 1993, Kardong 1999).

Brown treesnakes are considered dietary generalists, eating a wide variety of vertebrate prey, including reptiles, birds, and small mammals in both the snakes' native and introduced ranges (Savidge 1988, Shine 1991*a*). They seem to be opportunistic in their diet, and proportions of prey items tend to reflect local availability (Savidge 1988, Shine 1991*a*, Shivik et al. 2000). Following the drastic drop in bird and small mammal abundance on Guam (Savidge 1987*b*), lizards have become the main prey for the snakes on the island (Rodda and Fritts 1992*b*). Savidge (1988) viewed insect consumption as incidental, perhaps already consumed by the prey item. Brown treesnakes have been observed consuming carrion and various discarded human food items (Rodda et al. 1997, Rodda et al. 1999*b*, Shivik 1999, Jojola-Elverum et al. 2001).

There do not appear to be any differences in diet between sexes, only between age and size classes (Savidge 1988, 1991; Shine 1991*a*; Caudell et al. 2002). Brown treesnakes shift their prey selection and preference as they mature (Fritts 1988; Savidge 1988; Shivik and Clark 1999*a, b*). Juveniles (i.e., SVL <1,020 mm) rely exclusively on ectothermic prey (Savidge 1991, Linnell et al. 1997, Rodda et al. 1999*b*). Adults (SVL >1,050 mm) rely on endothermic prey because smaller, ectothermic prey (insects and lizards) cannot satisfy their physiological needs. Data collected during the population expansion period in northern Guam showed that medium-sized snakes (SVL 1,020 to 1,050 mm) had the most varied diet (Savidge 1988, 1991; Rodda and Fritts 1992*b*). Brown treesnakes collected during that time had been found to consume prey >30% of their body weight (Fritts 1988, Savidge 1988), and, under laboratory conditions, they have been known to consume prey ≤50% of their body weight (Chiszar et al. 1991) and in the wild 70% of their body weight, which is substantially greater than most non-viperid species studied (Fritts et al. 1994, Rodda et al. 1997).

Reproduction. Whittier and Limpus (1996) reported that brown treesnakes from Australia become sexually mature at about 70 cm SVL. However, Shine (1991*a*) showed that the size of males at maturity within the native range may vary among populations, and Aldridge et al. (2010) reported that male brown treesnakes from the native range reach maturity at smaller sizes than do snakes on Guam. The amount of fat reserves, or coelomic fat mass, does not appear to affect reproductive activity in males (Mathies et al. 2010). Reproduction in male brown treesnakes is seasonally restricted to the warmer, wetter months in Queensland, Australia, but is continuous with seasonal spermatogenesis and a brief stage of testicular regression from January to March in New Guinea (Bull and Whittier 1996, Bull et al. 1997). Aldridge and Arackal (2005) disputed this finding (supported in Mathies et al. 2010), and deduced that evidence from male specimens supported highly continuous reproduction in New Guinea, as supported by the continuous synthesis and secretory phases of the sexual segment of the kidney (Aldridge et al. 2011). In the southern hemisphere, female brown treesnakes begin ovulation in the summer (November and December) and produce eggs during the next spring (September and October), while males appear to maintain sperm throughout the year, with peak testicular volume in April (Shine 1991*a*, Whittier and Limpus 1996, Bull et al. 1997). Reproductive cycles appear to be influenced by climatic conditions, and, thus, change with latitude. In warmer, wetter climates, males appear able to inseminate receptive females throughout the year (Bull and Whittier 1996, Whittier and Limpus 1996, Mathies et al. 2010). When in captivity, both sexes of wild, brown treesnakes from Guam have exhibited the ability to alternate between continuous and seasonal reproduction due to changes in temperature (McCoid 1994, Greene and Mason 2000, Moore et al. 2005, Mathies et al. 2010), which potentially increases the capabilities of brown treesnakes as an invasive species (Mathies et al. 2010).

Brown treesnakes are an oviparous species, but fecundity is still poorly known. Clutch size varies widely within the snake's native range. Shine (1991*a*) reported a clutch size range of between 3 and 11 eggs (average 5.5), with larger females laying larger egg masses. Incubation periods of brown treesnakes in Australia ranged from 76 to 90 days, depending on incubation temperature (Shine 1991*a*). Mathies et al. (2004), suggesting that brown treesnake females may be induced ovulators, possibly requiring coitus for ovulation. Reproductively active females have been found at all times of the year (McCoid 1994), though not in large numbers. There has been no determined clutch size for brown treesnakes on Guam, and there is speculation that females could lay ≥1 clutch per year (Fritts 1988, Whittier and Limpus 1996, Savidge et al. 2007). Very few clutches have been found in the wild on Guam. Rodda et al. (1999*b*) speculated that gravid females may be under-collected (<0.5% of snakes sampled) due to their secretive behavior before laying a clutch. The few clutches found on Guam were located in varying types of substrate, including a tree hole, a coconut frond, and a solution hole on a limestone cliff face (Rodda et al. 1999*b*). The clutch sizes found on Guam typically have been 3 to 4 eggs, with up to 8 eggs per clutch (Fritts 1988, Shine 1991*a*, Rodda et al. 1997, Rodda et al. 1999*b*). Incubation periods for the clutches on Guam have been as short as 94 days and as long as 125 to 126 days (Linnell et al. 1997).

Behaviors exhibited by nocturnal, tropical snakes may have very few thermal limitations (Anderson et al. 2005). Mathies and Miller (2003) found that brown treesnakes respond to short periods of cool temperatures by increasing reproductive activity, but potential response to seasonally cold temperatures is yet unknown.

Sperm storage, a capability shared by many species of snakes, is speculated to occur in brown treesnakes, but there is some debate as to how and by which sex sperm is stored (Whittier and Limpus 1996, Pough 1998). Bull et al. (1997) found no special structures to support this idea and argued that it is the male that stores sperm for prolonged periods. Savidge et al. (2007) concluded that although sperm storage is crucial in certain areas of the native range, it may be uncalled for by either sex on Guam.

Typical courtship behavior displayed by male brown treesnakes includes tongue flicking and head jerking as the most obvious behaviors. Males and females show slightly different responses to each other's courtship behavior (Greene and Mason 2000). Methyl ketones, which have been identified as sex pheromones in *Thamnophis sirtalis*, have been found in the skin lipids of brown treesnakes (Murata et al. 1991). Brown treesnakes rely on sex pheromones for courtship and combat behaviors (Greene and Mason 2000, Greene et al. 2001). Greene and Mason (2003) found that release of female cloacal secretions prior to copulation may actually inhibit male courtship in brown treesnakes and act as a defense mechanism for females. Greene and Mason (2005) reported that aged cloacal secretions may elicit defensive behaviors from male snakes, which could be the cause of stress and high levels of corticosterone. There has been limited success in rearing these clutches in captivity, and resultant surviving hatchlings were smaller than their wild-born counterparts (Rodda et al. 1999*b*). There are only 2 known cases to date of brown treesnakes reproducing in captivity (Mathies and Miller 2003). Aldridge and Arackal (2005) showed that captivity causes decreased reproductive activity by preventing development and shutting down reproductive processes, possibly due to stress.

Reproductive data for brown treesnakes in the wild on Guam are scant, but Moore et al. (2005) gave evidence that the population on Guam is becoming less reproductively active, as shown by low proportions of reproductively active adults; they also reported that high levels of corticosterone in wild snakes may suggest that the prey resources on the island have been overexploited. Waye and Mason (2008) found lower levels of corticosterone in brown treesnake specimens collected in 2003 and suggested that the snakes were no longer experiencing high levels of stress and that few mature females appeared to be reproductively active. However, more recent studies suggested that because coelomic fat mass does not contribute to or reduce reproductive activity in male brown treesnakes (Aldridge et al. 2010, Mathies et al. 2010), high levels of corticosterone may be due to an increase in male–male encounters and combat (Aldridge et al. 2010).

Population expansion on Guam. Before World War II, there were no recorded instances of brown treesnakes on Guam. The possible transportation of snakes to the island in military equipment probably introduced them in extremely low numbers (Savidge 1987*a*, 1987*b*, 1991). Sometime during the 1950s, reports of snakes were made (Engebring and Fritts 1988, Fritts 1988), but skepticism and disbelief of the reports were common until 1955 when specimens were captured (Rodda et al. 1992*b*). Initial populations appear to have been concentrated around the main port of Apra Harbor, with island-wide dispersal occurring from this point, first south, then north, with rapid range expansion in the 1960s and 1970s (Savidge 1987*b*, Rodda et al. 1992*b*). The snakes probably spread with the relative availability of prey items, and peak population densities were not reached in the north of the island until the early 1980s (Savidge 1987*b*), followed by a population decline in the northern end of Guam starting in 1985 (Rodda et al. 1992*b*). Reasons for the increased rate of range expansion during the 1970s are still unexplained (Rodda et al. 1992*b*), though Vice and Engeman (2000) suggested that military movements, increases in training exercises, or response to natural disasters might have led to increased shipments of goods and materials around the island.

In their invaded range, brown treesnakes have unusually high densities for any snake species (Fritts 1988). Peak densities of 50 to 100 snakes/ha occurred on Guam in the 1980s, followed by a decline to persistent densities of 30/ha (Fritts 1988, Rodda et al. 1999*b*, Rodda et al. 1999*c*). The highest densities on Guam were described as irruptions within the population (Rodda et al. 1999*c*). Densities within parts of the snakes' native range are considerably less. Despite brown treesnakes' depletion of much of their prey base on Guam, they have proven to be persistent, with the population remaining at sufficient densities to warrant a control program to prevent them from colonizing additional locations. Despite the high densities recorded on Guam, brown treesnakes are solitary and do not generally aggregate, though some small groups have been observed in the native range (Pendelton 1947, Bull and Whittier 1996).

The smallest snakes found on Guam have been ≤350 mm SVL and retain an umbilical scar, which suggests that they are recent hatchlings (Rodda et al. 1999*c*). Jordan and Rodda (1994) classed brown treesnakes as juveniles (SVL <750 mm), sub-adults (SVL ≥750 to SVL < 950) and adults (SVL ≥ 950 mm). Savidge (1991) indicated that the adult population is skewed toward an abundance of males. This difference between the numbers of males and females becomes even more apparent when the snakes increase to SVL >1,200 mm. Jordan and Rodda (1994) support this observation, as well as affirming Savidge's (1991) finding that there is a ratio of 1:1 (M:F) among sub-adults and juveniles. Rural snakes rarely grow to SVL >1,300 mm, probably due to a scarcity of endothermic prey in rural areas (Savidge 1991). Larger snakes historically have been found in southern Guam, which has more savannah-like conditions than the rest of the island, and a relatively abundant rodant population (Savidge 1987*b*, 1991). Rodda et al. (1999*c*) showed that there is limited sexual dimorphism, as captive females can grow to sizes comparable to males and much larger than females in the wild when given a regular diet. Males were larger than females on Guam (Jordan 1991, Savidge 1991) and in the native range (Shine 1991*a*, Trembath and Fearn 2008).

Limiting factors. There are relatively few studies on brown treesnakes within their native range. There are 3 arboreal colubrid species within the native range of brown treesnakes (*B. irregularis*, *Dendrelaphis calligastra*, and *Dendrelaphis punctulata*; Shine 1991*a*). Shine (1991*a*) found that the diet of brown treesnakes within Australia is much more flexible than that of the other 2 arboreal snake species. Brown treesnakes consumed birds and bird eggs, as well as more mammal species, than did *D. calligastr*a or *D. punctulata*. The diet of brown treesnakes in Australia consists of 36% bird prey items and 23% mammal prey items, whereas these items made up <1% of the diets of *Dendrelaphis* spp. in the same area (Shine 1994). As adults, brown treesnakes also tend to be larger than either of the *Dendrelaphis* spp. (Shine 1994), which may have some effect on the types of prey they can consume. One of the main factors owing to these differences in prey consumption could be that brown treesnakes are nocturnal, while the 2 *Dendrelaphis* spp. are diurnal in Austrailia (Shine 1991*a*). Brown treesnakes in their native range and on Guam seem to lack any significant nocturnal arboreal competitor (Shine 1991*a*).

Studies of the Solomon Islands and native range in Australia show, with 1 exception, little obvious depredation of the snakes (Rodda et al. 1999*b*, Caudell et al. 2002). The mangrove monitor (*Varanus inidicus*) does prey on brown treesnakes, but not enough to significantly affect populations (Rodda et al. 1999*b*).

There appears to be few limiting factors for the brown treesnake population on Guam. Brown treesnakes have been observed being killed and eaten by monitor lizards and feral pigs (*Sus scrofa*). It has been speculated that rodent and crab species (*Birgus latro*) on Guam may attempt to take brown treesnakes as prey (Fritts 1988, Santana-Bendix 1994).

Some parasites and fungi have been found to contribute to captive brown treesnake mortality. Brown treesnakes in Queensland, Australia, are highly parasitized by haemogregarine parasites (Ewers, 1968, Mackerras 1961, Telford 1999), though Caudell et al. (2002) found no evidence to suggest that these parasites were regulating the brown treesnake populations. These parasites do not occur on Guam, and there is also almost no possibility of brown treesnakes acquiring parasites from the other snakes on Guam because the only other species is fossorial (Telford 1999).

The only factor that appears to have a potential to significantly impact population densities on Guam is prey availability. With the extirpation of avifauna and a low presence of rodents in the forested regions of Guam, reptiles are the major prey items of the current population of brown treesnakes. Lizards are a typical prey item of brown treesnakes, and Guam is now home to several introduced species of anurans (Christy et al. 2007). Brown treesnakes feed frequently (Jackson and Perry 2000), and the high densities of reptiles (mean of 13,290 lizards/ha) have helped to sustain the high density of brown treesnakes, despite the absence of birds and small mammals (Savidge 1991, Campbell et al. 1996).

Impacts on Guam

The severity of impact an invasive species has on any one resource may differ with species (Office of Technology Assessment [OTA] 1993, Aquatic Invasive Species 2003, Simberloff et al. 2005). Guam has suffered from the same fate as other islands invaded by other species (Elton 1958). It is difficult to estimate the overall damage to Guam's ecosystem, as there was no ecological monitoring of the environment to provide baseline data prior to the extensive research of the brown treesnake (Fritts and Rodda 1998, Rodda et al. 1999*b*). Brown treesnakes pose the same types of threats as do other invasive species, including impacts to ecology, economy, and human health.

Ecological. Several endemic species occurred on Guam, and the entire native fauna evolved in the absence of major predators. The historic lack of predators has led to a susceptibility to depredation, especially from nocturnal, arboreal predators, such as brown treesnakes. Brown treesnakes have been implicated in the extirpation of native and introduced forest, grassland, pelagic birds, native bat species, introduced rats, and native lizards on Guam (Savidge 1987*a*, Rodda and Fritts 1992*a, b*; Rodda et al. 1999*c*; Wiles et al. 2003). Savidge (1987*a*) traced the spread of the snake throughout the island during the disappearance of the native birds. This, along with a lack of convincing evidence implicating other potential causes of the disappearances, has led to the assessment that brown treesnakes are solely responsible for the losses (Engebring and Fritts 1988, Rodda et al. 1997, Fritts and Rodda 1998, Rodda et al. 1999*b*).

Wiles et al. (2003) found that brown treesnakes have extirpated or caused the severe declines (≥90%) in the 25 native bird species on Guam. These declines occurred rapidly, within an average of <9 years, and species with larger clutch and body sizes were more persistent (Wiles et al. 2003). Wiles et al. (2003) recorded the disappearance of 9 forest species in only 2.1 years at the Pajon Basin; this is the fastest bird population decline on record. Wiles and Brooke (2009) observed that medium and large young bats are rare within native bat populations on Guam; however, the loss of *Emballonura semicaudata* on Guam should not be attributed to brown treesnakes. By 1990, the only 3 surviving native vertebrate species in forested areas of Guam were lizards (Fritts and Rodda 1998). Surviving native lizard species are small in size and have high reproductive rates, thus, strengthening their population persistence (Rodda and Fritts 1992*b*). The success of introduced species on Guam keeps habitat suitability high for brown treesnakes (Rodda et al. 1999*c*).

It is highly probable that brown treesnakes caused the final demise of many of the bird species on the island, however, several other factors should be considered, as well. When research was initiated in the early 1980s, many of the bird species were already gone, and the dietary composition of the snakes was mainly composed of lizards, making it difficult to estimate the rate of depredation (Savidge 1988). To further compound matters, much of Guam's forest consists of second-growth invasive species, (e.g., *Leucaena leucocephla*). There have been several other non-native species introduced, including feral hogs and brown skinks (*Carlia fusca*). DDT use was extensive during post-World War II, and there is continued fragmentation of the island forest habitat by human development (McCoid 1991, Rodda and Fritts 1992*b*, Fritts and Rodda 1998, Wiles et al. 2003). It is reasonable to assume that these factors played some part in disrupting the ecosystem, further enabling the snakes to extirpate the affected bird and mammalian communities, and reptile species.

While the loss of individual species is lamentable, it is the likely long-term effects that brown treesnakes have had as a kestone predator that should produce the most concern.

In conjunction with some introduced lizard species, the basic assemblage of Guam's native lizards has been altered, and the extinction of bird species has removed pollinators and seed dispersers that help perpetuate native plant species (Savidge 1987*a*, McCoid 1991, Rodda and Fritts 1992*b*, Mortensen and Dupont 2008). Additionally, brown treesnakes appear to have altered the behavior of orb web-spinning spiders (*Argiope appensa*) on Guam, where there are reduced number of webs with stabilimenta, a silk web structure that may function to defend the spiders or to attract prey (Kerr 1993). Brown treesnakes have had effects on Guam that cascade throughout the island's ecosystem (Mortensen and Dupont 2008).

Health. Brown treesnakes are a threat to human health on Guam primarily because of their propensity to bite sleeping victims, usually small children <5 years of age, and infants (Fritts et al. 1994, Fritts and McCoid 1999). There is a significant increase in bite frequency during the wet season in Guam (August to October), which is probably related to the snakes' increased levels of foraging activity (Fritts 1988, Fritts et al. 1990, 1994, Rodda et al. 1999*b*).

Only speculation exists as to why these snakes attack infants and small children, especially as they have no hope of swallowing a child. As many of the bites occur on the extremities (e.g., hands, fingers), it is possible that the snakes cannot recognize the overall size of their prey choice, and so the extremities appear to be a viable prey item (Fritts et al. 1994). Additional evidence that indicates snakes perceive children as a prey item is that those snakes found attacking were also constricting their intended target (Fritts et al. 1990). So far, there have been no fatalities associated with bites from brown treesnakes. However, bites have induced a variety of reactions in humans, including swelling, blistering, respiratory distress, and lethargy (Fritts et al. 1990, 1994). These were the most serious symptoms, and they occurred only after severe envenomation. In general, it appears that the threat of human mortality from brown treesnakes is inconsequential. However, large snakes carry the greatest potential for causing a human death, as they these snakes carry the most toxic venom (Weinstein et al. 199l, 1993).

Economic. Brown treesnakes have produced 3 important economic impacts on Guam: (1) electrical outages; (2) attacks on domesticated animals; and (3) increased budgets for their control.

Because brown treesnakes are excellent climbers, unprotected power lines are easily accessible to them. Once a brown treesnake creates a connection between 2 high-voltage lines, a short-circuit results. Over a 7-year period (1991 to 1997) there were 934 electrical outages on Guam (Fritts 2002). These outages were of varying lengths and have been estimated to cost approximately $375,000 per hour during daytime on Guam, not including the cost of necessary power line and transformer repairs, which, together, extrapolates into losses that equal millions of dollars (Fritts 1988, 2002). Pimentel et al. (2005) conservatively estimated costs for power outages associated with brown treesnakes to be $1 million per year. This cost does not include all of the possible costs attributed to each outage due to loss or disruption of business in stores and online, as well as disruption of regular community processes, such as the traffic system (Rodda and Savidge 2007). The frequency of outages varies according to the season (wet versus dry); also, wet years produce more snake activity, correlating with increased number of power outages (Fritts et al. 1987, Fritts 2002). Brown treesnakes on Guam are responsible for approximately 1 outage every other day, typically affecting only 1 small area at a time (Rodda and Savidge 2007), but the costs add up quickly.

Fritts and McCoid (1991) found that 80% of respondents who raised chickens suffered from some form of depredation (dogs, monitor lizards, brown treesnakes), with 45% of their losses attributed to brown treesnakes. The overall economic impacts from these losses have generally meant that most of their poultry products have had to be imported, thus, raising the overall cost of the product to the residents of Guam (Fritts et al. 1987). Losses of pet puppies, kittens, and birds due to brown treesnakes have not been monetarily estimated.

Management for brown treesnakes across all participating agencies for 2004 cost approximately $10 million, with funding barely meeting costs (Brown Treesnake Working Group 2004). This estimate does not include any potential increase in shipping costs for

Guam, or cost of decreases in tourism of up to $1.5 billion annually that may have resulted from the snakes (Rodda and Savidge 2007).

Purpose of management

Because brown treesnakes are successful invaders and are capable of colonizing a variety of habitat types, it is critical that they be controlled in some manner (Fritts 1988, Aquatic Nuisance Species Task Force 1996*b).* Should brown treesnakes succeed in establishing in other areas, they will likely have some effect on susceptible species in the region where they colonize; whether there will be the same level of devastation are found on Guam remains to be determined. Early studies on brown treesnakes focused on understanding their ecology but have now expanded to include control efforts and public awareness campaigns on the threat of the snakes (Fritts 1988, Aquatic Nuisance Species Task Force 1996*a*, Rodda et al. 1998, Campbell et al. 1999, Burnett et al. 2008). The main goals of brown treesnake management are to keep the snakes from adversely affecting native wildlife restoration programs on Guam and to prevent their spread to other areas (Rodda et al. 1998). Rodda et al. (1998) cite 4 objectives, in declining order of importance for controlling the brown treesnake problem on Guam: (1) eradicate brown treesnakes; (2) greatly reduce snake populations permanently; (3) control snake populations over areas large enough for endangered species restoration; and (4) control snakes in small areas (i.e., cargo areas, transportation craft, etc.) to prevent further spread.

An organized management plan for the control of brown treesnakes is a relatively recent development of the 1990s (Rodda et al. 1998, Campbell et al. 1999). Research into a variety of control techniques has been occurring for a slightly longer period, but there was no widespread, unified effort against the snake. With the inclusion of brown treesnakes in the 1990 Nonindigenous Aquatic Nuisance Prevention Act, the development of a cooperative program has progressed to the point where the control program is a multi-agency effort involving federal, state, and local wildlife agencies across islands in the Pacific.

On Guam, the high densities of brown treesnakes, their willingness to utilize various habitat types, and their nocturnal movements in search of prey often lead them into cargo and aircraft areas (Fritts 1988, Aquatic Nuisance Species Task Force 1996*b*). Cargo and aircraft already have been sources of off-island transportation for brown treesnakes and are still considered the main vectors of dispersal, primarily because these modes of transport can provide suitable daytime refugia for snakes (Engeman and Linnell 1998, Rodda et a1. 1998, Fritts et al. 1999, Engeman and Vice 2002, Perry 2002). In rural areas, the snakes' ability to mimic vines and their lack of reflective eye shine make them difficult to locate or observe during nocturnal searches (Rodda et al. 1998). With their cryptic nature and ability to adapt to different environments, developing a single effective management technique is a daunting proposition.

Management techniques

The various management techniques currently being used by the agencies can be categorized into 4 major types of control: biological, ecological, chemical, and mechanical. Each of these methods has been attempted in some way to control the current population of brown treesnakes on Guam, but each is still under constant research to determine more effective methods of control. All techniques being developed in the control of brown treesnakes currently are being applied with varying degrees of success, each depending on goals and size of the area being treated (Aquatic Nuisance Species Task Force 1996*b*, Engeman and Linnell 1998). There are many large-scale control efforts around the world for various invasive species, but there is only 1 other large-scale snake control program currently in use. This program is in Japan to control for the highly venomous habu (*Trimeresurus flavoviridis*; Office of Technology Assessment 1993, Rodda et al. 1999*b*). However, the techniques applied to the management of the habu cannot readily be transferred to brown treesnakes, as the 2 snakes have very different ecologies (Campbell et al. 1999). The control efforts surrounding the Burmese pythons in south Florida are not as large scale as those for brown treesnakes and the habu (Willson et al. 2011). There are several factors that make the control of brown treesnakes difficult. Their ability to climb means that they can scale most barriers with ease. Their secretiveness makes them difficult to track and capture, and their high mobility makes them difficult to eliminate on a large scale. Each of the following techniques has the ability to control numbers with small-scale application, chemical control having the greatest promise on a larger scale of application.

Biological

Biological control can be defined as the management of a pest through the intentional use of living organisms (Lazarovits et al. 2007). To date, 2 techniques have been implemented or considered for biological control of brown treesnakes: pathogens (i.e., parasites and disease) and the introduction of a predator (Hoddle 1999, Nichols et al. 1999, Engeman and Vice 2002). Most biological controls that are successfully used for invasive species are generally used for insect control, and the overall efficacy is dependent on the characteristics of the pathogen (Dobson 1988). For brown treesnakes, research continues to look at the potential of introducing a biocontrol agent, but the potential of unintended consequences (i.e., infection of nontarget species) must be considered (Dobson 1988, Rodda et al. 1998, Engeman and Vice 2002).

Although limited knowledge and research on specific parasites associated with brown treesnakes is available, we do know that they carry blood parasites (Hoddle 1999, Telford 1999, Caudell et al. 2002). Additionally, Nichols et al. (1999) found that captive brown treesnakes were fatally susceptible to a dermal fungus, although, its use as a form of control is unknown. The difficulties associated with the use of parasites and disease stem from the overall lack of knowledge about brown treesnake epidemiology and the fact that there has been limited success in controlling vertebrates with introduced pathogens (Caughly and Sinclair 1994, Rodda et al. 1998). Successful biological control has been exhibited in agriculture (van Lenteren 2007, Wiedenmann et al. 2007), but only 3 successful forms of vertebrate pest control have been recorded: myxoma virus, rabbit hemorrhagic disease for rabbit control (Fenner and Ratcliffe 1965, Cook and Fenner 2002), and feline panleucopaenia virus for control of a small population of feral cats (van Rensburg et al. 1987, Saunders et al. 2010). The potential for successfully introducing a dominant predator is unlikely because most known predators are not generally considered effective at reducing brown treesnake populations, and the introduction of another potential predator (e.g., mongoose [*Herpestes* spp.]) could have undesired effects on nontarget species or on general ecosystem function (Fritts 1988, Rodda et al. 1998, Engeman and Vice 2002). Saunders et al. (2010) propose that biocontrol for vertebrate pests is never the final solution to the problem, and long-term mitigation will remain an essential component of management.

Ecological

Ecological control can be either a large- or small-scale endeavor, usually involving the alteration of habitat. However, ecological control is potentially limited to restricted areas, because brown treesnakes show little habitat preference and are found throughout Guam (Rodda et al. 1992*b*). Such methods would include clearing vegetation either mechanically or with herbicides (Fritts and Rodda 1999). This has the advantage of reducing the amount of habitat that snakes can utilize for cover. Additionally, the openness of the ground will increase wariness and perhaps discourage snake movement (Rodda 1991). Limited areas of control would include the immediate vicinities around cargo facilities and airports (Fritts 1988, Rodda et al. 1998). Ecological control techniques can be applied to urban areas, as these have surfaces and a vegetation structures that prove inhospitable to brown treesnakes (Rodda 1991). The use and placement of bright lights in snake capture has been considered, as brown treesnakes are nocturnal and may well avoid brightly lit areas, thus, detering their movements away from such areas (Campbell et al. 1999). Campbell et al. (2008) found in a laboratory-based study that moonlight affects microhabitat use by brown treesnakes, which use open ground more as light decreases and use the canopy for cover as the light increases.

Manipulation of the prey base of brown treesnakes has been suggested, although, difficulties arise when considering secondary impacts. However, the general belief is that the removal of a prey item from an area will make that area less attractive to brown treesnakes (Engeman and Vice 2002). Additionally, there are the problems of cost effectiveness and the unknown short- and long-term results of such a method (Campbell et al. 1999, Fritts and Rodda 1999). As with other control methods, ecological control requires serious consideration as to the potential to adversely affect nontarget species.

Chemical

Snakes, including brown treesnakes, generally use odor cues to track their prey (Rodda et al. 1999*b*, Shivik et al. 2000). With this knowledge, researchers have worked to develop attractants (for traps), repellents, and lethal toxicants. Research on attractants has focused on finding the best odors that attract snakes into traps. In general, snakes have shown preference for whole blood and carcasses of preferred prey (birds and rodents) over synthetic odors (Shivik and Clark 1997, Shivik 1998, Shivik et al. 2000, Chiszar et a1. 2001, Stark et al. 2002). However, despite some success in the laboratory, more research is necessary for application in the field (Chiszar et al. 1997, Shivik and Clark 1999*a*, Shivik et al. 2000).

Shivik et al. (2002) examined the aerial delivery of toxicants by implanting acetaminophen into dead mice and dropping them into the canopy. Radiotransmitters were implanted in the bait for data collection on movement, and the authors reported that snakes moved from 1 to 70 m within 5 to 11 days after bait consumption, and snakes that consumed baits were comparable in size and body condition to other snakes captured in the field. This technique is believed to be the best technique for depopulating brown treesnakes on Guam (Shivik et al. 2002). Savarie et al. (2001) conducted a promising study in the use of acetaminophen as a toxicant, which has the advantage of being effective, inexpensive and easily accessible. Savarie and Tope (2004) found that the best method for aerial delivery is to drop bait in paper food cups. In comparison to 4 other types of flotation materials, paper food cups were easiest for researchers to put together and deploy into the canopy.

In the search for repellents, research findings differ in regard to the reactions of brown treesnakes to carrion. Some experiments with a synthetic pheromone from monkeys and components of carrion odors elicited avoidance behavior in snakes used for the experiments, but extensive field research is required to overcome delivery and human health issues (Chiszar et al. 1997, Clark 1997, Engeman and Vice 2002). In contrast, Torr and Richards (1996) reported that brown treesnakes eat carrion. Shivik and Clark (1997) found that carrion cues attract brown treesnakes to traps. One issue associated with both attractants and repellents (primarily to reduce costs and labor) is longevity (Engeman and Vice 2002). Clark and Shivik (2002) examined the effects of natural compounds and aerosolized oils as chemical irritants for brown treesnakes as remedial snake repellents and found several that could be used instead of harmful organochlorines. Repellents used for brown treesnake control would potentially be successful in small, restricted areas, but would not be effective in completely eradicating the snake from a more widespread location, such as Guam.

There are numerous literature sources from the 1950s, 1960s, and 1970s detailing that organochlorine chemicals (e.g., DDT) are viable repellents for snakes (Savarie and Bruggers 1999). Such chemicals acted as repellents, in addition to being lethal to the target species, and they can be applied orally (i.e., bait) or dermally (i.e., spraying). However, the difficulty associated with these methods is finding the appropriate delivery system (Rodda et al. 1998, Engeman and Vice 2002, Shivik et al. 2002). The search for toxic chemicals for eliminating brown treesnakes has found several potential lethal toxicants, including rotenone, propoxur, and pyrethrins (Johnston et al. 2001, Brooks et al. 1998, Savarie and Bruggers 1999). Different levels of lethality occur when these chemicals are applied via dermal or oral doses, independent of application type (Brooks et al. 1998, Savarie et al. 2000, Johnston et al. 2002, Shivik et al. 2002). Maudlin et al. (2000) found a simple analytical method using high-performance liquid chromatography to identify the residual capacity of rotenone, and possibly other toxicants, in brown treesnakes.

Several factors must be considered before there can be widespread use of toxicants. Any application must consider the potential impact on nontarget species and the environment (Rodda et al. 1998, Savarie and Bruggers 1999, Savarie et al. 2001, Johnston et al. 2002). Commercially available toxicants, such as Dr. T's Snake-A-Way, that have been advertised on Guam as a product for control of brown treesnakes, but are ineffective (McCoid et al. 1993). There have been no studies to examine the residual effects of this type of commercially available toxicant on nontarget species.

With the many economic and ecological disadvantages to using chemicals for species eradication, it is important to consider other options. Thermal fumigation also has been examined as a potential alternative to chemical fumigation of cargo containers leaving Guam. Perry and Vice (2007) found that passive thermal fumigation used along with snake barriers may be an economically advantageous tool for areas in the Commonwealth of the Northern Mariana Islands receiving shipments from Guam. Passive thermal fumigation uses sunlight and ambient temperatures to warm cargo boxes beyond the point of snake survival. Inconsistencies of daylight and heat patterns, as well as differences in cargo, make this technique unpredictable (Perry and Vice 2007).

Mechanical and physical

This kind of control involves traps or some form of barrier. Traps (with lures) have been used effectively since the beginning of brown treesnake research, and trap designs continue to be evaluated for improvement (Savidge 1987*b*, Fritts et al. 1989, Rodda et al. 1992*a*, Linnell et al. 1998, Engeman and Vice 2002). Engeman and Vice (2002) cite trapping as central to brown treesnake control activities on Guam. Funnel traps have 1-way doors, with a secondary chamber located inside the trap that contains a 1ive mouse as a lure (Fritts 1988, Linnell et al. 1998, Engeman and Vice 2002). Early traps may have allowed 80% of snakes to escape under certain conditions, but newer designs are more effective at retaining captured snakes (Rodda et al. 1992*a*, Linnell et al. 1998, Rodda et al. 1999*a,* Engeman and Vice 2002) and immigration of snakes or inadequate trapping effort are likely the cause of persistence of snakes in long-term trapping areas (Rodda et al. 2007*a*). Traps can be valuable tools because they can be placed in areas that cannot adequately be patrolled by either people or dogs (Fritts 1988, Rodda et al. 1992*a*, Vice 1999, Engeman and Vice 2002). Because brown treesnakes respond to polymodal stimuli, experiments have focused on how to make traps more attractive and reduce the dependence on live mouse lures, a logistically intensive operation (Rodda et al. 1998, Vice 1999, Lindberg et al. 2000). Mechanical mouse lures have been experimented with, but a life-like representation is still under long-term development (Lindberg et al. 2000).

The most effective form of trap placement has been on a perimeter around forest edges; this placement covers a greater area and reduces the amount of trap maintenance time (Engeman and Linnell 1998, Engeman and Vice 2002). Problems do arise, however, when considering how large an area to cover with traps. Traps are very effective in small discreet areas. Increasing the distance between traps both reduces the chance of a snake encountering a trap and increases labor time. Capture-rates are highly dependent on the local density of snakes, as well as the abundance of the prey base (Rodda et al. 1992*a*, Engeman and Linnell 1998, Rodda et al. 1999*a,* Engeman and Vice 2002). Engeman et al. (2003) analyzed models of capture rates for management purposes of brown treesnakes to predict capture rates over time, based on the number of snakes captured per trap-night. Gragg et al. (2007) found that capture rates of brown treesnakes were higher in areas with lower rodent abundance, such as Guam. Brown treesnakes on Guam enter traps more readily in search of prey than do brown treesnakes in locations with higher mammalian prey abundance. This implies that the lowered rodent abundance may actually enhance brown treesnake control (Gragg et al. 2007). Rodda et al. (2007*a*) and Tyrell et al. (2009) found traps to be more successful in capturing larger snakes SVL > 900 mm than smaller snakes SVL <700 mm, and the authors suggest that trapping can be used to capture sexually mature adults if used as a continuous management tool.

Because brown treesnakes are adept climbers, it has been difficult to develop an effective barrier for this species, but there are some in use. Rodda et al. (1998) found barriers to be the best tools for mid-scale control of brown treesnakes on Guam. Barriers are typically placed in and around urban areas, government facilities, and areas that are being used to reintroduce native wildlife (Rodda 1991; Aguon et al. 1999, 2002). Problems with barriers are the costs (dependent on materials used), the amount of area they can cover, and potential damage from typhoons

(Rodda et al. 1998, Campbell 1999, Engeman and Vice 2002). The success of a barrier is dependent on the material used and the size of any particular snake (Campbell 1999, Engeman and Vice 2002, Rodda et al. 2007*b*). Rodda (1991) tested the validity of chain-link fences as a collection point for the snakes (Figure 1). The fence helped to facilitate their capture due to brown treesnakes' willingness to climb the barrier and the ease with which they could be spotted and collected. Perry et al. (1998*a*) found permanent barriers to be more cost-effective than temporary barriers and metal mesh barriers and vinyl seawall barriers to be highly effective as permanent barriers against brown treesnakes.

Figure 1. Chain-link fences can be used as collection points for brown treesnakes.

Detection

Humans and dogs are used in inspection processes, but mainly they are the last line of defense and are useful in limited areas only (Orcutt 1997, Engeman and Vice 2002). A rapid-response team developed in 2002 performs searches to detect and capture snakes following credible sightings (Stanford and Rodda 2007). Human searchers are used in cargo areas, airports, along fence lines, and transects in forest areas to locate brown treesnakes (Rodda and Fritts 1992*a*, Rodda et al. 1992*a*). Spotlighting perimeter fences at night to find snakes for hand-capture has become a generally efficient technique, as well (Vice and Pitzler 2000).

While hand-capture is effective, there are problems involving time constraints, fatigue, observation capabilities, and also problems of overcoming a natural fear of snakes (Rodda and Fritts 1992*a*, Rodda et al. 1998, Campbell et al. 1999). Dogs (primarily Jack Russell terriers) are trained to detect snakes by odor and are used by the U.S. Department of Agriculture (USDA) to inspect outbound cargo and aircraft wheel wells. Detection of snakes by dogs may differ by the form of dog training, such as whether dogs are trained using pre-handled snakes, which may affect the odor of the snake that the dog is trained to detect and may differ from snakes in the wild (Imamura 1999). This presents the difficulty with having trained brown treesnake detector dogs in currently uninhabited locations for detection and rapid response. In order for the dogs to continue maintenance training with the brown treesnake odor, a population would have to be maintained under security for these training purposes, and this is unacceptable on all snake-free islands (Imamura 1999). Costs, time, physical limitations, and protocol associated with dog-team training and searches can lead to policy and management issues (Imamura 1999, Engeman and Vice 2002). Canine detection for brown treesnakes does work on Guam, although a 100% inspection goal for cargo is not realistic due to personnel and scheduling limitations and overall volume of inspections (Imamura 1999).

Education and awareness

Getting the public involved in brown treesnake control and prevention could be one of the most effective forms of management. Biocontrol studies have had success when involving public education systems in pest management through teacher training, student research, and outdoor application (Wiedenmann et al. 2007). Public and military support and education at transport locations is critical for brown treesnake prevention and may increase detection (Engeman and Vice 2002). Educational materials, such as flyers, posters, rapid response cards, and general information for the public are available from different sources (U.S. Department of Agriculture 1997, North American Brown Treesnake Control Team [NABTSCT] 2008, U.S. Geological Survey [USGS] 2007). Furthering public education and awareness could also benefit brown treesnake control through increases in funding support from individuals and groups.

The catastrophic results from a long list of invasive species and the well-documented results from the study of the brown treesnake colonization prompted the development of the Brown Treesnake Working Group (BTSWG) and the NABTSCT. The latter is a multi-agency effort to develop a model for prevention of brown treesnake invasion into continental North America through education and awareness, as well as rapid response assessments of potential sightings (Henke 2002). The stakeholders involved include government officials from the U. S. Fish and Wildlife Service, U.S. Geological Survey, USDA/APHIS/Wildlife Services, and various groups from the public, including, but not limited to, herpetological groups, the Audubon Society, and the pet industry. These groups develop a public awareness plan to alert people to the dangers associated with the brown treesnake, something that is missing for a great many invasive species. By developing a preemptive plan and refining control methods on Guam, the NABTSCT hopes to prevent another invasive species from entering the continental United States (Acquatic Nuisance Species Task Force 1996*a*).

Future plans

Complete eradication of brown treesnakes from Guam is probably unrealistic (Rodda et al. 1998). Thus, preventing further spread, which is still feasible, should be considered successful management. Therefore, increased research opportunities to refine and implement prevention techniques are necessary. Continued research is needed, not only on Guam, but also in regions considered under threat. Because the invasion success of brown treesnakes are dependent on ecological preadaptation (Shine 1991*a*), it may be possible to further refine definitions of areas that are most at risk. This can be accomplished by focusing research on pathway analysis, potential species competition, and resource-use in areas receiving shipments from Guam, thus, focusing management, rapid response, and education programs in those areas to increase detection probabilities and jumpstart management to prevent brown treesnake introduction. Further research is needed on introduction and transport pathways and cost-effective control of those pathways, including ways to enhance technique, speed, scheduling and management of inspections in order to increase productivity. Future efforts should also include the latest research for management, control, and eradication. Several studies have been published that have yet to be widely implemented, such as the use of acetaminophen-baited mice over large areas (Savarie et al. 2001, Shivik et al. 2002, Savarie and Tope 2004), to kill brown treesnakes.

There is, of course, no certainty that brown treesnakes will be as devastating on a continental scale as it has been on the island of Guam. However, on a local scale, new invasions could be as devastating. Certainly, brown treesnakes pose a threat to Hawaii and Florida, 2 geographic areas that are very hospitable to many other invasive species (Office of Technology Assessment 1993, Kraus and Cravalbo 2001). By 2008 there had been 14 credible brown treesnake sightings in Hawaii and 3 confirmed sightings in the mainland United States (Perry and Vice 2008), including one in Texas in May 1993 (McCoid et al. 1994), one in Anchorage, Alaska (Stanford and Rodda 2007), and one in McAlester, Oklahoma, in 2005 (S. H. Henke, NABTSCT, unpublished report). The most recent credible sighting on the mainland was in August, 2011, near San Antonio, Texas, but the snake was not captured (S. H. Henke, North America Brown Treesnake Control Team, personal communication). The increase in dispersal events has raised the interest of military authorities on Guam (McCoid et al. 1994). Management for brown treesnakes in Hawaii and on other at-risk islands in the Commonwealth of the Northern Mariana Islands is difficult due to several uncertainties, including knowledge of the number of snakes currently located there and the minimum viable population size for brown treesnakes (Burnett 2007). Without proper management, islands in the Pacific are at high risk for receiving brown treesnakes due to military restructuring and increased military movements in the region as Guam increases in strategic importance (Pitt et al. 2010).

Pathway risk assessments and ecological modeling are the cutting edge in invasive species prevention (Hulme 2009). Pathway analysis allows researchers to define the most likely transport pathways to the most at-risk locations, providing a focus for management of those pathways on Guam and giving priority to inspections of those pathways, thus, making inspections more cost-effective. Climatically suitable areas for brown treesnakes within the U.S. mainland are located in California, the Southwest, and the Southern Coastal Plain where temperature and precipitation most closely match those of the tropics (Rodda et al. 2007*c*, Wisniewski 2010). San Diego, California, receives more shipments from Guam than any other location in the continental United States, and is, therefore, at relatively high risk for the potential transfer of brown treesnakes, especially with the expected increase in shipments due to military restructuring on Guam (Wisniewski 2010).

Spread of brown treesnakes from Australia and New Guinea is much less likely due to lower densities there (Rodda and Savidge 2007). Rödder and Lötters (2010) projected climatic suitability for brown treesnakes in the Pacific and found that the highest suitability is located in the Commonwealth of the Northern Mariana Islands, Hawaiian Islands, Madagascar, New Caledonia, and the Fiji Islands. The island of Oahu holds approximately 150,000 ha of brown treesnake habitat (Burnett et al. 2008). Burnett et al. (2008) found that it is economically advantageous to actively search for a potential population of snakes in Hawaii, rather than to wait for discovery. Alien species invasions are one of the most serious problems hindering conservation programs, and, due to their likely irreversibility, have the potential to undo other conservation programs (Howarth 1999).

Acknowledgments

We thank G. Perry (Texas Tech University), L. Brennan (Caesar Kleberg Wildlife Research Institute), and M. Tewes (Caesar Kleberg Wildlife Research Institute) for their professional review and helpful comments on this manuscript prior to submission. We thank the U.S. Fish and Wildlife Service for funding. This is manuscript number 11-111 of the Caesar Kleberg Wildlife Research Institute.

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