

The Risk to Hawai'i from Snakes¹

Fred Kraus² and Domingo Cravalho³

Abstract: We assessed the risk to Hawai'i's native species and human quality of life posed by the introduction of alien snake species. An examination of Hawai'i Department of Agriculture records from 1990 to 2000 indicated hundreds of credible snake sightings in the state, mostly of free-roaming animals that were not recovered. These snakes arrived primarily through smuggling of pet animals, but some snakes are accidentally introduced as cargo stowaways. Most recovered specimens are of species potentially capable of inflicting substantial harm to native birds and the poultry industry if they become established. Some may affect native freshwater fish. An analysis of the frequency with which snakes are smuggled into the state, the suitability of the local environment to snake welfare, and the ecological threats posed by recovered snake species leads us to conclude that snakes pose a continuing high risk to Hawai'i. Mitigation of this threat can only be achieved by altering the human behavior leading to their widespread introduction. There are a variety of reasons why this behavior has not been successfully curtailed heretofore, and we propose a series of measures that should reduce the rate of snake introduction into Hawai'i. Failure to achieve this reduction will make successful establishment of ecologically dangerous snakes in Hawai'i a virtual certainty.

CONSIDERABLE EFFORTS HAVE been expended by the federal and State of Hawai'i governments over the past several years to exclude brown tree snakes, *Boiga irregularis* (Merrem), from Hawai'i because of the recognized threat that they pose to the state's remaining native birds, its tourist and electrical industries, and quality of life. Federal activity is largely based on Guam, where efforts are directed to keeping snakes out of the transportation network via trapping, searching of outbound cargo with snake-detecting dogs, erection of barrier fences, and reduction of prey bases—all focused around port areas. Prevention efforts by the State of Hawai'i consist of searching most inbound flights from Guam with canine units to verify

that the flights are snake-free and responding to likely *B. irregularis* sightings with search and trapping efforts utilizing agency staff and volunteers. Since establishment of a comprehensive federal interdiction program on Guam in January 1995, only one verified *B. irregularis* has turned up in Hawai'i (dead), whereas seven (at least three alive) had been detected in the period 1981–1994 (Fritts et al. 1999). It appears that this interdiction program has been effective in reducing the frequency with which *B. irregularis* reaches Hawai'i.

Unfortunately, *B. irregularis* is widely viewed in Hawai'i as the only snake threat to the state's native species and economy, and reduction of the likelihood of receiving *B. irregularis* from Guam has frequently been interpreted as synonymous with success in reducing the threat of snakes to Hawai'i. This conclusion, however, is excessively optimistic. As discussed by Rodda et al. (1997) and Loope et al. (2001), the ecological attributes that have made *B. irregularis* an ecological disaster in Guam are shared with hundreds of other snake species worldwide, which could prove equally devastating to naive faunas endemic to other oceanic islands in Polynesia or

¹ Manuscript accepted 23 February 2001.

² Department of Land and Natural Resources, Division of Forestry and Wildlife, 1151 Punchbowl Street, Room 325, Honolulu, Hawai'i 96813.

³ Department of Agriculture, Plant Quarantine Branch, 701 Ilalo Street, Honolulu, Hawai'i 96813.

Micronesia, should they be introduced. Recognition of this fact has led the State of Hawai'i to prohibit importation and possession of all snake species within the state; however, we argue that enforcement of this prohibition has not been commensurate with the real threats posed by snakes to Hawai'i. Herein we assess the ecological risk posed to Hawai'i by snakes.

MATERIALS AND METHODS

We assessed Hawai'i Department of Agriculture (HDOA) interception/capture records of snakes to identify the frequency with which snakes appeared in the state for the 10-yr period from June 1990 to June 2000. We were concerned only with credible sightings and, hence, excluded obvious hoaxes, misidentified items such as radiator hoses or eels, and sightings of the widely established blind snake, *Ramphotyphlops braminus* (Daudin), present in Hawai'i since 1930 (Oliver and Shaw 1953). Data recorded by HDOA, when available, included species identification, date of report/capture, location of sighting, and whether retrieved snakes were dead, captured roaming freely, surrendered voluntarily by snake owners under HDOA's amnesty program, or confiscated as part of an HDOA investigation. For analysis, the surrendered and confiscated snakes were lumped together by us as "captive." Ecological information on particular snake species was taken from the literature.

Risk is defined to be a conditional probability for experiencing a hazard or harm (Rowe 1977, Hohenemser et al. 1982, Cutter 1993). In the context of alien-species invasions, risk is the product function of the probability of a species being introduced to an area, the probability of its becoming established once introduced, and the ecological hazard the species poses. Consequently, simply noting ecological similarities between *B. irregularis* and other snakes (Rodda et al. 1997, Loope et al. 2001) is necessary but insufficient to establish risk. Although the risk of snakes to Hawai'i cannot be meaningfully

quantified at this time, it can be qualitatively categorized.

RESULTS

For the 10-yr period under study, 236 credible sightings of snakes were reported in Hawai'i. Variation in numbers of sightings among years was considerable, with 1992 having 57 and 1994 only seven (Figure 1). Of the total 236 reports, 22 snakes were found dead, 41 were captured roaming free, and 74 were captive animals surrendered voluntarily under HDOA's amnesty program or confiscated by its personnel. This leaves 99 presumptive snakes roaming free but uncaptured. It is apparent that the ability to retrieve snakes in Hawai'i, relative to the numbers reported, is not great (Figure 1), especially for snakes reported to be free roaming ($41/140 = 29\%$). However, considering the cryptic habits of most snakes and the heavy cover at many sighting locations, it is perhaps more surprising that so many free-roaming snakes were captured.

Snakes arrive in Hawai'i via one of two pathways: intentionally smuggled in to serve as pets or unintentionally hitchhiking in shipped cargo. It is immediately obvious from the large number of snakes voluntarily surrendered to or confiscated by HDOA that intentional smuggling of pets is of tremendous importance as a mechanism for introducing snakes to Hawai'i. This is confirmed by consideration of the identities of retrieved snakes (Figure 2). The genera *Boa*, *Python*, *Elaphe*, and *Lampropeltis* apparently arrived in Hawai'i in the 1990s strictly as pet animals: each species is frequently kept and widely available as pets in the United States, all Hawaiian animals that could be unambiguously associated with a pathway were associated with pet keeping, and none was associated with cargo during our study period (although one *Boa* and one *Python* were associated with cargo transport to Hawai'i in the 1970s [Fritts 1987]). Species of *Thamnophis*, *Pituophis*, and *Coluber* are also frequently kept as pets in the United States, although some specimens have arrived in Hawai'i as stow-

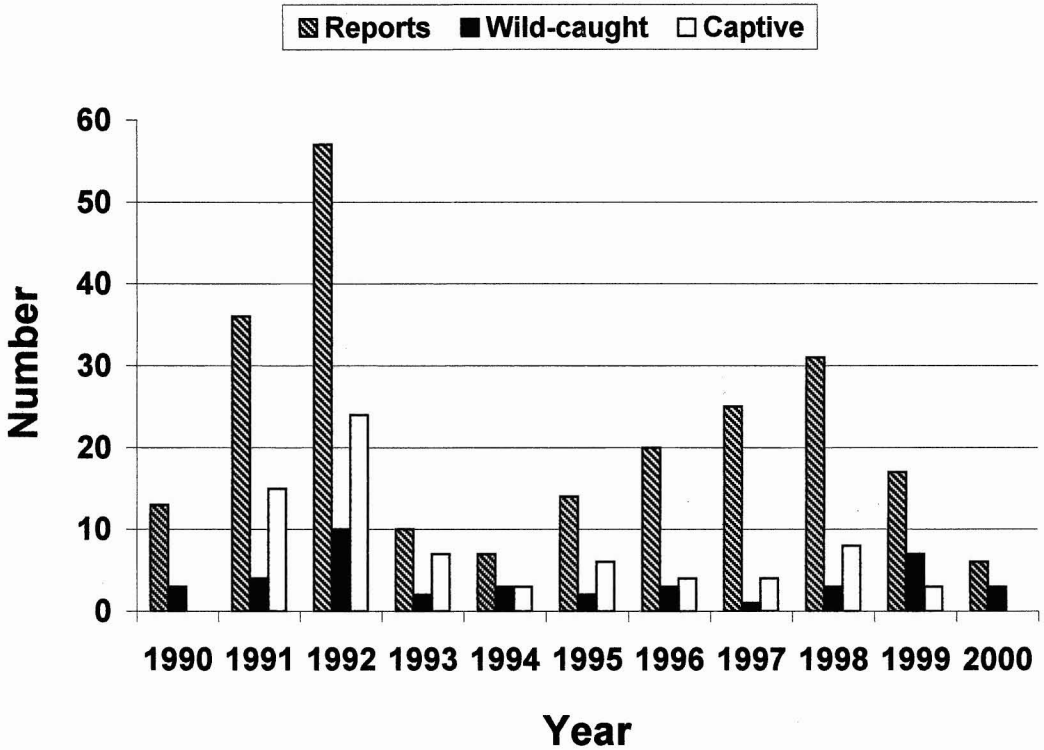


FIGURE 1. Numbers of credible snake reports received, free-roaming snakes captured, and captive animals confiscated by or surrendered to Hawai'i Department of Agriculture from June 1990 to June 2000.

aways in cargo, frequently in hay bales or Christmas trees. Of the 137 retrieved snakes during this period, however, only 22 arrived as unintentional hitchhikers, including the four *B. irregularis*.

The ecological hazard posed by the commonly encountered snakes in Hawai'i may be assessed by comparison with the ecological characteristics of the well-studied and destructive invasive *B. irregularis* (Table 1). This species has proven invasive in Guam because of its catholic diet, arboreality, nocturnality, and the abundance of alien prey species to maintain its high population densities (Campbell 1996, McCoid 1999, Rodda et al. 1999b). The species of *Boa*, *Python*, *Elaphe* (corn and rat snakes), *Pituophis* (bull and gopher snakes), and *Lampropeltis* (king snakes) share several relevant ecological attributes with *B. irregularis*, including nocturn-

ality, consumption of endothermic prey, and, for some, arboreality (Table 1). The clearest distinction between *B. irregularis* and the species commonly encountered in Hawai'i is that the latter are even more fecund, often to a considerable degree (Table 1). A further distinction is that *B. irregularis* is capable of attaining elevations of 1400 m in its native range (O'shea 1996), indicating that it is probably more tolerant of cooler temperatures than *Boa* and *Python* would be. This limitation, however, would be unlikely to apply to the temperate North American *Coluber*, *Elaphe*, *Lampropeltis*, and *Pituophis*. *Thamnophis* may pose less of a threat to native wildlife because the species commonly encountered in Hawai'i feed primarily on anurans and earthworms, both of which are alien introductions to Hawai'i. However, some *Thamnophis* species likely to be imported to

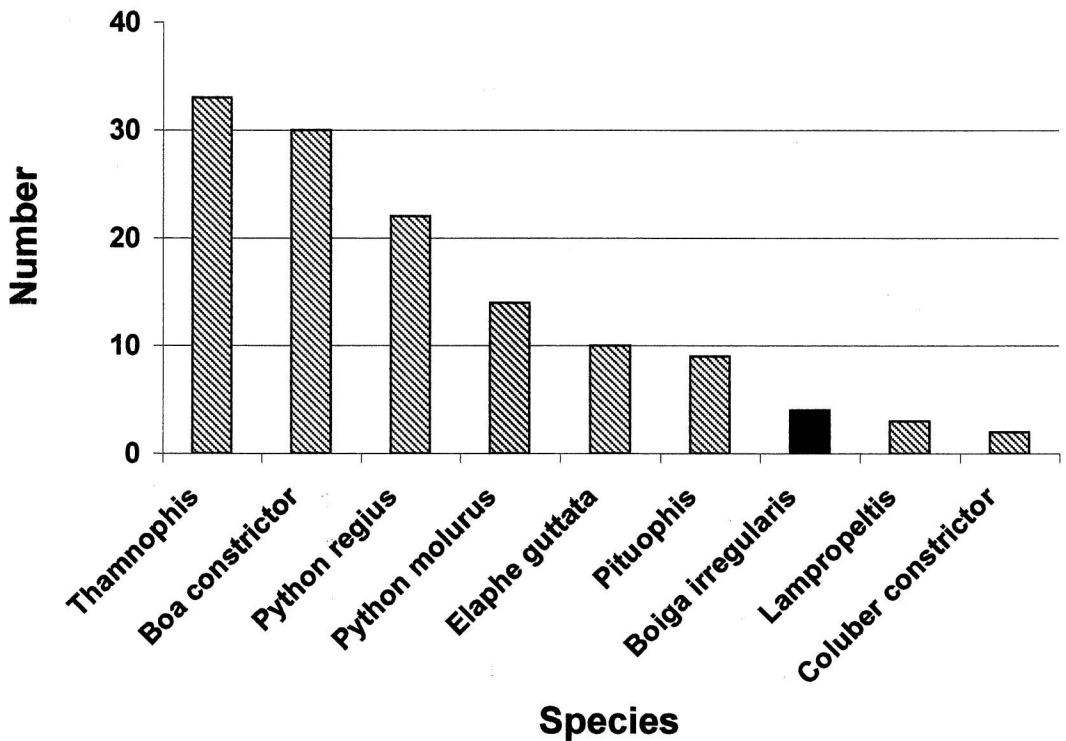


FIGURE 2. Numbers of each of the snake taxa most commonly retrieved and identified by Hawai'i Department of Agriculture from June 1990 to June 2000. Black bar highlights for perspective those instances of brown tree snakes (*Boiga irregularis*) retrieved during this period. In addition to these species, there have been retrieved one specimen each of *Diadophis punctata*, *Heterodon nasicus* (from cargo), *Nerodia rhombifera*, *Ninia sebae* (from cargo), and *Python reticulatus*. The *Lampropeltis* comprised two *L. getula* and one *L. alterna*.

TABLE 1
Ecological Characteristics of Frequently Encountered Snakes in Hawai'i

| Characteristic | Genus | | | | | | |
|----------------|-----------------------|------------|---------------|-------------------------|-----------------------|------------------|-----------------------|
| | <i>Boiga</i> | <i>Boa</i> | <i>Python</i> | <i>Elaphe</i> | <i>Lampropeltis</i> | <i>Pituophis</i> | <i>Coluber</i> |
| Prey | Vertebrate generalist | Endotherms | Endotherms | Endotherms ^a | Vertebrate generalist | Endotherms | Vertebrate generalist |
| Arboreal? | Y | Y | Y | Y | N | N | N |
| Nocturnal? | Y | Y | Y | Y | Y | Y | N |
| Clutch size | 4-12 | 12-64 | 15-107 | 3-21 | 5-17 | 3-22 | 4-25 |
| Broods/year | 1-2 | 1 | 1 | 1-2 | 1 | 1-2 | 1 |

Note: Data taken from Fitch (1963, 1970, 1985), Tryon and Murphy (1982), Brown and Parker (1984), Tryon (1984), Stafford (1986), Seigel and Ford (1987), Savidge (1988), Greene (1989), Rosen (1991), Shine (1991), Campbell (1996), Shine and Seigel (1996), Rodda et al. (1999a).

^a Has an ontogenetic dietary shift from ectotherms to endotherms.

Hawai'i [e.g., *T. couchii* (Kennicott), *T. elegans* (Baird & Girard)] also feed significantly on fish (Rossman et al. 1996) and may pose a hazard to Hawai'i's native gobies.

Three species of abundant alien lizards, five birds, and five small mammals are believed to have fueled the expansion of *B. irregularis* on Guam and maintained its high population densities following the population declines and extinctions of native vertebrates (McCoid 1999, Rodda et al. 1999b). This abundance of alien prey items is matched, and probably exceeded, in Hawai'i, which has five small mammals, three frogs, seven lizards, and dozens of birds that are extremely abundant statewide and could serve as food sources for expansion of the snake species discussed here. Rigorous population estimates have not been generated for these potential prey species in Hawai'i, but many are as abundant or more so than their taxonomic counterparts are in Guam (F.K., pers. obs.), and the taxonomic and ecological diversity of Hawai'i's alien vertebrates is greater.

DISCUSSION

Three requirements must be met to demonstrate substantial ecological risk from an alien species: that the probability of introduction is high, that establishment of wild populations upon introduction is likely, and that the species poses an ecological hazard. The first criterion is a function of rate of human movement of the alien, the second reflects the favorableness of the recipient environment to the alien, and the last concerns the ecological damage that the alien is capable of inflicting. All three conditions are met in Hawai'i for a variety of snakes and will be considered in turn.

The large numbers of yearly sightings of free-roaming snakes, the high frequency with which snakes are surrendered or confiscated, their wide distribution around the state, and the casual manner in which many sightings are reported to authorities make it likely that scores or hundreds of snakes—a considerable proportion of them free roaming—are present in Hawai'i at any one time. Clearly,

snakes are being smuggled into Hawai'i in large numbers and a substantial, though unknown, percentage of these escape or are deliberately released each year, presenting a clear possibility for establishment of wild populations. The likelihood of establishment may be increased by the apparent ability of some of the most commonly smuggled species to reproduce via facultative parthenogenesis in the absence of males (Schuett et al. 1997). Hence, it is conceivable that even single, unimpregnated females may be capable of establishing snake populations in Hawai'i.

The probability of establishment of these free-roaming snakes appears even higher because of the poor success in retrieving snakes once released (Figure 1), the equitable climate in Hawai'i, and the rich prey base available to support population growth. The snakes most frequently captured in Hawai'i are of either tropical or temperate origin, and, because both subtropical and temperate climatic regimes are widely distributed throughout the state, released snakes generally find themselves in areas favorable to their growth and reproduction. Furthermore, food items occur in abundance throughout the lower elevations (0–1000 m) of the state. Given Guam's experience with dense populations of *B. irregularis* maintained by alien prey species (Campbell 1996, McCoid 1999, Rodda et al. 1999b), the richness of alien prey in Hawai'i is an ominous portent.

Finally, the hazards associated with the introduction of snakes to Hawai'i, or to other oceanic islands, are high. For Hawai'i, ecological concerns are largely focused on loss of native forest or water birds because these are the native species most likely to be impacted by alien snakes. However, native stream-dwelling fish may also be affected. Most snake species recovered in Hawai'i feed largely or partly on birds, and the thermal tolerances of several would allow them entry into at least midelevation (up to ca. 1500 m) habitats. Most native forest and water birds have part or all of their ranges included within the zones that many of these snakes could inhabit. Consequently, most native bird species could be expected to sustain substantial harm

if these snake species should become widely established.

Direct human economic and health threats are also posed to Hawai'i by snakes. Although none of the species yet recovered in Hawai'i is dangerously venomous to humans, rumors are occasionally received that such snakes are maintained in captivity in the state. Even should these rumors be incorrect, venomous snakes are widely kept in the mainland United States and would be just as easy to smuggle into Hawai'i as any other species. The occasional use of venomous snakes to guard drugs or other illicit materials (Chiszar et al. 1992, 1993) provides an additional motive to smuggle these animals into Hawai'i. The health and economic drawbacks to having such snakes become established should be obvious, although it would certainly make hiking a more exciting activity.

Economic damage to the electrical industry's infrastructure on Guam results from the arboreal proclivities of brown tree snakes leading them to cross and short-circuit power lines (Fritts et al. 1987). This same problem would no doubt lead to millions of dollars of economic loss if *B. irregularis* arrived in Hawai'i, and it is possible that the other arboreal species frequently encountered in Hawai'i would cause similar problems if established. Substantial losses to the poultry industry are also likely, as have occurred in Guam (Fritts and McCoid 1991).

One economic impact of unknown potential is the effect that established snake populations might have on Hawai'i's tourist industry. The dependence of that industry on myriad social factors makes any impact from snakes inherently difficult to predict, but there is reasonable cause for concern. Because many tourists to Hawai'i are from the mainland United States, and fear of snakes or their association with evil is widespread in Western cultures, it is possible that tourist visits from the mainland could decline considerably if snakes became established in Hawai'i. At the very least, substantial publicity would be likely to attend such a discovery. Although we do not predict hysteria to result, the publicity might be sufficient to, at least temporarily, induce some mainland tourists to seek recre-

ation elsewhere. Whether or not a permanent market depression would ensue is impossible to predict.

It should be obvious from this discussion that three factors are interacting to make the threat of snake invasion in Hawai'i high: the biology of the commonly retrieved snakes is ecologically destructive and conducive to easy establishment; the environment is climatically equable, food-rich, and prone to easy invasion; and human activities are widely and frequently disseminating the threatening organisms. Under the circumstances, establishment of ecologically destructive snake species in Hawai'i seems assured. To avoid this outcome logically requires modifying one of the three factors combining to produce the risk. The hazardous biology of the snakes themselves cannot be changed, and alteration of the food-rich environment is physically impossible at this late date. Consequently, alteration of human practices introducing the threat is the only means of averting invasion. To this end, the State of Hawai'i has made possession of snakes illegal, with large associated penalties (up to \$200,000 fine and 3 yr imprisonment). Given this severe response, it is reasonable to inquire why smuggling persists and what is further required to terminate it.

Snake smuggling persists in Hawai'i because it is relatively simple and safe to accomplish, and enforcement tools to apprehend smugglers are grossly inadequate. Smuggling at airports is easy because inspection is based on an honor system: passengers are requested to voluntarily identify prohibited articles in their possession and have them searched by inspectors. However, passengers can exit the airports without encountering inspectors, unsolicited baggage checks by inspectors are rare because too few inspectors are available to adequately cover arriving flights (for example, in fiscal year 2000, only 2% of parcels arriving in Hawai'i were detained and the large majority of these were agricultural items), and inspectors have no authority to stop and search baggage and passengers without probable cause because of 4th Amendment protections. Tools that could be used to provide probable cause, such as trained

detector dogs and X-ray machines, are not employed to interdict smugglers. Finally, even when probable cause is available to justify searching an item, HDOA inspectors lack authority to detain or arrest smugglers. Hence, most arriving passengers never encounter (and can easily avoid) an inspector, all passengers and most baggage cannot legally be searched, and passengers cannot be arrested by inspectors even if their baggage contains prohibited items.

For constitutional reasons identical to those noted above, nondeclared mail and express packages also arrive in the state without inspection and these provide alternate routes of easy entry of smuggled animals. Thus, in summary, it is easy to bring illicit animals into the state, and the probability of being detected is low.

Confiscation of animals already imported into the state is of similarly low probability because of lack of appropriate law-enforcement staff and training for the State agency having jurisdictional authority. Consequently, investigation of smuggling cases is devolved onto inspectors whose lack of law-enforcement training forbids or restricts their ability to: (1) obtain background information on suspects in a timely manner; (2) obtain search or arrest warrants; (3) serve warrants; and (4) directly discuss such cases with the State prosecutors expected to try cases. Cases that were successfully pursued during the period studied by us relied on assistance offered by concerned personnel from other agencies, but the ad hoc nature of these collaborations has resulted in few cases being prosecuted. The last indictment for snake possession in Hawai'i was in 1995 even though 99 credible reports and 36 actual snakes have been received by officials since then.

One additional problem is that the seriousness of smuggling invasive animals has not yet been generally appreciated among significant sectors of the law-enforcement, legal, and judicial communities in Hawai'i. This serves to ensure that even when warrants are obtained and served, receipt of a meaningful penalty by the perpetrator is doubtful. For example, within the 10-yr period studied by us, the cases that were eventually submitted

for prosecution resulted in only two defendants receiving the maximum fine and additional jail sentence, eight the minimum fine (bail forfeiture), four reduced fines, four probation or never prosecuted, and two successfully fled the state before prosecutorial action was taken.

In contrast to the current situation, a credible deterrent to smuggling can only be provided by enhancing the likelihood that smugglers be intercepted either at the port of entry or upon subsequent receipt of tips from the concerned public. To meet the former need, a single point of exit where all baggage and hand-carried items are liable to search is needed in clearing airports. At these points, use of technology, such as X-ray machines and dog teams, appropriate for identifying illicit items in baggage is required. This reconfiguration and enhancement of inspection capability would provide an increased deterrent against smuggling and result in improved interception of smuggled animals at the ports. Additional authorities are also needed to allow inspectors to stop and search persons at airports if given good cause. Without these tools, evasion of detection at the port of entry will continue unabated.

To provide meaningful enforcement of state laws prohibiting snake possession, the Hawai'i Department of Agriculture, charged with the enforcement of these laws, but not provided the proper tools to do so, must be given a small (two to four staff), but properly funded, law-enforcement arm. Other law-enforcement agencies lack the authority or funding to meet this need and cannot provide a meaningful deterrent. Legislative action will be required to provide these police powers, training, personnel, and operational funding.

It is not biologically inevitable that ecologically destructive snakes colonize Hawai'i, but human activities, if allowed to maintain their current course, make it highly likely. To avoid this socially determined outcome is, of course, a matter of choice, but it requires acceptance of important attitude and behavioral changes by society and government in Hawai'i. These changes depend upon recognition that alien-species invasions constitute a major threat to human ecological wel-

fare, are a cost imposed by assorted small interest groups on society as a whole, and require vigorous and comprehensive responses by those entrusted with managing the public welfare. At this time, these facts are not widely recognized by the State of Hawai'i. Consequently, it remains an open question whether society and government in Hawai'i have the will to adopt the necessary protective measures that will determine whether Hawai'i in the twenty-first century will host populations of ecologically or economically destructive snakes.

ACKNOWLEDGMENTS

We thank Gordon Rodda and an anonymous reviewer for helpful suggestions on the manuscript, G. Phocas for helpful discussions of current enforcement restrictions, and L. Jones and A. Resetar for kindly providing us with critical literature.

Literature Cited

- Brown, W. S., and W. S. Parker. 1984. Growth, reproduction and demography of the racer, *Coluber constrictor mormon*, in northern Utah. Pages 13–40 in R. A. Seigel, L. E. Hunt, J. L. Knight, L. Malaret, and N. L. Zuschlag, eds. Vertebrate ecology and systematics: A tribute to Henry S. Fitch. Univ. Kans. Mus. Nat. Hist., Spec. Publ. 10.
- Campbell, E. W. 1996. The effect of brown tree snake (*Boiga irregularis*) predation on the island of Guam's extant lizard assemblages. Ph.D. diss., Ohio State University, Columbus.
- Chiszar, D., H. M. Smith, and W. D. Costain. 1992. Reptiles in association with illicit drugs. Bull. Chic. Herpetol. Soc. 27:1–4.
- Chiszar, D., L. Jones, W. D. Costain, and H. M. Smith. 1993. Another association between reptiles and illicit drugs. Bull. Chic. Herpetol. Soc. 28:60.
- Cutter, S. L. 1993. Living with risk. Edward Arnold, London.
- Fitch, H. S. 1963. Natural history of the racer *Coluber constrictor*. Univ. Kans. Publ., Mus. Nat. Hist. 15:351–468.
- . 1970. Reproductive cycles in lizards and snakes. Univ. Kans. Mus. Nat. Hist. Misc. Publ. 52:1–247.
- . 1985. Variation in clutch and litter size in New World reptiles. Univ. Kans. Mus. Nat. Hist. Misc. Publ. 76:1–76.
- Fritts, T. H. 1987. Movements of snakes via cargo in the Pacific region. 'Elepaio 47:17–18.
- Fritts, T. H., and M. J. McCoid. 1991. Predation by the brown tree snake *Boiga irregularis* on poultry and other domesticated animals in Guam. Snake 23:75–80.
- Fritts, T. H., N. J. Scott Jr., and J. A. Savidge. 1987. Activity of the arboreal brown tree snake (*Boiga irregularis*) on Guam as determined by electrical outages. Snake 19:51–58.
- Fritts, T. H., M. J. McCoid, and D. M. Gomez. 1999. Dispersal of snakes to extralimital islands: Incidents of the Brown Treesnake (*Boiga irregularis*) dispersing to islands in ships and aircraft. Pages 209–223 in G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka, eds. Problem snake management: The habu and brown treesnake. Comstock, Ithaca, New York.
- Greene, H. W. 1989. Ecological, evolutionary, and conservation implications of feeding biology in Old World cat snakes, genus *Boiga* (Colubridae). Proc. Calif. Acad. Sci. 46:193–207.
- Hohenemser, C., R. E. Kasperson, and R. W. Kates. 1982. Causal structure: A framework for policy formulation. Pages 109–139 in C. Hohenemser and J. X. Kasperson, eds. Risk in the technological society. Westview Press, Boulder, Colorado.
- Loope, L. L., F. G. Howarth, F. Kraus, and T. K. Pratt. 2001. Newly emergent and future threats of alien species to Pacific landbirds and ecosystems. Stud. Avian Biol. 22:291–304.
- McCoid, M. J. 1999. Established exotic reptiles and amphibians of the Mariana Islands. Pages 453–459 in G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka, eds.

- Problem snake management: The habu and brown treesnake. Comstock, Ithaca, New York.
- Oliver, J. A., and C. E. Shaw. 1953. The amphibians and reptiles of the Hawaiian Islands. *Zoologica* (N.Y.) 38:65–95.
- O'shea, M. 1996. A guide to the snakes of Papua New Guinea. Independent Publishing, Port Moresby, Papua New Guinea.
- Rodda, G. H., T. H. Fritts, and D. Chiszar. 1997. The disappearance of Guam's wildlife: New insights for herpetology, evolutionary ecology, and conservation. *BioScience* 47:565–574.
- Rodda, G. H., T. H. Fritts, M. J. McCoid, and E. W. Campbell III. 1999a. An overview of the biology of the brown treesnake (*Boiga irregularis*), a costly introduced pest on Pacific islands. Pages 44–80 in G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka, eds. Problem snake management: The habu and brown treesnake. Comstock, Ithaca, New York.
- Rodda, G. H., M. J. McCoid, T. H. Fritts, and E. W. Campbell III. 1999b. Population trends and limiting factors in *Boiga irregularis*. Pages 236–256 in G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka, eds. Problem snake management: The habu and brown treesnake. Comstock, Ithaca, New York.
- Rosen, P. C. 1991. Comparative ecology and life history of the racer (*Coluber constrictor*) in Michigan. *Copeia* 1991:897–909.
- Rossman, D. A., N. B. Ford, and R. A. Seigel. 1996. The garter snakes: Evolution and ecology. University of Oklahoma Press, Norman.
- Rowe, W. D. 1977. An anatomy of risk. John Wiley & Sons, New York.
- Savidge, J. A. 1988. Food habits of *Boiga irregularis*, an introduced predator on Guam. *J. Herpetol.* 22:275–282.
- Schuett, G. W., P. J. Fernandez, W. F. Gergits, N. J. Casna, D. Chiszar, H. M. Smith, J. B. Mitton, S. P. Mackessy, R. A. Odum, and M. J. Demlong. 1997. Production of offspring in the absence of males: Evidence for facultative pathogenesis in bisexual snakes. *Herpetol. Nat. Hist.* 5:1–10.
- Seigel, R. A., and N. B. Ford. 1987. Reproductive ecology. Pages 210–252 in R. A. Seigel, J. T. Collins, and S. S. Novak, eds. Snakes: Ecology and evolutionary biology. McGraw-Hill, New York.
- Shine, R. 1991. Strangers in a strange land: Ecology of Australian colubrid snakes. *Copeia* 1991:120–131.
- Shine, R., and R. A. Seigel. 1996. A neglected life-history trait: Clutch-size variance in snakes. *J. Zool. (Lond.)* 239:209–223.
- Stafford, P. J. 1986. Pythons and boas. T. F. H. Publishing, Neptune City, New Jersey.
- Tryon, B. W. 1984. Additional instances of multiple egg-clutch production in snakes. *Trans. Kans. Acad. Sci.* 87:98–104.
- Tryon, B. W., and J. B. Murphy. 1982. Miscellaneous notes on the reproductive biology of reptiles. 5. Thirteen varieties of the genus *Lampropeltis*, species *mexicana*, *triangulum* and *zonata*. *Trans. Kans. Acad. Sci.* 85:96–119.