ECOLOGY, BEHAVIOR AND CONSERVATION OF THE JAPANESE MAMUSHI SNAKE, *GLOYDIUS BLOMHOFFII*: VARIATION IN COMPROMISED AND UNCOMPROMISED POPULATIONS

By

KIYOSHI SASAKI

Bachelor of Arts/Science in Zoology
Oklahoma State University
Stillwater, OK
1999

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
December, 2006

ECOLOGY, BEHAVIOR AND CONSERVATION OF THE JAPANESE MAMUSHI SNAKE, *GLOYDIUS BLOMHOFFII*: VARIATION IN COMPROMISED AND UNCOMPROMISED POPULATIONS

Dissertation Approved:

Stanley F. Fox

Dissertation Adviser

Anthony A. Echelle

Michael W. Palmer

Ronald A. Van Den Bussche

A. Gordon Emslie

Dean of the Graduate College

ACKNOWLEDGMENTS

I sincerely thank the following people for their significant contribution in my pursuit of a Ph.D. degree. I could never have completed this work without their help. Dr. David Duvall, my former mentor, helped in various ways until the very end of his career at Oklahoma State University. This study was originally developed as an undergraduate research project under Dr. Duvall. Subsequently, he accepted me as his graduate student and helped me expand the project to this Ph.D. research. He gave me much key advice and conceptual ideas for this study. His encouragement helped me to get through several difficult times in my pursuit of a Ph.D. degree. He also gave me several books as a gift and as an encouragement to complete the degree. Dr. Stanley Fox kindly accepted to serve as my major adviser after Dr. Duvall's departure from Oklahoma State University and involved himself and contributed substantially to this work, including analysis and editing. Dr. Michael Palmer was more than just a committee member, he provided me with various insights into the life sciences, as well as valuable opportunities and experiences. His family has contributed to making my stay in Stillwater memorable. Dr. Anthony Echelle, his wife, Alice, and her father, Dr. Henry Fitch, have not only given me important suggestions for this study, but also made my stay in Stillwater memorable. Dr. Ronald A. Van Den Bussche helped to improve analysis and writing. Dr. Robert Capers, though he was not on my committee, reviewed and helped to improve this dissertation. Dr. James Shaw helped to write grant proposal for this work. Dr. Aaron Place helped and encouraged me especially during my difficult times. Dr. Sen Takenaka from Hokkaido Tokai University helped me in various ways, including providing helpful suggestions for this study, as well as some equipment. Day Ligon, a graduate student, helped with some analysis.

My parents, Yoshinori and Mitsuko Sasaki, were extremely supportive in various ways. My father's contribution was significant. He found locales of mamushi populations by asking government officials and local people. Without such help, I could not even have begun my study. Gathering information and references for religious aspects of snakes in Japan was mostly done by my father, which was not possible for me to do while staying in the U.S. Mr. Masanori Sasaki, my father's former student, also helped to find mamushi populations. Dr. Hifumi Tsuruga and colleagues taught me environmental characteristics of my study area, including vegetation of the area. My wife, Fumiko, helped me a great deal with many aspects during my pursuit of a Ph.D. She also assisted me in the field, especially when I was incapacitated by snakebites. Her help was essential. Local people at my study site were very supportive and helped me during my stay there, especially the Furudate family, Otani family, and Murotsuka family. Mr. and Mrs. Furudate kindly let me stay in their house and cooked and did laundry for me. Mr. Takahashi (my father's former student) and Mr. Tahata took me to a hospital when I was bitten by a mamushi. I would be dead if they had not helped me. Many people, including my relatives and the Inoue family, took care of me when I was bitten by mamushi on three occasions. Mr. Mukai and Haru Koike kindly volunteered in some fieldwork. Songoku restaurant served a lot of good food, including sake, often free of charge. Dr. Kawamata and others in Kawamata Animal Hospital kindly took X-ray pictures of snakes free of charge. Mr. Shuzo Sugai, the principal, and other personnel of Chiisago elementary school were very supportive of my snake conservation education activities. Hokkaido University allowed me to use their facilities and experimental forest. Dr. Kyo Matsuda kindly taught me about the forest.

TABLE OF CONTENTS

Chapter Page

I. SURVEY OF LITERATURE

II. A NATURAL EXPERIMENT

LIST OF TABLES

Table Page

Chapter II.

LIST OF FIGURES

Figure Page

Chapter I.

Chapter II.

CHAPTER I

SURVEY OF LITERATURE

Introduction to the Japanese Mamushi

Conservation concerns

Japanese mamushi (*Gloydius blomhoffii*; hereafter, mamushi; Figure 1), belonging to the subfamily Crotalinae, family Viperidae, are Old World pitvipers that are endemic to the Japanese archipelago (Paik et al. 1993; Toriba 1996; Hikida 2002). They occur on all four major islands of Japan, including Hokkaido, Honshu, Shikoku, Kyushu, and on several small islands (Figure 2). Though similarities occur between this species and the many mainland (Eurasian and Asian continent) forms of this genus (Gloyd and Conant 1990), the mamushi is unique and important in one key respect: it is an exclusively island form, with all that this implies in a biogeographic ecological context (MacArthur and Wilson 1967; Grant 1998).

Mamushi populations in many places appear to be declining or are already extirpated (e.g., Sato 1990), though quantitative data are non-existent. Although mamushi have existed on the lands that humans (i.e., the people of Japan) have occupied for thousands of years, it was probably not until around 1900 that mamushi began to be seriously impacted by humans, when dramatic cultural and societal transformations (i.e., adoption of the "western" ways) occurred in Japan.

Just as it is for so many other kinds of fauna and flora, significant habitat loss is involved. The decline of mamushi populations appears most notable in lowland and hilly terrain in which extensive anthropogenic modification is taking place. In Hokkaido, for example, road installations and associated modifications around the roads appear to have lead to extirpations of several local populations (personal observation).

As with many snakes of the world (e.g., Klemens and Thorbjarnarson 1995; Zhou and Jiang 2004), potential additional threats to mamushi are commercial (Goris, cited in Gloyd and Conant 1990; Conant 1992) and non-commercial (Sato 1990) harvesting. The genus *Gloydius*, which includes the mamushi, has long been known for its medicinal value in Asia. In Japan, the oldest Japanese medical dictionary, Daidoruijuho, which was written in 808, reports such use of mamushi (Kurihara 1963). The company Tohtohshu, originating in 1690, is one of the largest wholesalers utilizing mamushi today. A prominent herpetologist of Japan, Dr. Richard Goris, who performed Tohtohshu's bookkeeping as a general curator of snakes, describes mamushi harvesting as follows (personal communication via email, 2001):

> 30 some years ago snake whiskey companies like "Tohtohshu" collected at least 40,000 mamushis per year… In the early 70's they were unable to get enough to keep up their production of whiskey, so they took to importing other species of *Agkistrodon* (i.e., *Gloydius*) from Korea and China, and continue to do so today. Other heavy users of mamushis are the Chinese medicine places. They rely

heavily on imports also, mostly from Fukien Province in China. They are able to obtain only a few hundred local specimens in the summer.

In the update from him (email, 2006), he stated:

> Tohtohshu recently ceased operating because of bankruptcy. Ultimately, the cause of the bankruptcy was their rapacious overcollection of mamushi, and the defection of the farmers who used to do the collection. The farmers could no longer collect enough snakes to make it worth their while to collect for the pittance they were being paid. To compound matters, their import sources dried up. Because of the SARS epidemic and cover-up scandal, China outlawed export of all animals indiscriminately; and Korea passed an environmental protection law that made it illegal to even collect mamushi.

Added to such exploitation, mamushi are also impacted by malicious, indiscriminate, and/or seemingly irrational killing, which is a common source of snake mortality the world over today, especially for venomous species like mamushi. In today's highly fragmented and reduced habitats, such killing of mamushi may be detrimental to many of the declining populations. Mamushi are removed (usually killed) in/around not only residential areas, but also wildlife protection areas and parks. In Teuri Island, a quasi-national park, for example, the municipal government has been enforcing a "removal program" by employing a local resident to kill mamushi to "protect" tourists (personal communication with the hunter). Dr. Goris goes on to say (in the above email communication):

> Self-sustaining populations of mamushi remain only in the undeveloped hills and terraced rice fields in unimproved valleys. In parks and near housing developments they are hunted and killed; or they die off because of disturbance to the food chain. Their reproductive capability is also low, 3–5 babies once every couple of years. They are capable of producing 10 and more babies every year, but you need a big population, lots of food, and older females for that. Existing populations are now generally fairly young, so the females are small.

What his observations imply, and particularly germane to this dissertation, is that human attitude and actions towards snakes and nature (e.g., snake habitats) not only can directly reduce population size via direct mortality, but also can change the age and size distribution of the afflicted populations. Reduction in body size, and consequent change in life history traits, is one of the most notable genetic and evolutionary consequences that has long been argued theoretically and recently shown empirically in exploited fish and trophy-hunted ungulate populations. Evolutionary changes in traits of afflicted species are not trivial because whereas the changes may allow the affected populations to persist via "adaptations," such presumptive adaptations could actually lower the ability for population recovery, and, therefore, have important implications for species persistence, conservation, and management (discussed elsewhere in this dissertation).

Mamushi biology and ecology

Mamushi are typically 30–50 cm in snout-vent length (SVL) (Toriba 1996; Goris and Maeda 2004) and 35–150 g in body mass (Toriba 1996). Mamushi in Hokkaido, however, are larger than southern counterparts (Ota and Nakagawa 1985; Moriguchi and Takenaka 1984), and SVL is typically 49–56 cm (see Chapter II). Longevity is reported to be more than 10 years in captivity (Fukada 1989). Though not known in nature, longevity may be similar in nature based on preliminary skeletochronological analyses on mamushi from Hokkaido (Sasaki, unpublished data).

Males reach sexual maturity in about three years when total body length reaches about 40 cm, whereas females become mature when body size reaches 40–45 cm (data based on mamushi in Kyushu). Data collected in my study (see Chapter II) are consistent with such figures: the smallest female found to be pregnant in Hokkaido was 52.5 cm. Mamushi are known to mate in August–September in Kyushu, the southernmost main island of Japan (Figure 2) (Isogawa and Kato 1995; Central Research Laboratories 1999). Though no information is available for Hokkaido populations, the mating season in Hokkaido may also occur at about the same time of the year based on my observations of male aggregations (2–4 individuals), high encounter rates with males, and occurrence of seemingly synchronous shedding during mid August through early September (Figure 3). Mamushi are known to give birth to 2–13 young in August–October (Toriba 1996). In Hokkaido, August parturition appears to be non-existent or rare, with births later, in mid-September through late-October (see Chapter II).

Mamushi are frequently found in diverse habitats, including agricultural lands, usually within or adjacent to forests (Goris and Maeda 2004; personal observation).

Hokkaido populations appear to use the same general area year after year (Sasaki, this study). Microhabitat association, daily activities and seasonal movements appear to differ among males and nonpregnant and pregnant females, especially between the former two groups and the latter (see Chapter II). Mamushi emerge from hibernation in April–May and retreat underground in October–November (Toriba 1996; personal observation). Pregnant females remain in areas termed “basking spots” (Sasaki and Duvall 2003) during June–October (the timing and duration varies between locations and between individuals), which are small, sunny areas with abundant crevices and sparse vegetation. At basking spots, pregnant females appear to confine their movements to an area of a few square meters until parturition, presumably to behaviorally thermoregulate (see Chapter II). Parturition appears to take place outside of basking spots, but not far from them (personal observation). Soon after parturition, they move away from these basking spots, presumably for foraging (personal observation). In contrast to pregnant females, most males and nonpregnant females appear to stay only briefly at a basking spot and are mostly found in other places (personal observation). Mamushi of both sexes appear to be active only in daylight hours; however, during the warmest time of the year, i.e., August, they appear to be active also after dusk (personal observation).

Mamushi mainly feed on frogs and small rodents (Toriba 1996; Sasaki, unpublished data) but also take other snakes, lizards, birds, fish, and centipedes (Toriba 1996). The “natural” (i.e., non-human) predators include raptors, crows and ravens (*Corvus* spp.), weasels (*Mustela* spp.), Japanese four-lined snakes (*Elaphe quadrivirgata*), and boar (*Sus* spp.; absent in my study area) (Toriba 1996). Feral/domestic cats (personal observation), and probably red fox (observations by local people at my study sites), also prey on mamushi. General antipredator behavior has been described by Goris and Maeda (2004) as, "When approached by humans, it often does not flee but remains motionless, relying on its camouflage…Bites occur in such situations when it is inadvertently stepped on or otherwise touched." Mamushi studied in Hokkaido exhibit a characteristic defensive sequence, similar to that described by Duvall et al. (1985). Mamushi at first depend on procrypsis, remaining immobile and silent, to avoid detection. If that fails, most snakes attempt to escape by locomotion. If that is inefficacious (e.g., when a predatory encounter is sudden) or threat escalates/continues, some snakes turn to threat displays (vibrating tails, flattening body, striking) and biting attempts, though the latter action is rare unless the snake is touched.

Conservation through Traditional Religious/Spiritual Beliefs in Japan

There is no question that increasing human populations and activities have diminished suitable habitat for many species of plants and animals. However, many flora and fauna, as well as relicts of less disturbed terrestrial and aquatic areas, have found refuges in areas where the force of traditional (also referred to as "indigenous" or "local"), spiritual/religious/customary beliefs still prevail (e.g., Osemeobo 1994; Colding and Folke 2001; Bernard 2003). A notable example is so-called sacred forest/groves, which have been protected through strong traditional beliefs upheld by the local people's spiritual, religious, and cultural attachments to them (Barrow and Pathak 2005).

Similar examples are found in various parts of the world, and Japan is no exception. During more than 2000 years of Japan's civilization, most of the archipelago's accessible primeval forests were cut and replaced with plantations or left to naturally regenerate (Diamond 2005). Much of the accessible lands have been converted to rice paddies, farmland, residential areas, and other human construction. However, though greatly reduced in area during the last 100 some years, especially the last 50 years, there still remain ancient forests even in such human-disturbed areas, and those are the places where human use or access has been constrained by religious, spiritual, and customary beliefs. Because Japanese traditionally believe that *kami* (spirits, souls, or something revered and/or awe-inspiring) resides in nature(Senda 1992), particular areas, such as the land around shrines, are considered holy or untouchable by people, and thus, have been kept free from destructive human activities (Omura 2004) (though such beliefs and practices have been eroding rapidly in contemporary time).

Examples include the 300-ha Kasugayama Primeval Forest, which has been protected from logging and hunting as the sacred place of Kasuga-taisha (a Shinto shrine) for more than 1100 years (Mizuno et al.1999; Omura 2004). This forest is today designated by UNESCO as a World Cultural Heritage Site. Deer there are believed to be a messenger of *kami*, and accordingly, respected and protected (Omura 2004). Tatera Forest Reserve (ca. 100 ha) of Mt. Tatera (559 m) on Tsushima Island also has been free of human disturbance for centuries because the mountain has been revered by local people. According to a local resident, some elders call a portion of the mountain "dreadful place" and do not even approach it, believing that such an act would bring a curse.

I herein highlight the importance of traditional beliefs held by the people of Japan, especially those associated with snakes, to the future of Japanese snakes. Beliefs presented here include published accounts, what I was taught during my life in Hokkaido, and interviews with local residents (by my father and myself).

Snake- and nature-beliefs

During the Neolithic, Jomon period of Japan (ca. 14,500–300 BC), the snake was a powerful, omnipotent ancestor-*kami* (Yoshino 2000, 2001). Similar beliefs about snakes as ancestral deities also exist in other cultures, such as the Paiwan tribe in Taiwan, who considers hundred-pace snakes (a pitviper similar to mamushi) as its ancestors. Since the end of the Jomon period, however, such indigenous belief about snakes has been modified as Toraijin (people from the Asian continent; the modern Japanese contain a large proportion of Toraijin genes) immigrated into Japan and increased their social and political power (Daniels 1960; Yoshino 2000, 2001; Arakawa 1996; Nago 2001). Toraijin introduced their own cultures and religions, including those influenced by the "West", along with irrigated rice farming systems and metallurgy, which drastically changed the very way of life for the people of Japan, including belief systems and legends.

Snakes are commonly perceived as a *kami* or *kami*'s messenger, which has aspects of ancestors, the deceased, water-*kami*, thunder-*kami*, or mountain/forests-*kami*. Snakes are also called *nushi*, creatures that have long been living and have control over areas—of houses, land, water bodies, mountains, etc (Kojima 1991; Kawanabe 2003). In villages in Shikoku, snakes are considered as a *kami* of mountain, and the villagers are said to chant before burning fields for slash-and-burn agriculture: "Mountain-*kami*, big-snakes, beg your pardon, beg your pardon" (Kojima 1991; Sasaki 2006).

Snakes are believed to possess supernatural powers over the welfare of humans and can deal harm (i.e., cast divine curses) to humans when not treated appropriately, but they become guardians or play beneficial roles when treated appropriately. For example, a local resident informed me that people in Nishinogami (Hyogo prefecture) perceive snakes as something they must not kill because snakes are believed to be water-*kami*, to which the local Suwa Shrine is dedicated. As suggested by Daniels (1960), there is a general belief that killing or harming snakes will bring divine curses on the person involved, on his/her family, or on the entire community. Similar beliefs associated with snakes appear to be widespread in various cultures, such as in many Native American tribes (Klauber 1972; Sasaki et al. in press) and Southern African Bantu-speaking peoples (Bernard 2003).

Snakes that visit or are found in/around houses are regarded as *nushi* of the house or the ancestor of the family, and they are believed to be the guardian of the house and family (Kojima 1991 and references therein). People of Japan traditionally regard harming and killing of such snakes as taboo. Matsutani (2003) documented a family that enshrines snake-*kami*. Every time a snake is found around the house, the grandmother of the family makes offerings of rice and sake to the snake and preys for the welfare of the family. Matsutani (2003) also documented other cases where snakes in and around the houses are protected and where unfortunate incidences (death and other undesirable consequences) were attributed to harming and killing of such snakes.

Albino snakes, so called “white snakes”, are especially the target of worship, generally considered as a *kami* or *kami*’s messenger by the people of Japan. The representative example is the “naturally” occurring population of albino Japanese rat snakes (*Elaphe climacophora*) in the city of Iwakuni (Sengoku 1996). The occurrence of albino snake populations in nature is extremely rare because they are conspicuous to predators. It is said that the local people have acted as a selective force in which they have avoided killing white snakes even though they killed regular-colored rat snakes. The Japanese government designated the localities and these albino snakes as natural monuments in 1924 and 1972, respectively. White snakes are still revered by the local people and receive active protection.

Though a general taboo against killing and harming of snakes may be more commonly applied to non-venomous snakes (Daniels 1960), such a taboo also exist for venomous snakes even today and was probably common at least in the past based on existing legends, stories, and proverbs. For example, a legend, “The Snake that Returns a Favor,” told in the area of Taihakuku, Miyagi prefecture, relates that mamushi is a *nishi* of a hill called Mt. Taihaku-san (321 m) and a family involved in this story quit hunting mamushi for medicinal use on this mountain (Aihara et al. 1997). The legend of “The shed skin of snakes,” told also in this area, explains that mamushi is a messenger of *kami* and a guardian of this mountain who punishes reckless people who disturb the mountain and that mamushi’s shed skin is a good medicine for verruca/warts (Aihara et al. 1997).

Actual taboos against killing venomous snakes are still practiced today in some areas. For example, a tiny shrine, erected near a mineral spring on Mt. Futagoyama (635 m; Iwate prefecture, located in Honshu), is devoted to a *kami* called *Futago-daimyojin*, in which local people have a strong belief. According to an elder woman who guards the shrine, *Futago-daimyojin* is a mamushi-*kami* (Naito 1987). Mamushi are said to (actually do) abound in the area and even enter beds at night. However, it is believed that mamushi living around the shrine do not coil and never bite people. If people act inappropriately, mamushi are believed to cast a curse on the person. It is also believed that if one kills a mamushi, mamushi will come to attack people in great numbers (Naito 1978). The son of the person who erected the shrine tells a slightly different story. According to him, the *kami* of the area is a *ryujin* (dragon/snake-*kami*), not mamushi themselves. However, killing of mamushi is believed to bring a curse to the persons involved, and therefore, local people, even today, do not kill mamushi on Mt. Futagoyama. He also added that mamushi there do not attempt to bite people, and therefore, people leave them alone. He said that the mineral spring is so good that local villagers still go to the spring for daily drinking water.

In Samukawa hamlet in Hokkaido (people occupied the area over 1884-1957), located at the foot of a mountain along the coast, people worshiped *kuroki-hachidai-ryujin* (*kuroki* = black tree, *Hachidai* = the eighth generation), one of the *kami* of the sea/water (Nakamura and Furusho 2004). According to a former villager, success and safety of fishing was believed to be controlled by the *kami*. It also appears that the local people perceived the *kami* as the guardian of the hamlet and people. According to the villager, for example, people carried flags of the *kami* with them when they went to war and nobody died, thanks to the *kami*. Mamushi are believed to be the manifestation of the *kami*, and accordingly, people did not kill mamushi.

For another example, in the town of Kaminokuni, Hokkaido, a fisherman informed me that he regarded sea snakes (venomous species belong to the family Elapidae) as a *ryujin*, a *kami* who controls the catch and safety. The fisherman offers *sake* (Japanese rice wine) whenever he accidentally captures a sea snake and releases the snake after the offering. His house has an altar where his family makes offerings (e.g., eggs) to the *ryujin*. In the town of Samani, Hokkaido, a fisherman informed me that although he does not like snakes and fears them, fishermen are not to kill snakes, including mamushi. I observed a fisherman driving a pickup truck who stopped and waited until a mamushi finished crossing a road.

In Tokunoshima Island (south of Kyushu), about 100 people get bitten annually by large, venomous snakes called habu (*Trimeresurus flavoviridis*) (Hattori 2002), and Kagoshima prefecture has been buying up habu since ca. 1880 to reduce the number of habu (Yoshida 1980; Hattori 2002). In contrast to such a detrimental-to-snake attitude and action, people in older times used to associate habu with *kami* and avoided killing habu. When a habu was found in a garden, people did not kill it; instead, they chanted particular words and prayed so that the snake would go away (Nakamura 1998).

Beliefs about snakes as a *kami* or the like are not limited to reduction of human-caused direct mortality of snakes. It extends also to habitat and even ecosystem protection. Snakes are often regarded as *kami* dwelling in the mountains (Czaja 1974). A *kami* of a hill called Mt. Miwa (467 m) is believed to be the snake (Arakawa 1996; Yoshino 2000). This mountain has restricted access, and all animals and plants living there have been protected to this day (Antoni 1995). In the case of Mt. Nonogami-dake (550 m), a big snake, or the snake as a *kami*'s messenger, is believed to reside on the mountain. This mountain is perceived as a place where *kami* reside by the people who have faith in Kunitsu and Ogami shrines. Accordingly, entrance to this mountain has been tabooed even today. In Iwagami Shrine's Shasou ("*kami*'s forests," "sacred forests," also called "chinjuno-mori"), covering about 2 ha, remain broad-leaved evergreen trees, which have been lost from most of the rest of their historical ranges. It is said that such original vegetation communities persist today because people did not cut trees in the area, believing that logging would bring curses by a white snake living on a huge rock revered by the local people. The forest is today designated as a natural monument of the city of Matsuyama on Gogoshi Island. Mt. Tonochigo-yama on Tokunoshima Island is still covered by ancient forests (though the size is greatly reduced today, 0.7 ha) because of the belief that cutting trees on the mountain will bring a curse (Matsuyama 1998). Habu is believed to protect the mountain from those that do not obey "*kami*'s rule" by biting the offender (Matsuyama 1998). It is said that one must not kill habu on the mountain because such an act is believed to bring a curse to the person involved (Matsuyama 1998).

In Bise hamlet of Okinawa Island, there is a traditional "prayer ground" called gusukuyama in the forest. This forest is still covered with ancient vegetation because local people believe that reckless entrance to this forest will bring a divine curse (Takara 1998). According to an elder, *nushi* of the forest is believed to be a large habu and guarding the forest (Takara 1998). Killing of habu in this forest is believed to bring a curse not only to the person who killed the snake, but also to other fellow villagers (Takara 1998).

In some cases, entire islands are protected. For example, Kasim Island (3 ha), just offshore of Wakayama prefecture, is preserving ancient nature, covered by broad-leaved evergreen forest and designated as a natural monument by the government in the early 1900s. The island has been largely free from human disturbance because the local people generally have recognized the island as where *kami* of dragon-snake (guardian of the sea) resides (Sato 1952). Kumagus Minakata (Blacker 1983), who is largely responsible for the designation of this island as a natural monument and who recognized the biological and ecological values of this relict of ancient nature, wrote in 1911: "This island has not been inhabited by people since ancient times because people feared snake-*kami* residing on the island" (Association of Minakata Kumagusu Archives 2006).

As in other traditional/indigenous societies, oral traditions play an important role in strengthening and transmitting traditional beliefs and practices (e.g., Sasaki et al. in press). Legends are generally based on what actually happened in the past and have a clear message about what are and are not right deeds (Sasamoto 1994). In 1844, many people died due to a severe landslide in the town of Nagiso. Local people were aware of the risk of logging along the headwaters of a stream. The legend reads as follows: Before the incident, local villagers were logging the area, obeying the order of Owari-fief. One night, a woman in white appeared and told a logger, called Yohei, that further logging would lead to a disaster. Yohei, the next day, told others about it, but officials enforced the logging despite the loggers' opposition. The next day, as the woman warned, a severe landslide occurred and all houses were completely destroyed. During the landslide, Yohei saw a white snake sliding down and realized that the woman in white was the white snake. From that day, Yohei quit working as a logger (Sasamoto 1994).

In another example, a local newspaper in 1923 (cited in Sasamoto 1994) reported a massive flood that destroyed an entire village and killed the construction workers involved in land development there. This disastrous incident was attributed to the killing of snakes by the workers and disrespectful development of the land. According to the article, the workers killed many snakes while developing the land. On the same day, a snake appeared in a dream of one of the villagers and said, “Your people killed snakes, so I will destroy the whole village.” As the snake said, a massive flood and landslide destroyed the entire village on the following day. Thirty-eight workers were killed and their bodies were never found.

In the case of a waterfall in Heijigawa River falling into a seemingly bottomless pool, the *nushi* of the pool is believed to be a snake, who gets offended when the surrounding valley is made dirty. In 1912, a family built a cottage to log the area. As they were doing laundry upstream of the waterfall, it began to rain hard and a landslide destroyed the cottage and killed the entire family (Matsutani 2003).

Imperiled divine snakes and nature

Snake beliefs, and nature worship in general, have helped to reduce not only the frequency of human-caused mortality of snakes in Japan, but also to preserve indigenous natural systems, including snake habitats. Without these beliefs, many snake populations and habitats would probably have disappeared from the islands of Japan in the history of the more-than-2000-year-old civilization. However, such a nice-to-snake attitude/behavior has deteriorated rapidly due largely to the Meiji Restoration (1868-1912) and World War II, which brought radical societal and cultural transformation to Japan (e.g., adoption of Western education, values, beliefs, agriculture, farming, forestry, technology, and economics) and drastic changes to the very way of life (e.g., adoption of the Western calendar, houses, food, hair style, and clothes). In Hokkaido, for example, guided and assisted by foreign advisers like Dr. W. S. Clark (a former President of the Massachusetts Agricultural College, now the University of Massachusetts, Amherst) and

D. Edwin (an Ohio rancher), much of the primeval forest that covered most of Hokkaido was converted to agricultural land, ranches, and forestry plantations, and Japanese wolves were driven to extinction mainly to benefit ranching (McClain 2001; Walker 2004; Dudden 2005).

During such modernization/westernization/industrialization, many places that had been protected through religious or spiritual beliefs were destroyed. For example, Yanagita (1935) documented a place earlier called ryu-no-mori ("dragon forest"), but Nomoto (2004) failed to find such a place in recent searches. Yanagita (1935) documented the place as follows (originally in Japanese):

> Throughout villages there are places that children do not approach. Ryu-no-mori is one such a place. ... There are several very old Japanese horse chestnut trees. Numerous arrowheads are stabbed on ground around the trees…this forest is deep and ominous… A stream runs through this forest. It is told that a villager in the past fished a trout-like fish and incurred a divine curse. It was taboo to take anything living in this forest, including snakes and plants. People avoid entering this forest. When people cannot avoid passing through this forest, they must face the chestnut trees and pray to prevent *kami* from getting offended.

Much of folk religions/beliefs, especially phallic/sex beliefs (which are associated with snake beliefs), were also suppressed during the Meiji Restoration. Snakes are now perceived by many people as a "biological" animal, not as a supernatural being or *kami*. The fact that more and more people kill snakes on sight, especially venomous ones such as mamushi (as mentioned in the beginning of this chapter), reflects extensive erosion of traditional beliefs. Many water bodies and expanses, which used to be "protected" by dragon/snake-*kami*, have also been destroyed recklessly. Development of land and deforestation are now conducted without any concerns about a curse by snake's or nature's *kami*.

Given that nature worship extended its influence not only to snakes and their habitats, but also to ecosystems, I recommend strengthening and restoring snake and nature beliefs in Japan to enhance biological conservation and ecological restoration efforts. This is not impossible because even today actual examples of nature-worship, spirit-worship, fetishism, and even phallicism still exist in some rural areas and "…highly educated people living in a technologically advanced country still following superstitious, magical beliefs" (Macer and Boyle 1995). Many psychics even today emphasize not to kill snakes. Many people possess shed snake skins, believing that they will bring wealth. There are still hospitals that hang snake sheds to bring good fortune. There are many regions throughout Japan that still have Shinto-related beliefs; followers make motifs of the snake and pray for fertility and safety. Many shrines still have sacred areas, sometimes an entire mountain, where entrance is prohibited or restricted to special occasions.

Lastly, regarding the beliefs about mamushi on Mt. Futagoyama and in Samukawa hamlet, it is worth noting that the local people's attitudes and actions toward venomous snakes, mamushi, are quite rational. On Mt. Futagoyama, local people leave mamushi alone because mamushi there are known not to attempt to bite people. In the case of Samukawa hamlet, where mamushi are left alone, a local resident said:

> The mamushi is a quite rational animal and does not bite people indiscriminately. City people visiting this place fear mamushi more than necessary. The local people know where mamushi abound and avoid such locations. Even when encountered, mamushi usually become aware of approaching people and flee to their home. That city people get bitten is inevitable because they walk outside of paths, sticking their feet into the mamushi's home.

These statements by local people are in good agreement with my own observations that no mamushi bit me when walking by very close to them. Indeed, several venomous snake species rarely attempt to bite people when encountered by humans, unless cornered, inadvertently stepped on, or handled (e.g., Duvall et al. 1985; Gibbons and Dorcus 2002), which is consistent with my own four instances of snakebite. Such attitudes and treatment of venomous snakes exhibited by the local people near Mt. Futagoyama and in Samukawa offer an excellent example of how people ought to act toward venomous snakes. As in the case of other venomous snake species (Greene 1997, 1999), informing people about accurate mamushi biology, ecology, and behavior can ultimately help to reduce irrational (from my standpoint) killing of mamushi.

Rapid Evolution

Though evolutionary changes are historically thought to occur gradually over geological time (Darwin 1859), accumulating evidence has shown that changes can occur extremely rapidly over a wide array of free-ranging taxa, from viruses (Van Valen 1973), many insects (e.g., Kettlewell 1973 and Grant and Wiseman 2002 for industrial melanism), and herbaceous plants (e.g., Maron et al. 2004 for introduced St. John's wort), to western red cedar (Vourc'h et al. 2002), fish (Reznick et al. 1990; Magurran 1999; Reznick and Ghalambor 2001), and bighorn sheep (Coltman et al. 2003). Because phenotypic change can occur sufficiently fast such that it has the potential to impact population dynamics, community interactions, and ecosystem processes, ignorance about rapid evolution in systems under consideration can lead to inaccurate understanding of the systems (Hairston et al. 2005 and references therein). For example, Yoshida et al. (2003) demonstrated that the observed period of oscillations and the phase relations between rotifers (predator) and algae (prey) were not driven by classical predator-prey interactions, but by rapid evolutionary change in the prey (i.e., resistance to predator) (see also Turchin 2003; Hairston et al. 2005). More and more findings of rapid evolution in nature, such as evolution in response to fluctuating rainfall in finches and copepods (Grant and Grant 2002) and to variation in fish predation pressure in copepods (Hairston and Dillon 1990), suggest that rapid evolutionary responses may be inherent to and play a significant role in biological systems. Rapid evolution would seem to be a necessary working hypothesis in the study of such systems (Thompson 1999; Hairston et al. 2005). The question, "To what extent are succession, population dynamics, and ecosystem dynamics—historically considered to be solely ecological processes—governed by rapid evolutionary change in species and their interactions?" was identified in discussion in 1999 at The National Science Foundation as one of the key research frontiers that was crucial for our understanding of the ecological dynamics of biocomplexity (Thompson et al. 2001).

Much of earth's creatures and environment are impacted from the unsustainable way of modern life, including value and belief systems, and from the side-effects of an exploding human population, including habitat fragmentation and degradation, species introduction, overexploitation, and climate change. It implies that a species' phenotype that has evolved in an environment in which natural forces have prevailed may no longer be adaptive in an environment in which anthropogenic forces are powerful. If so, a species' traits must undergo evolutionary change for continued persistence of that species in a human-dominated world. Indeed, an increasing number of studies have detected such changes (Palumbi 2001a, 2001b). For example, changes in life history traits of prairie chickens (*Tympanuchus pallidicinctus*) have been suggested to be a rapid evolutionary response to modified mortality rates caused by habitat fragmentation (Patten et al. 2005). Other examples include squirrels in response to climate change (Berteaux et al. 2004), various native species in response to introduced species (reviewed in Strauss et al. 2006; Callaway et al. 2005), and *Daphnia* in response to pollution (Hairston et al. 1999). Because humans often act to create evolutionary forces and because afflicted populations often undergo evolutionary changes in response to them, we need to understand what and how human activities act as evolutionary forces and how such forces affect populations and associated communities. Only with such knowledge can we act wisely and effectively in land use and exploitation of wildlife populations, as well as succeed in conservation, restoration and management practices. Amidst today's human-dominated world, evolutionary thinking is crucial in conservation and management (see Ashley et al. 2003 for discussion).

Human predation as an evolutionary force

One of the most notable human impacts on natural populations of plants and animals is related to predation force. Predation is a strong selection force that causes evolutionary change in numerous traits of affected species at the population level, i.e., local adaptation (Seeley 1986; Lima and Dill 1990; reviewed in Ducey and Brodie 1991; Fuiman and Magurran 1994; Kats and Dill 1998; Huntingford et al. 1994; Coss 1999; reviewed in Magurran 1999; Reznick and Ghalambor 2001; Stoks et al. 2003; Åbjörnsson et al. 2004; Bell et al. 2004). Rapid changes can take place especially when prey species are subjected to novel predation regimes (e.g., Cousyn et al. 2001; Losos et al. 2006). For example, transplantation of guppies (*Poecilia reticulate*) in the wild (Strauss 1990; Reznick et al. 1990; Reznick et al. 1997) revealed that fish in high predation environments rapidly evolved (i) smaller body size and reduced size and age at maturity, which are expected in populations experiencing high adult (larger individual) mortality (e.g., Endler 1995; Reznick and Bryga 1996) and (ii) traits associated with predator avoidance and antipredator behavior (Endler 1995), such as increased distance from potential predators (Magurran et al. 1992) and escape ability (O'Steen et al. 2002). Introduced species also create novel predation regimes and act as an evolutionary force for native species (Schlaepfer et al. 2005). Rapidly modified antipredator responses of native frogs in response to introduced bullfrogs (Kiesecker and Blaustein 1997) are an example.

Commercial harvesting by humans today has unprecedented predatory force and efficiency. Commercial fishing, as it has long been argued on both empirical and theoretical grounds (Rutter 1902; Borisov 1978; Ricker 1981; Nelson and Soulé 1985; Law and Grey 1989; Stokes et al. 1993; Hutchings 2000; Law 2000; Stokes and Law 2000; Ratner and Lande 2001), can lead to evolutionary change in exploited fish populations. Fishing gear is typically designed to remove large, usually older, individuals (Law 2000). Life history theory predicts that when mortality rates increase in one age class, then the optimal reproductive effort increases before that age (Michod 1979). High predation rates in larger and older individuals are expected to select for decreased age and size at maturity (Charlesworth 1980). As predicted, Olsen et al. (2004, 2005) demonstrated that exploited fish populations rapidly evolved to maturity at younger age or smaller size in response to predation pressure created by commercial fishing.

Unlike fishing, terrestrial systems have received little attention until recently. Among the earliest, Duvall et al. (1996) found that rattlesnakes were extremely phlegmatic in areas where human-rattlesnake confrontations were frequent. He speculated that in the past, snakes that had made their presence known to humans by rattling as they were encountered were killed, and, they disappeared from the population. Fincher and Duvall (1998 for abstract; Fincher, uncompleted Master's thesis) provided support for that speculation by demonstrating reduced body size and rattling in rattlesnake populations hunted intensively for rattlesnake roundups versus unhunted populations. Recent reviews by Harris et al. (2002) and Festa-Bianchet (2003) have called attention to the genetic consequences of selective hunting on wild ungulates. The only compelling evidence of rapid evolution mediated by human hunting comes from the recently published data on a long-term study of the effect of trophy hunting on a population of bighorn sheep in Canada. Coltman et al. (2003) demonstrated that trophy hunting—targeting rams with large horns—has depleted the genes that confer rapid early body and horn growth, and, thus, body weight and horn size have declined significantly over 30 years.

Occurrence of rapid evolution in exploited species has important implications for persistence, conservation and management of afflicted species. On the one hand, rapid changes may enable affected populations to persist in the face of human exploitation pressure. On the other hand, because many traits covary with each other (Endler 1995), a change in one trait, presumably adaptive to human predation, can lead to "undesirable" changes in other traits that lower vital rates of the population (Hutchings 2005). Harvesting targeted at large individuals often results in evolution of earlier age and/or smaller size at maturation. Such changes have been hypothesized as the reasons why harvested fish populations have failed to recover following careful management that aims to rebuild affected stocks (Barot et al. 2004), even after a decade-long moratorium on harvest (Olsen et al. 2004). Walsh et al. (2006) also suggest that genetically based changes reduce the capacity for population recovery because harvesting of larger individuals can cause changes in numerous other traits, including (for fish species at least) fecundity, egg volume, larval size at hatching, larval viability, larval growth rates, food consumption rate and conversion efficiency, vertebral number, and willingness to forage.

CHAPTER II

A NATURAL EXPERIMENT

Objectives and Associated Hypotheses

Like some snake species of the world (Lillywhite 1991; Dodd 1987; Klauber 1972; Greene 1997; Schlaepfer et al. 2005), the mamushi in Japan have not only been hunted for individual and/or commercial uses (Goris, cited in Gloyd and Conant 1990), but also been killed indiscriminately by both individuals and organizations in large numbers. For example, in Utochaya, located in central Honshu of Japan, commercial harvesting of mamushi began since in the 1910s and, in a good year, more than 80,000 snakes were exported to medicine stores in Osaka (Shiki Elementary School 1979; current harvesting status is not reported). On Teuri Island, a small island (12-km perimeter) just offshore of Hokkaido, hunters employed by the local government have hunted mamushi for many years to keep the island “safe” for tourists. A second-generation hunter informed me that his father had hunted 60 mamushi in a good day, but in recent years, he can kill only around 100 a year. Given such hunting pressure, as in the cases of commercial fishing and trophy hunting, mamushi may be undergoing evolutionary change in some key fitness-related traits.

My study has taken advantage of the existence of several local populations of mamushi in Hokkaido that have been experiencing regular hunting (‘compromised’) and little or no hunting (‘uncompromised’). It can be assumed as a ‘natural experiment’ where uncompromised populations serve as a ‘before selection’ condition and compromised populations as an ‘after selection’ condition. This setting provided me with an opportunity to explore how fundamental ecological and evolutionary processes work, while simultaneously obtaining basic ecological, behavioral, and evolutionary data important for conservation and management of this species.

Objective 1. Investigate the effects of mamushi hunting on key morphological, behavioral, life history, and reproductive traits

Predation pressure is generally selective with respect to size or age, and can have important consequences for prey populations. High adult mortality often drives afflicted populations to exhibit smaller body size, as documented in both non-human (e.g., piscivorous fish predation on guppies, Endler 1995) and human (e.g., commercial fishing, Stergiou 2002) predatory environments. Also, life history theory predicts that if mortality increases after certain sizes, individuals that increase reproductive effort before the afflicted sizes will become prevalent in a population (reviewed in Stearns 1992).

Anecdotal evidence suggests that frequent hunting and killing of mamushi have driven mamushi populations to exhibit smaller body size (Goris, personal communication; see Chapter I). Accordingly, I predicted that (i) larger mamushi would be killed by humans in greater numbers than smaller counterparts, and, consequently, (ii) compromised populations would exhibit a truncated size distribution that lacks larger individuals, and, therefore, mean body size of compromised populations would be smaller than that of uncompromised populations, and, as a result, (iii) reproductive effort (measured as litter size) would be higher for smaller individuals in compromised versus uncompromised populations.

The most effective antipredator tactic always is not to be detected in the first place (Edmunds 1974; Duvall et al. 1985; Goode and Duvall 1989). To avoid detection, snakes in high risk environments may do things such as using microhabitats that make them less noticeable and/or moving around less, as reported frequently in predator-prey systems (Lima and Dill 1990; Abramsky et al. 1996; Kiesecker and Blaustein 1997). I hypothesized that mamushi hunting has caused compromised populations to exhibit a range of behavior that buffers against detection by humans. I predicted that (i) individuals of compromised populations would exhibit greater occurrence in densely vegetated or covered microhabitat versus the more open or only sparsely vegetated, (ii) movements would be reduced in compromised versus uncompromised populations, and (iii) hiding time would be greater for snakes belonging to compromised than uncompromised populations.

Like many other snake species, such as rattlesnakes (Klauber 1972; Duvall et al. 1985), the first thing most mamushi do is to rely on procrypsis, remaining immobile and silent, to avoid detection (my study). If procrypsis fails (in the snakes' perception), mamushi in most cases attempt to escape by locomotion, and occasionally they employ threatening displays, such as vibrating tails, flattening body, striking, but rarely attempt to bite unless touched. However, unlike against non-human predators, threatening displays or biting attempts simply do not work against human hunters equipped with boots and snake-catching equipment. I hypothesized that hunting has caused mamushi to modify antipredator tactics: when and how to escape once procrypsis fails. I predicted that (i) individuals that allow closer human approach and those that stand up to humans by threatening displays or biting attempts, instead of fleeing, would be taken more frequently by human hunters, (ii) individuals that flee at a greater distance from humans would be more prevalent in compromised versus uncompromised populations, and (iii) frequency of threat display and biting attempts would be reduced in compromised versus uncompromised populations.

The ability to reduce a behavioral response with repeated exposure to stimuli that are not followed by biological consequence for the organism, the process termed as habituation (Thorpe 1963), is ubiquitous among animals (reviewed by Harris 1943; Thorpe 1963). Learning not to respond to non-predatory stimuli, such as simply bypassing humans in uncompromised sites, would allow animals to conserve time and energy, and to continue other important activities. Conversely, habituating to predatory stimuli, such as motivated by mamushi hunters in compromised sites, would be fatal. I hypothesized that hunting has affected the way mamushi snakes process experiences. In fish, studies have shown that individuals in low-predation sites habituate, but those in high-predation sites do not or do so only slowly (Huntingford and Coulter 1989). I predicted that mamushi from compromised sites would not habituate to repeated human approaches whereas those from uncompromised sites would.

However, the use of alternative behavioral tactics will come at some cost in the form of time and energetic loss, and disruption of other important activities such as thermoregulation and feeding. I predicted that individuals of compromised populations would (i) be in poor condition (i.e., thinner), and (ii) delay the timing of parturition due to interrupted thermoregulation and, resultant slowed embryogenesis.

Objective 2. Examine whether differences in traits between compromised and uncompromised populations are the result of selection acting to produce genetically based changes.

Are the changes detected in compromised populations the result of cumulative genetic changes (evolution) mediated by phenotypic selection (i.e., the within-generation change in the trait distribution among cohorts, independent of genetic basis; Endler 1986) and/or some proximate effects such as the immediate result of removing larger individuals from populations or learning to avoid humans? I hypothesized that mamushi hunting has acted as phenotypic selection in body size and behavioral traits. For phenotypic selection to occur, affected traits must have individual variation and consistent relationship with fitness (Endler 1986). Accordingly, I predicted that (i) significant variance in a trait was accounted for by differences between individuals versus variation within an individual, (ii) individuals would express consistency in states of the trait, and (iii) hunting mortality was not random with respect to the state of the trait.

I also hypothesized that the changes in trait states in compromised versus uncompromised populations would be the result of response to selection imposed by mamushi hunting. For a trait to respond to selection, the trait must have a heritable component (Endler 1986). Accordingly, I predicted that (i) differences observed between adults of compromised and uncompromised populations would also be evident in naïve, experience-free offspring, and (ii) littermates would resemble each other compared to members from other litters.

Objective 3. Investigate the extent to which suites of traits differ between male and female mamushi from compromised versus uncompromised populations.

Why would hunting pressure be expected to affect males and females differently? Males and females of many snake species differ in many important ways. In general, females increase reproductive success by foraging, feeding and thermoregulating as effectively as possible whereas males realize increased reproductive success with numerous matings (Duvall et al. 1993). Males and females also exhibit evolutionarily established physiological (e.g., pregnancy, hormonal) differences. These sex differences can affect their day-to-day activities, movement patterns, and activity levels (e.g., Duvall et al. 1993; Graves and Duvall 1995). For example, females may be constrained by the need for basking so as to accomplish normal embryogenesis such that their antipredator tactics may be limited and different from males. Additionally, sex differences in activity and movement may expose the respective sexes to different temporal and spatial patterns of variation in human predation regimes.

Methods

Study area

My study was conducted in Hokkaido, the northernmost main island of Japan (Figure 2). Due to potential risks of attracting commercial harvesting, the exact location of the study area is not published here, and the names of the sampled sites are given as informal abbreviated names. Much of the study area is covered by natural and plantation forests, but interrupted by rivers and roads, and by interspersed agricultural fields, quarries, abandoned coal mines, hamlets, and abandoned hamlets. Elevation of the study area varied from coastal to 200 m.

The Ainu subsisted with hunting, fishing, and gathering in this region prior to Japanese invasion. Traditional use of mamushi is not known among the Ainu. The Japanese arrived in this area by 1200 and subsequently invaded and destroyed the traditional Ainu way of life. Information about how people treated (e.g., killing, harvesting) mamushi in the earlier times could not be obtained. According to information obtained from local elders, non-commercial harvesting of wild mamushi was already widespread in the early 1900s. Hunting varies from opportunistic to active searching by local people or seasonal hunters from adjacent regions.

Human predation pressure on mamushi varies spatially throughout my study sites (Figure 4). In some areas, usually close to human habitations, people have been frequently killing or collecting mamushi mainly at or around commonly known basking spots (see Chapter I). I considered mamushi populations around these areas to be “compromised” (Figure 5) only if they have experienced such impact during the last 60 years (ca. $\leq$ 20 generations). This time span was selected because it seems ample for evolutionary change based largely on other exploited species (fish and sheep) and on potential rapid evolution in morphological traits of Australian snakes (Phillips and Shine 2004). Other basking spots have no evidence, or apparent history of substantial hunting or have experienced hunting only during the last 6 years (ca. $\leq$ 2 generations). I considered populations around these areas to be “uncompromised” (Figure 5). In both site types, non-hunting peoples (e.g., those who are visiting for fishing and gathering edible wild plants and mushrooms) visit there occasionally (probably several times a day or week). I designated each area as compromised or uncompromised after data were collected based on information from local people and hunters, and site histories.

Given the small size of some of my compromised populations (Figure 4), the impact of hunting seems quite large, even considering that actual population sizes must be much larger (partly because males and immature snakes were underrepresented in all my samples). At the TD site (n = 39 mamushi), one of the compromised sites, a hunter with whom I accompanied to the site spotted 18 mamushi within 15 minutes (he did not capture them at that time). I observed four other hunters during my study period. At the CS site (n = 14), another compromised site, indiscriminate killing appeared to be the major cause of mamushi mortality. Based on information from 8 local people at this site, the number of mamushi killed was 1–4 snakes per year. If all 74 households are assumed to kill that number of mamushi, mamushi killed at the entire CS site would be 8–296 snakes per year. However, because not every household is likely to kill mamushi, the estimate is likely to be inflated. In the other two compromised sites (n = 4 and 31), local farmers and foresters appeared to be the major cause of mamushi mortality. A forester informed me that she killed about 30 mamushi in 1997.

General study methods

In each of four seasons (June 16-July 30, 1999; July 2-August 4, 2000; August 13-October 12, 2001; May 28-Oct 23, 2002), I captured mamushi by hand (with tongs), recorded certain variables, and then released and observed them. The recorded variables snout-vent length (SVL) and tail length (TL) in cm, body temperature (T_b) in ºC, body mass ([BM] in g, sex by probing for hemipenes, and female reproductive condition by ventral palpation. Individuals were marked by injection of PIT-tags, ventral scale clipping, and painting small numbers on the dorsum with nail polish). X-ray pictures were taken at the Kawamata Animal Hospital for a limited number of females to "calibrate" my palpation technique. Data were also taken opportunistically on such aspects as feeding and shedding.

Twenty snakes (8 males, 9 nonpregnant females, and 3 pregnant females) were equipped with individually unique, T_b-sensitive radiotelemetry tags (Holohil Systems and AVM). Prior to implantation, transmitters were calibrated at 3°C intervals over the range 5-40°C in a constant-temperature water bath. Five individuals received external attachment at the dorsal, caudal region using tape. This method allowed tracking for only 2–4 weeks. Nine individuals received coelomic implantation. Snakes were anesthetized with Halothane inhalant during surgical procedures. Surgically implanted individuals were kept at about 20ºC for several days to allow recuperation from surgery. Snakes were then released where they were captured. When possible, radiotagged individuals were located daily. Due to the almost immediate failure in the field of several radiotags and due to unforeseen incidents (e.g., hospitalizations due to snake-bites), the amount of telemetry data varied between snakes and duration of data collection was short.

Each time a radiotagged snake was located and/or relocated, I recorded the date, time of day, air (T_a) and microhabitat (T_m) temperatures, the pulse interval of the telemetry signal (to later convert to T_b), the snake's general behavior (e.g., moving or stationary), general habitat and microhabitat features, and the location. Standardized photographs of a 80-cm diameter circle centered on the snake's head location were taken (usually the next day or after snakes moved away from the location to minimize disturbance to snakes; locations were marked by placing flagging) to determine surface cover percentages for dense vegetation that potentially acts as concealment for snakes. Cover percentages were determined by overlaying a transparency with grids over the pictures. Locations of each snake fix were recorded on a map and by a Global Positioning System (GPS) receiver.

Non-radiotagged snakes were similarly sampled. To minimize disturbance to non-radiotagged snakes, identification of relocated snakes was accomplished by scanning PIT-tag ID with the hand-held AVID Microchip Reader affixed to a 76-cm pole (see Sasaki 2005 for the photographic figure). This allowed identification of PIT-tagged snakes from >1.5 m away. To account for potential differences in microhabitat characteristics between compromised and uncompromised sites, measurements and photographs were also taken at "random" locations at and near basking spots where most snakes were captured.

Characteristics of mamushi hunting

At the HMSC site (not assigned to either compromised or uncompromised because of insufficient information), I conducted behavioral trials (see below) for as many snakes as possible (n = 42), and captured, marked, and recorded a suite of variables on each individual. Then, I released them and their survival was tracked. Every time the only hunter at this site killed a mamushi, he left the killed snakes on the ground so that I could come to identify which individuals were killed.

Antipredator behavior

Non-radiotagged, free-ranging snakes were approached and ‘threatened’ in a standardized manner. When I spotted snakes that were not yet “responding” (e.g., no apparent sign of fleeing or defensive actions), I approached individuals at a slow and regular walking pace (1 step/5 sec). As a function of the snakes’ responses (fleeing, tail vibration, body flattening, striking, or biting attempt) to this approach, individuals were “attacked” (i.e., lightly touched) successively twice at 1-s interval. Individuals that remained motionless until my foot was within 5 cm of it were not included in the behavioral trial and were simply captured to obtain non-behavioral data. These standardized approaches and attacks comprised one trial. In each trial, a maximum of 3 behavioral units thus could occur, e.g., flee → flee → “threatening defensive behavior” (TDB). I included tail vibration, body flattening, striking, and biting attempts as TDB. I considered all of these actions as TDB because any of such actions would increase the likelihood of being captured or killed by humans. I ranked the 3-unit behavioral sequences in order of increasing defensiveness, with rank 1 being the least defensive and 8 being the most defensive: 1 = flee → flee → flee, 2 = flee → flee → TDB, 3 = flee → TDB→ flee, 4 = flee → TDB → TDB, 5 = TDB → flee → flee, 6 = TDB → flee → TDB, 7 = TDB → TDB → flee, and 8 = TDB → TDB → TDB. For each trial, I also measured flight threshold radius (FTR) as the distance between the experimenter and the snake when the snake initiated escape.

I tested subsamples of individuals multiple times in the same manner described above to assess individual variation and consistency (see Analysis) in the behavioral traits. The trial intervals varied from daily to a few months in a given growing season.

Offspring born to wild-caught females (see the section below), which were relocated after their release as neonates (see below), were tested in the same manner as adult snakes. Multiple measurements for offspring could not be obtained because I failed to relocate them more than once after their release. Microhabitat data (i.e., photographs) for offspring also could not be obtained due to time constraints and camera damage caused by confrontation with a bear.

Eleven snakes were tested for possible habituation to human disturbance. These snakes were approached in the same manner, but were neither attacked nor recaptured (other than the time when I first captured them). They were tested daily over 8 days to examine behavioral responses to repeated human approaches.

For a limited number ($n = 5$ for each site type) of the relocated snakes, I measured the time taken (latency) for snakes to emerge from refuge after their escape from my approach (hereafter, emergence latency). I waited for a maximum of 90 minutes. I sampled these individuals 2–3 times.

Reproduction and offspring

I kept 27 wild-caught pregnant females in individual cages (40 × 25 cm plastic cages with mesh tops) until parturition (fifty females were kept originally, but I had to release about half of them because I was hospitalized a few times due to snake bites). Water and shelter were provided all the time. Immediately after parturition, I weighed the females and sexed, measured and weighed neonates. For litter size and mass, I included stillborn and deformed embryos with fully-developed size and morphology, but not expelled unfertilized eggs or yolk masses. Additional data on litter size were obtained from one pregnant female that ws found killed by traffic (data on body size of the neonates from this female could not be obtained due to poor condition for taking measurements and weight).

All offspring were marked by nail polish for short-term identification after they completed the first shedding of their skin, which mostly occurred within a few minutes of birth. Within a few hours of birth, mothers and their offspring were released at the location where the mothers were captured.

Analysis

Data from all years were pooled for analyses because sample size of the first two years of the study and of males in all years was small and because separate multiple regression analyses of adult SVL, BC, FTR, defensiveness, microhabitat cover, and T_a (dependent variables) on site type, sex/reproductive condition, and year (independent variables) showed that year effect was not significant (each with $P > 0.05$). Also, because both site types were sampled every year, pooling years should not bias comparisons between site types. All data were tested for normality and homoscedasticity before analyses (except for logistic regression analysis). For data on neonatal SVL, adult SVL, adult FTR, and microhabitat cover, multiple attempts to transform the data to make them normal and homoschedastic failed; therefore, I used rank transformation (Zar 1996). Data on parturition date also did not meet the parametric assumptions, so I used a Mann-Whitney U-test to compare compromised and uncompromised populations.

To examine whether mamushi hunting is selective with respect to trait values in SVL, FTR, and defensiveness, I tested the probabilities of mortality as a function of these variables for the HMSC site using logistic regression (Hosmer and Lemeshow 2000).

Body condition (BC) can be used to assess individual physical condition or nutritional status (Bonnet and Naulleau 1994; reviewed in Green 2001). It was estimated as standardized residual score derived from a general linear regression of log10-transformed BM against log10-transformed SVL (Secor and Nagy 2003). Theoretically, this measure reflects the extent to which the mass of a snake deviates from that expected for its body length (SVL) within the entire population of the study area. However, caution must be applied to the interpretation of results using this estimate because body mass in my study was obtained from individuals with various times since last feeding and some in various stages of pregnancy.

To assess how noticeable or visible the snakes were, percentage of "cover" for a given snake within an 80-cm diameter circle (see above) was recorded. By cover, I mean any structural cover that potentially makes snakes less noticeable or visible to humans, such as dense vegetation and piled fallen branches and plant debris.

To determine the effects of site type (compromised, uncompromised) and sex/reproductive condition (males, pregnant and nonpregnant females) on a suite of dependent variables (body size, FTR, defensiveness, microhabitat cover, and movement), this "natural" experimental study takes the form of a 2 (site type) ×3 (sex/reproductive state) between-subjects factorial design. Accordingly, factorial analysis of variance (ANOVA) was used to examine the main effect and interaction of these factors.

To test the prediction that snakes from uncompromised populations would habituate whereas those from compromised populations would sensitize, I used repeated-measures ANOVA of FTR. General response decrement was considered as habituation, the waning of a behavioral response to a repeated stimulus (approaching human) that tends to be non-threatening (c.f. Thorpe 1963). “An augmentation of a response to a stimulus” (Teyler 1984) was considered as sensitization. To test whether the pattern of differences between mean FTR for the two site types changed over time, I examining the time (day) by site type interaction in a repeated-measures ANOVA with site type (uncompromised or compromised) as the between-subjects factors and FTR as the dependent variable. I used data obtained from 11 relocated individuals that I tested daily over 8 consecutive days: day 1 represented the first trial when a snake was first encountered and tested (it was then captured and processed, and subsequently released within a few minutes); day 2 was the first trial after the release trial; and day 8 was the final trial.

Repeatability (*t*) is the measurement of consistent individual differences and expressed as the proportion of total phenotypic variance of a trait that is due to differences between (rather than within) individuals, both genetic and environmental: $t = (V_G + V_{Eg})/V_P$, where V_G is genotypic variance, V_{Eg} is general environmental variance, and V_P is phenotypic variance (Falconer 1981; Lessells and Boag 1987; Falconer and Mackay 1996). I estimated repeatability of a given trait (FTR, emergence latency, defensiveness, and microhabitat cover) as the intraclass correlation between repeated measures of that trait on the same individuals. Intraclass correlation is the ratio of among-individual ($\sigma^2_{\text{among individual}}$) to the total ($\sigma^2_{\text{among individual}} + \sigma^2_{\text{within-individual}}$) variance, and these variance components were calculated from the mean squares ($MS_{\text{among-individual}}$, MS_{error}) in one-way ANOVA with individual as the main effect (Lessells and Boag 1987). I estimated repeatabilities separately for each site type.

I assessed individual consistency in FTR to repeated human approaches using the data obtained from 4 individuals for which multiple tests were conducted daily over 8 consecutive days across years (2001 and 2002), separated by a 6-month hibernation period. I performed separate linear regression analyses for each individual's FTR over trials (i.e., days) for each year (Bowers 1992). The intercept provides an estimate of initial responsiveness, and the slope corresponds to the rate of response change over the trials (Bowers 1992). All regression analyses were performed on the FTR measurements from trial 2 to trial 10. Trial 1 (conducted when a snake was first captured) was excluded because all animals showed an initial increase (sensitization) between trial 1 and trial 2 (Bowers 1992). Then, individual consistency was assessed by testing correlations of intercepts and slopes between 2001 and 2002.

Body size and many behavioral traits are quantitative (continuous) and are affected by many genes. It is not simply genotypic properties, but instead, a particular genetic property known as additive genetic value of parents that encodes the transmission of traits to offspring that produce resemblance of their offspring. Thus, a parent's phenotypic value is composed of an additive genetic value that is transmitted to offspring and a part not transmitted to offspring, which is composed of nonadditive genetic effects (due to dominance and epistasis) as well as purely environmental effects (Arnold 1994). The component of phenotypic variance due to additive effects of genes is the additive genetic variance (V_A), and the proportion of the phenotypic variance due to additive genetic factors is termed (narrow-sense) heritability (h_N^2), which determines the degree of heritable resemblance between parents and offspring and determines the response to selection by quantitative characters (Brodie and Garland 1993). Other components of phenotypic variance include dominance (V_D), epistatic or interaction (V_I), environmental (V_E), and common family environmental (V_{Ec}) variance.

The most common means of partitioning phenotypic variance (e.g., in snakes, Brodie and Garland 1993; Arnold 1994; King et al. 2004) is to compare the resemblance among siblings by analyzing patterns of variation within and between families. Such a "full-sib" (assuming single paternity) analysis provides what Brodie and Garland (1993) refer to as 'full-sib' heritability (h^2_{FS}). To estimate h^2_{FS} for a given trait, I first tested family differences using ANOVA with family as a factor for a given trait. Then, I computed intraclass correlation of the trait in the same manner as repeatability estimates described above. Assuming full-sib relationships within a litter and because full-sibs on average share half of the V_A and a quarter of the V_D, the intraclass correlation must be multiplied by a factor of 2 to compute h^2_{FS} (Brodie and Garland 1993). The h^2_{FS} is then: (V_A + ½ V_D + ½V_I + 2V_{Ec})/V_P (Brodie and Garland 1993). Interpretation of h^2_{FS}, thus, should recognize that a full-sib comparison does not allow isolation of pure V_A, and, therefore, the estimates of additive genetic parameters will be potentially inflated by effects of dominance, epistasis, and common family environmental factors, including maternal effects (Brodie and Garland 1993; Arnold 1994; Garland 1994). Maternal effects have recently been shown to be more important than were previously thought (King et al. 2002).

To partly remove the influence of maternal effects, as suggested and used by others (e.g., Garland 1988; Brodie and Garland 1993; Arnold 1994; Garland 1994), I conducted separate stepwise multiple regression analyses of neonatal SVL, neonatal FTR, and neonatal defensiveness on a series of potentially significant independent variables:

maternal SVL and BC (because much of neonates' size is probably due to variation in age and/or past nutritional history of the mother), offspring SVL (not used when used as dependent variable), offspring BC, litter size, and birth date. Standardized residuals from the regressions (after examining normality and homoschedasticity) were used to estimate h^2_{FS}. However, it should be recognized that several problems still persist. For example, a common uterine environment (e.g., nutritional, hormonal, and thermal), which was not measured in my study, cannot be accounted for in the present analyses. All these analyses were conducted for each site type separately because heritabilities may differ under differing predation environments (Relyea 2005).

I calculated two movement parameters: total distance moved in September and the number of movements (i.e., displacement > 2 m) in September. As mentioned above, because I could not obtain thorough movement data, a comparison between site types was performed for data obtained only during September, the month with the most data. Even so, tracking periods and frequencies still varied between individuals. Although I was unable to collect data on every major movement, my data should be unbiased for comparisons made between site types because both kinds of movement data were obtained similarly for both site types. Also, I pooled all years and sexes to increase sample size ($n_{\text{uncompromised}} = 7$, $n_{\text{compromised}} = 2$). Pregnant females were not analyzed because they did not "move" (based on the criterion of > 2-m displacement). Because data on the number of moves did not meet the parametric assumptions, I used a Mann-Whitney U-test to compare site types.

All statistical analyses, except otherwise noted, were performed using SPSS 14.0 for Windows (SPSS Inc).

Results

Body size

Characteristics of mamushi hunting

Although preference for and intentional targeting of adult or larger individual mamushi appeared to be nonexistent, direct mortality caused by human hunters in the HMSC site was biased toward larger size, indicating that mamushi hunting is in fact size-selective. Logistic regression analysis revealed that the probability of mortality increased for larger (SVL) individuals ($\chi^2 = 8.75$, df = 1, $P = 0.003$; Figure 6).

Adult body size

Summary data are shown in Table 1. An expected truncated size distribution that lacks larger individuals was evident in compromised populations (Figure 7). Snout-vent length was affected by site type (main effect: $F_{1, 286} = 44.85$, $P < 0.001$) and sex/reproductive condition (main effect: $F_{2, 286} = 11.70$, $P < 0.001$), but not by an interaction between these two factors ($F_{2, 286} = 0.25$, $P = 0.780$) (Figure 8). Specifically, all mamushi (males, pregnant and nonpregnant females) were smaller in compromised versus uncompromised populations ($P \leq 0.001$ for each pairwise comparison). In uncompromised populations, pregnant females were larger than males and nonpregnant females ($P < 0.001$ for each pairwise comparison), and the latter two groups did not differ from each other ($P = 1.000$). In compromised populations, pregnant females were larger than males ($P = 0.025$), but not than nonpregnant females ($P = 0.181$); males and nonpregnant females were similar in size ($P = 0.721$).

No site type effect was detected in adult body condition (BC: $F_{2, 280} = 1.01$, $P = 0.316$). Sex/reproductive condition effect was significant ($F_{2, 280} = 65.64$, $P < 0.001$). The interaction between the two factors was not significant ($F_{2, 280} = 0.39$, $P = 0.680$). Pairwise comparison at each site type revealed that pregnant females were fatter than nonpregnant females, and the latter were fatter than males, at both site types ($P \leq 0.002$ for each comparison).

Neonate body size

Consistent with adults, an expected truncated size distribution that lacks larger individuals was evident in compromised populations (Figure 9). Neonatal SVL was affected by site type (main effect: $F_{1, 178} = 125.9$, $P < 0.001$), but not by sex (main effect: $F_{1, 178} = 1.27$, $P = 0.262$) nor an interaction between these two factors ($F_{1, 178} = 1.36$, $P = 0.245$) (Figure 10). Specifically, neonates from compromised populations exhibited reduced body size than those from uncompromised populations. This trend persisted after statistically controlling for the potential effects of maternal SVL and BC, and birth date (ANCOVA: $F_{1, 175} = 49.55$, $P < 0.001$ for site type; $F_{1, 175} = 0.81$, $P = 0.369$ for sex; $F_{1, 175} = 0.52$, $P = 0.474$ for interaction by the two factors). Figure 11 shows neonatal SVL in relation to maternal SVL.

Neither site types ($F_{1, 178} = 0.59$, $P = 0.444$), sex ($F_{1, 178} = 0.28$, $P = 0.596$), nor interaction of these factors ($F_{1, 178} = 1.35$, $P = 0.248$) was significant in neonatal BC. These results were unchanged even after statistically controlling for the effects of maternal SVL and BC, and birth date (site type: $F_{1, 175} = 0.99$, $P =0.322$; sex: $F_{1, 175} = 0.13$, $P = 0.721$; interaction: $F_{1, 175} = 0.84$, $P = 0.360$).

Full-sib heritability estimates for SVL at 1-day of age

The number of families used in analyses was 11(with mean number of offspring per mother ranging from 4 to 9) and 15 (with mean number of offspring per mother ranging from 3 to 11) for compromised and uncompromised populations, respectively. Stepwise multiple regression analyses revealed that parturition date was significant predictor of neonatal SVL in compromised populations ($F_{1, 27} = 16.06$, $P < 0.001$), and maternal SVL in uncompromised populations ($F_{1, 100} = 30.15$, $P < 0.001$). Parameter estimates below were generated from analysis of the resulting residuals. ANOVA indicated that family membership had significant effects on SVL in both compromised ($F_{10, 63} = 3.11$, $P = 0.003$) and uncompromised ($F_{14, 87} = 4.92$, $P < 0.001$) populations. Full-sib heritabilities of SVL at birth were estimated to be 0.48 and 0.74 for compromised and uncompromised populations, respectively.

Flight threshold radius (FTR)

Characteristics of mamushi hunting

The probability of mortality increased with decreasing FTR (logistic regression: $\chi^2 = 13.39$, df = 1, $P < 0.001$; Figure 12), indicating that individuals that allowed closer approach by human hunters were killed more than those that kept a greater distance. In my study, mamushi in compromised populations were very hard to capture because they often fled before I could reach them. I failed to capture 44% of the snakes (n = 88 of 198 attempts) in compromised sites, whereas only 13% of the snakes (n = 31 out of 245) in uncompromised sites. This difference was statistically significant ($\chi^2 = 56.3$, df = 1, $P <$

0.001).

Adult FTR

Summary data again can be found in Table 1. FTR in adults was affected not only by site type (main effect: $F_{1, 266} = 126.95$, $P < 0.001$) and sex/reproductive condition (main effect: $F_{2, 266} = 15.74$, $P < 0.001$), but also by a significant interaction between these two factors ($F_{2, 266} = 3.74$, $P = 0.025$; Figure 13). Specifically, all snakes, regardless of sex and female reproductive condition, fled at a greater distance from the investigator in compromised versus uncompromised sites ($P < 0.001$ for each pairwise comparison). In uncompromised populations, pregnant females allowed closer approach than nonpregnant females, which was followed by males ($P \leq 0.001$ for each pairwise comparison). To the contrary, in compromised populations, all snakes fled at a similar distance ($P > 0.100$).

Neonate FTR

Offspring differed between site types in FTR (main effect: $F_{1, 40} = 64.20$, $P < 0.001$; Figure 14). Pairwise comparisons revealed that all offspring (males and females) from compromised sites fled at a greater distance from the predator than those from uncompromised sites ($P < 0.001$ for each sex). Neither sex (main effect: $F_{1, 40} = 1.48$, $P = 0.230$) nor interaction effects was significant ($F_{1, 40} = 0.32$, $P = 0.574$).

Repeatability estimates for adult FTR

Adults in uncompromised ($t = 0.73$, ANOVA: $F_{27,\,133} = 13.49$, $P < 0.001$) and compromised ($t = 0.41$, ANOVA: $F_{6,\,44} = 5.97$, $P < 0.001$) sites showed consistent FTR across trials (days).

Heritability estimates for FTR at 1-day of age

The number of families used in the full-sib heritability estimate was 9 and 8 (with mean number of offspring per mother ranged from 2 to 3) for compromised and uncompromised populations, respectively. Stepwise multiple regression analyses revealed that significant predictors of offspring FTR were mother's BC in both compromised ($F_{1,\,22} = 6.89$, $P = 0.015$) and uncompromised ($F_{1,\,18} = 13.26$, $P = 0.002$) populations. Thus, residuals obtained from multiple regressions with these independent variables were used in the following analyses. ANOVA indicated that family membership had significant effects on SVL in both compromised ($F_{9,\,14} = 2.66$, $P = 0.0493$) and uncompromised ($F_{7,\,12} = 2.96$, $P = 0.0475$) populations. Full-sib heritabilities of SVL at birth were estimated to be 0.88 and 0.82 for uncompromised and compromised populations, respectively.

Defensiveness

Characteristics of hunting

As expected, more defensive individuals (those that tended to stand up to human hunters via threatening displays and/or biting attempts) were killed in greater numbers than those that fled (logistic regression: $\chi^2 = 9.97$, df = 1, $P = 0.002$; Figure 15).

Adult defensiveness

See again summary data shown in Table 1. Threatening defense in adults was affected by site type (main effect: $F_{1, 265} = 28.37$, $P < 0.001$) and sex/reproductive condition (main effect: $F_{2, 265} = 7.36$, $P = 0.001$) (Figure 16). The interaction between these two factors was not significant ($F_{2, 265} = 2.38$, $P = 0.095$). Specifically, male ($P < 0.001$) and nonpregnant females ($P < 0.001$) in compromised sites tended to flee more than those in uncompromised sites. No site type difference was evident for pregnant females ($P = 0.136$). In uncompromised sites, males and nonpregnant females tended to turn to threatening defense more than pregnant females ($P < 0.001$ for each pairwise comparison), and the former two groups did not differ from each other ($P = 1.000$). To the contrary, no sex or reproductive condition differences were evident in compromised populations ($P > 0.500$).

Neonate defensiveness

Threatening defense in neonates was affected by site type (main effect: $F_{1, 40} = 29.42$, $P = 0.006$), but neither by sex (main effect: $F_{1, 40} = 0.06$, $P = 0.805$) nor interaction between these two factors ($F_{1, 40} = 0.01$, $P = 0.916$) (Figure 17). Both female ($F_{1, 40} = 18.43$, $P < 0.001$) and male ($F_{1, 40} = 12.08$, $P = 0.001$) neonates from compromised sites were less defensive than those from uncompromised sites.

Repeatability estimates for defensiveness in adult

Adults in uncompromised ($t = 0.89$, ANOVA: n = 23, $F_{22, 105} = 41.62$, $P < 0.001$) and compromised ($t = 0.59$, ANOVA: n = 4, $F_{3, 27} = 11.89$, $P < 0.001$) sites showed consistent FTR across trials (days).

Heritability estimates for defensiveness

The number of families used in the full-sib heritability estimate was 8 and 9 (with mean number of offspring per mother ranging from 2 to 3) for uncompromised and compromised populations, respectively. Stepwise multiple regression analyses revealed that significant predictors of neonate defensiveness were maternal SVL and BC in uncompromised ($F_{2, 17} = 145.46$, $P < 0.001$), and neonatal SVL in compromised ($F_{1, 21} = 46.79$, $P < 0.001$) populations. The residuals that were obtained from multiple regressions with these independent variables were used in the following analyses. ANOVA indicated that family had significant effects on defensiveness in compromised populations ($F_{9, 14} = 2.78$, $P = 0.0422$), and h^2_{FS} was estimated to be 0.85 for neonate defensiveness. Significant family effects were also evident in uncompromised populations ($F_{7, 12} = 2.97$, $P = 0.0472$), and h^2_{FS} was estimated to be 0.88.

Response to repeated exposure to an approaching human

Overall, mamushi in uncompromised populations exhibited habituation to repeated human approaches, whereas those in compromised populations exhibited sensitization (Figure 18). These patterns were confirmed by repeated-measures ANOVA. Significant interaction of day and site type ($F_{7, 63} = 20.79$, $P < 0.001$) indicates that FTR exhibited by snakes in the two site types changed over time in different ways. Pairwise comparisons revealed that snakes in both site types increased FTR between the first trial and the second trial ($P = 0.001$ for each comparison). Flight threshold radii exhibited by snakes in uncompromised populations declined to their original level ($P = 0.201$) whereas FTR of snakes in compromised populations remained high throughout ($P < 0.001$). The tests of between-subjects effects confirmed that snakes in compromised populations fled at a greater distance than those in uncompromised populations ($F_{1,9} = 17.88$, $P = 0.002$).

Individual consistency across years in adults

Individual adults showed consistent responsiveness and rate of change in FTR between 2001 and 2002 (separated by the 6-month period of hibernation) (Figure 19). Formally, correlations of regression coefficients between the years were positively correlated ($r_{intercept} = 0.988$, $n = 4$, $P = 0.012$; $r_{slope} = 0.998$, $n = 4$, $P = 0.002$).

Latency to emerge from refuge

Mamushi in compromised populations ($n = 5$, $\bar{x} \pm 1SE = 41 \pm 9$ min) took more time to emerge from a refuge than those in uncompromised ($n = 5$, $\bar{x} \pm 1SE = 7 \pm 1$ min) populations ($t = 3.81$, df = 8, $P = 0.005$; Figure 20).

Individual consistency

Adult individuals showed consistency in latency to emerge in both uncompromised ($t = 0.567$; ANOVA: $F_{4,9} = 4.75$, $P = 0.025$) and compromised ($t = 0.74$; ANOVA: $F_{4,9} = 8.78$, $P = 0.004$) populations. The intervals of the trials ranged from 2-6 days.

Microhabitat cover

Summary data again are shown in Table 1. Not only did site type (main effect: $F_{1, 269} = 25.33$, $P < 0.001$) and sex/reproductive condition (main effect: $F_{2, 269} = 25.72$, $P < 0.001$) affect the use of microhabitat cover, their interaction did so as well ($F_{2, 269} = 6.47$, $P = 0.002$; Figure 21). Specifically, males and nonpregnant females (each pairwise comparison, $P \leq 0.001$) were found among or near denser cover (mostly dense or tall vegetation) in compromised versus uncompromised habitats. In contrast, pregnant females were found in more open microhabitat regardless of site type (pairwise comparison, $P = 0.828$). Pregnant females were invariably found in more open microhabitat than either male or nonpregnant females regardless of site type ($P < 0.05$ for each pairwise comparison).

Difference in microhabitat association between site types was not simply the result of inherent differences in microhabitat cover available at each site type. No difference was detected in microhabitat cover at random locations between the site types ($t = 1.09$, df = 322, $P = 0.28$).

Repeatability estimate for microhabitat use

The use of microhabitat cover was consistent within adult individuals. It was evident in both uncompromised ($t = 0.67$, ANOVA: $F_{27, 133} = 10.17$, $P < 0.001$) and compromised ($t = 0.50$, ANOVA: $F_{6, 44} = 8.38$, $P < 0.001$) populations.

Movement and activity

Descriptive data are summarized in Table 3. Mean total distance moved during

September was smaller for compromised (n = 3, $\bar{x} \pm 1SE = 35 \pm 15$ m) versus uncompromised (n = 7, $\bar{x} \pm 1SE = 43 \pm 9$ m) populations, but the difference was not statistically significant ($t = 0.48$, df = 7, $P = 0.646$; Figure 22). However, this failure in rejecting the null hypothesis of no difference may be due to insufficient sample size. A retrospective power analysis (SamplePower 2.0, SPSS Inc.) indicated that this analysis had a low chance (power = 0.25) of producing a statistically significant result, given that the null hypothesis is false. In addition, three individuals from uncompromised populations were tracked for only half of the month and, therefore, movement parameters are likely underestimated. The number of moves was fewer for compromised (n = 3, $\bar{x} \pm 1SE = 1 \pm 0.0$) than uncompromised (n = 7, $\bar{x} \pm 1SE = 3 \pm 0.6$) populations, but not statistically so (Mann-Whitney U = 1.0, $P = 0.072$; Figure 23).

Reproduction

Parturition occurred later among females in compromised versus uncompromised populations (Mann-Whitney U = 29.0, $P = 0.003$; Figure 24).

All smaller females (< 52.7 cm, the body size at which the probability of mortality is 75%) of compromised populations (n = 5) produced greater than or equal to 6 offspring, whereas only 1 out of 4 smaller females of uncompromised populations produced greater than or equal to 6 offspring (Figure 25). A comparison of the number of offspring produced per litter by smaller females revealed that females of compromised populations gave birth to greater number of offspring than those of uncompromised populations ($t = 2.37$, df = 13, $P = 0.034$). In addition, smaller females of compromised sites produced smaller offspring given their number of offspring per litter and maternal

SVL (ANCOVA with litter size and maternal SVL as covariates: $F_{1, 9}$= 20.82, P = 0.001).

Thermal ecology

One-way ANOVA detected an overall difference in T_b among non-radiotagged males and pregnant and nonpregnant females ($F_{2, 238}$ = 5.00, P = 0.007) and pairwise comparisons showed that pregnant females had higher T_b than either nonpregnant females (P = 0.003) or males (P = 0.001), that were in turn, similar (P = 0.826). In addition, pregnant females more so than males and nonpregnant females maintained constant T_b (ANCOVA: sex/reproductive condition [males, pregnant and nonpregnant females] × T_a interaction; $F_{2, 238}$ = 3.66, P = 0.027; Figure 26). This trend was also evident in radiotagged snakes (Figure 27).

Discussion

My study reveals a clear association between human predation pressure (e.g., harvesting for medicinal use, indiscriminate killing) and a suite of fitness-related traits—morphology, behavior, reproduction, and life history—among mamushi populations in Hokkaido, Japan. The question arises as to whether my study design transcends a descriptive, correlational approach. My study was not a controlled experiment in the strictest sense. However, it is a natural experiment in which populations can be categorized into “manipulated” versus “controlled,” revealing differences in directions expected from behavioral ecology and life history theories. Moreover, mamushi hunting probably (i) constitutes the largest source of mortality and (ii) can alter evolutionarily established mortality schedules, from low to high adult mortality. Thus, it is likely that mamushi hunting, rather than other potential location-specific abiotic and biotic factors, is the chief underlying cause of any changes in traits of snakes of compromised populations. In this section, I first discuss the overall patterns of observed differences in a suite of traits between compromised and uncompromised populations. Next, I discuss each trait more closely, focusing on underlying mechanisms responsible for such differences.

Like many cases of commercial fishing and sport hunting, mamushi hunting was found to target adult individuals, especially those with larger body size. As expected from populations experiencing such a predation pressure, compromised mamushi populations exhibited a truncated size distribution that lacked larger individuals, and the mean body size was smaller than that of uncompromised sites. Such a size-biased mortality would lower the expected future reproduction, and consequently it should lead to increased reproductive effort at smaller sizes (e.g., Schaffer 1974; Law 1979; Charlesworth 1980; Wellborn 1994). In close agreement with such a life history prediction, in the comparison of life histories of mamushi from compromised and uncompromised sites, I found that smaller females from compromised sites produced more offspring and smaller ones per litter than their counterparts from compromised habitats. Smaller average size of pregnant females in compromised versus uncompromised populations also suggests increased reproductive effort at smaller sizes.

With respect to behavioral traits, the findings of my study agree with expectations of behavioral ecology. Because the most effective antipredator tactic is not to be detected in the first place (e.g., Edmunds 1974), animals in high predation-risk environments are expected to use microhabitat that makes them less noticeable, and/or they move around less (e.g., Lima and Dill 1990). My study found that individuals of compromised populations inhabited in densely vegetated or covered microhabitat versus that more open or only sparsely vegetated. Mamushi movement and activity also appeared to be reduced as reflected in reduced distance moved and reduced number of moves. This conclusion about movement and activity, however, is tempered by the lack of daily-based monitoring in my study. Nonetheless, the greater emergence latency from a refuge after escaping from a human (myself) observed among individuals of compromised populations suggests that activity is reduced in such populations, at least when humans are nearby.

Owing to their technological inventions, such as "snakebite-proof boots" and snake-catching equipment, human hunters are not intimidated by snakes' deimatic behavior, such as threatening displays or retaliatory biting attempts. The only way snakes can survive a confrontation with human hunters is to flee, instead of standing up to the threat. Accordingly, frequency of occurrence of deimatic behavior would be expected to be reduced in compromised populations because individuals that tend to stand up to humans would be extirpated from the populations. My study confirmed that individuals that allowed closer approach and those that defended against humans by deimatic behavior sustained higher hunter-caused mortality. As expected, individuals of compromised populations tended not to turn to deimatic behavior; instead, they tended to initiate flight at a greater distance from human hunters and to continue their efforts to flee. Such increased wariness and greater FTR are widespread phenomena among hunted populations of mammals, such as ungulates (e.g., de Boer et al. 2004) and camelids (Donadio and Buskirk 2006).

A wide array of animals has been documented to reduce behavioral response to a repeated stimulus that tends to be unthreatening, the adjustment known as habituation (c.f. Thorpe 1963). In habitats where human confrontations rarely lead to a lethal consequence, animals would be better off by not “overly” reacting to such a nonthreatening stimulus (i.e., humans). To the contrary, in habitats where hunting is common, humans truly are threatening stimulus and habituation to any approaching humans can be fatal. Accordingly, using FTR as the variable, I tested whether individuals of uncompromised populations would habituate to my regular approaches such that they gradually allowed my closer approach and whether those of compromised populations would not habituate. The result was consistent with this prediction. In fact, individuals of compromised habitats increased their FTR such that the probability of successful hunt became progressively lower. Such an augmented response (i.e., sensitization) was the major cause of the high rates of my failure to capture more snakes in compromised habitats.

Thus, mamushi in compromised habitats exhibited modified behavior compared to those in uncompromised habitats. Such alternative behavioral tactics are expected to come at some cost. I found that compromised populations exhibited delayed timing of parturition, presumably due to interrupted foraging and thermoregulation and, consequently, slowed embryogenesis. Although I predicted that individuals of compromised populations would be in poor body condition, no such evidence was detected. However, this may partly be due to the way I computed the BC index. Because

I captured, measured, and weighed individuals with different elapsed time since last feeding, and with different stages of developing embryos in the case of pregnant females, BC used in my study was probably confounded by such biases and, hence, it may not reflect pure “health” or “fatness” of the animals. Alternatively and additionally, snakes in compromised habitats might have compensated costs resulting from alternative behavioral tactics by some other means, such as foraging at night (which was not investigated in my study).

Body size

Truncated size distributions that lack larger individuals and a reduced mean body size are ubiquitous among populations in a wide array of species experiencing high mortality among adult and/or large-sized individuals, whether or not the mortality is natural (including introduced species) or anthropogenic (via harvesting) predators (e.g., Endler 1995; Stergiou 2002; Coltman et al. 2003). Mamushi populations studied in Hokkaido were no exception, and other hunted populations on a different main island of Japan, Honshu, appear also to show the same phenomenon (Goris, personal communication). Several alternative and nonexclusive hypotheses may explain body size reduction in compromised mamushi populations versus uncompromised ones.

The first hypothesis is that the size reduction is a result of an ongoing, consistent loss of larger individuals from the populations. This can explain why larger individuals are missing from the populations. However, this hypothesis cannot explain why neonatal snakes at birth were already smaller even when potentially confounding factors, including maternal SVL and BC and birth data, were taken into account.

A second hypothesis is that the size reduction has resulted from lower prey availability in compromised versus uncompromised habitats. Compromised sites may have lower prey availability because insecticides, herbicides, or rodenticides are often sprayed for agriculture or for forest management. Madsen and Shine (2000) showed that python born in years of low prey availability tended to exhibit slower growth rate throughout life and suggested that two populations might differ in mean body size because of some prior event such as low food supply. They concluded that body size variation among individuals has been shown to be caused by environmental rather than genetic factors (Madsen and Shine 2000). Also, Madsen et al. (2006) showed that mean body size was lower in some years than others because of annual variation in the proportion of the animals that were subadults rather than adults. The reduced body size in neonate offspring belonging to compromised populations may result from maternal nutritional factors that were not reflected in maternal BC calculated in my study.

A third hypothesis is that reduced body size is the result of human disturbances that are mediated through maternal effects. Early influences on phenotypic development are not restricted to the individual's own hormonal secretions, and the maternal environment experienced during development can contribute indirect genetic and/or environmental effects (reviewed in Dufty et al. 2002). Many of these effects are mediated through the endocrine system, and are increasingly recognized as being important in shaping phenotypic plasticity in offspring even to adulthood (reviewed in Dufty et al. 2002). Maternal hormone signals modify organizational pathways of developing brain nuclei, affecting physiological and behavioral responses in adult offspring in ways that influence their survival and reproductive success in a given environment (reviewed in Dufty et al. 2002).

Mamushi in compromised habitats experience greater human disturbance than those in uncompromised populations. In most vertebrates, including reptiles (Elsey et al.1990; reviewed in Guillette et al. 1995b), circulating levels of stress hormones (e.g., corticosterone) increase when exposed to stressors, and chronically elevated levels cause various negative effects, including reduced growth rates and elevated corticosterone at an early age, which have negative physiological consequences for individuals later in life (reviewed in: Romero 2004; Walker et al. 2005). Juvenile hoatzin (*Opisthocomus hoazin*) living at tourist-exposed sites, for example, had lower survival, lower body mass, and a strongly elevated corticosterone level than those living at undisturbed sites (Müllner et al. 2004). Müllner et al. (2004) hypothesized that the lower body mass of tourist-exposed juveniles most likely was a result of repeatedly elevated levels of corticosterone.

Another physiological consequence of human disturbance may be related to thermal condition. Inadequate thermoregulation may retard growth, which, in turn, can result in smaller body size for a given age. Also, inadequate thermoregulation by pregnant females can reduce offspring body size. Webb et al. (2001) found that snake offspring from a variable incubation treatment were shorter. Pregnant female mamushi of compromised populations are frequently disturbed by humans such that behavioral thermoregulation is frequently interrupted. Another potential factor underlying reduced body size may be related to the use of insecticides, herbicides, and/or rodenticides in compromised habitats. These may disrupt normal endocrine systems (Guillette et al. 1995a) and may cause reduction in body size.

A fourth hypothesis is that the reduced body size reflects the net directional changes in body size over generations (evolution) as a result of phenotypic selection that favors smaller body size. Individual variation, which is one of the prerequisite for phenotypic selection to occur, exists for body size in the mamushi populations, among both adults and neonates. Examination of marked individuals at the HMSC site revealed that direct hunting-caused mortality increased with increasing body size; that is, smaller-bodied individuals were favored in compromised habitats. The tight relationship between body size and direct hunting-caused mortality (i.e., differential survival) suggests that phenotypic selection, and not random genetic drift, is the chief force determining distribution of body sizes in compromised mamushi populations within a generation. Thus, findings in my study support the hypothesis that mamushi hunting has acted as phenotypic selection.

To support the other part of the fourth hypothesis (evolution), body size must be shown to be heritable for the within-generation changes in the trait distribution to be transmitted to the next generation. My study provides two lines of evidence that support heritability of body size. First, the differences in mean and distribution of body sizes observed between adults of compromised and uncompromised populations were also evident in neonatal snakes at birth. Neonates of wild-caught females of compromised populations were smaller regardless of their maternal body size compared to those of females of uncompromised populations. A second line of evidence is that neonatal body size was similar among littermates, and full-sib heritabilities of body size at birth were estimated to be 0.48 and 0.74 for compromised and uncompromised populations, respectively. Unfortunately, the full-sib heritability estimate is not a clean estimate of additive genetic variance (which determines the degree of heritable resemblance between parents and offspring and determines the response to selection by quantitative traits) because it was estimated from the within- and among-sibship components of variance, where the latter component estimates additive genetic variance plus some of the dominance, epistatic, and common family environmental variance (Brodie and Garland 1993; Arnold 1994). Common environment experienced by neonates in their mother's uterus may greatly increase similarity in phenotype among siblings and, thus, it can greatly inflate the estimate of heritability (King et al. 2001).

A difference in heritability estimates found between compromised and uncompromised populations is noteworthy. The estimate was high (0.74) for uncompromised populations and low (0.48) for compromised populations. This discrepancy between site types may simply be the result of insufficient sample size. However, past strong selection can reduce genetic variation, hence, heritability (Price and Schluter 1991). Due to strong selection pressure favoring smaller body size, body size in compromised populations might be approaching its minimal size. Relyea (2005) also found different heritabilities (narrow-sense) of predator-induced traits (tail depth in particular; body length and depth to lesser degree) in larval wood frogs (*Rana sylvatica*) in predator and no-predator environments.

Thus, body size reduction in compromised mamushi populations is highly likely to reflect evolutionary change as a result of selection from hunting that favors small individuals. Change in reproductive efforts in the direction expected from life history theory further supports this conclusion. Findings of my study and others on exploited fish (e.g., Concover and Munch 2002) and trophy-hunted bighorn sheep (Coltman et al. 2003) suggest that evolutionary change in body size in response to human predation pressure may be the rule rather than the exception. However, non-genetic factors, such as history of food abundance and maternal effects discussed above, are also likely contributing factors for the observed differences between site types.

Flight threshold radius (FTR)

Mamushi of compromised populations, whether they were males or females, pregnant or not, adult or neonate, were less tolerant of human approaches, fleeing at a greater distance from me than those of uncompromised ones. In uncompromised habitats, pregnant females allowed the closer approach than either nonpregnant females or males. In compromised populations, however, pregnant females exhibited a FTR of similar distance as nonpregnant females and males. This can be explained in the context of different use of microhabitat cover among these groups. Nonpregnant females and males of compromised populations, compared to their counterparts of uncompromised ones, were associated with more densely vegetated or covered microhabitats, whereas pregnant females were invariably found in more open or only sparsely vegetated microhabitats. These results suggest that pregnant females were less likely to give up such open, insolated microhabitat, but they increased distance at which they initiated fleeing from human hunters. For pregnant females, giving up well-insolated basking spots is probably not an option. My study found that pregnant females, compared to males and nonpregnant females, kept relatively constant and higher body temperature, presumably to achieve necessary temperatures for embryogenesis. An alternative way to avoid falling prey to human hunters is to increase FTR. Like other animal taxa (reviewed in Lima and

Kill 1990), such alternative tactics reflects trade-offs between the risk of predation and the benefit to be gained from engaging in a given activity.

Many hunted populations of mammals (e.g., roe deer, de Boer et al. 2004; guanacos and vicuñas, Donadio and Buskirk 2006; moose, Altmann 1958; impalas, Matson et al. 2005; caribou, Aastrup 2000) exhibit augmented FTR (often known as flight initiation distance or approach distance) compared to unhunted populations. Studies of FTR in various taxa reveal that it is very flexible, being influenced by many variables, such as angle of approach (Burger and Gochfeld 1990, 1991), time of year (Richardson and Miller 1997), time of day (Delaney et al. 1999), reproductive state (Bauwens and Thoen 1981; my study), distance to refuge (Dill and Houtman 1989), human visitation rates (Labra and Leonard 1999), and predation pressure (Diego-Rasilla 2003). Blumstein et al. (2004) reported very low (0.09) repeatability of FTR in yellow-bellied marmots (*Marmota flaviventris*), indicating the highly context-dependent nature of FTR. A review by Lima and Dill (1990) revealed that animals can assess their risk of being preyed upon in ecological time (i.e., during their lifetime) and incorporate this information into their decisions about whether or when to attempt escape given an encounter. For example, many game bird (e.g., Madsen 1985) and mammal (Behrend and Lubeck 1968) species change FTR depending on whether hunting seasons are open or closed.

Antipredator behavior in snakes is usually highly plastic, changing onotogentically (Herzog et al. 1992) or through experiences (Herzog and Burghardt 1988; Herzog 1990). Changes in FTR in response to repeated human approaches found in my study also indicate that FTR is highly plastic. Thus, a longer FTR exhibited among individuals of compromised populations may be a flexible behavioral modification in response to high predation risk imposed by human hunters.

Divergent expression of FTR between populations experiencing disparate hunting pressures appears common among populations of various species (de Boer et al. 2004; Donadio and Buskirk 2006; Altmann 1958; Matson et al. 2005; Aastrup 2000). Having been reported repeatedly, we now have a good deal of phenomenological understanding of "visible" changes in behavior and their consequences (e.g., reproduction, habitat use) in response to hunting However, we lack a mechanistic understanding about underlying causes of such changes, and, therefore, we need to ask questions like: Are behavioral changes in hunted populations solely a phenotypic change as the result of learning (including habituation and sensitization)? Alternatively, do the changes involve a net directional genetic change (evolution) as a result of phenotypic selection imposed by human hunters?

My study showed that FTR was variable among individuals, yet individuals were quite consistent in their FTR. Also, mortality was not random with respect to FTR; individuals that allowed too close an approach sustained higher mortality. Thus, two conditions for selection to occur—individual variation and fitness differences—are present in the mamushi populations.

For selection to result in evolution, the trait must be heritable. Two lines of evidence suggest that FTR is heritable. First, the differences observed between adults of compromised and uncompromised populations were also evident in naïve (experience-free) neonatal snakes. Second, full-sib heritability for FTR measured at birth was high in both compromised (0.82) and uncompromised (0.88) populations. As noted elsewhere, these estimates are probably inflated by nonadditive genetic effects (due to dominance and epistasis) as well as purely environmental effects. Studies on other snake species also have shown that much antipredator behavior in snakes is heritable (Arnold and Bennett 1984; Brodie 1989, 1992, 1993; Burghardt and Schwartz 1999; Mori and Burghardt 2000), including response distance (the distance at which a snake first responded, e.g., by orienting towards the threat or fleeing backward, King 2002). Heritability estimates in my study were higher than those reported in these studies ($h^2_{\mathrm{FS}} \leq 0.65$). The higher values I found are probably due to common environmental conditions when neonate offspring were tested. Neonate offspring were often found with other siblings or with other adult snakes (regardless of their blood relationship). When approached, they appeared to initiate escape perhaps in response to escape by other individuals near them.

Although all this evidence suggests the involvement of genetic changes, changes in FTR could be due solely to maternal effects. King et al. (2001) showed that heritability of antipredator behavior may be lower and maternal effects larger. Littermates share the common maternal uterine environment, and, consequently, maternal genotype may affect offspring phenotype. It has become evident that the prenatal environment can have profound effects on offspring traits, both as juveniles and as adults (e.g., Clark and Galef 1998; Dufty et al. 2002). Prenatal exposure to relatively high, stress-induced levels of corticosterone may lead to changes in postnatal behavior (Thompson 1957; Weinstock 2001), such as novelty-induced escape behavior (Vallée et al. 1997). Most reptiles (Lance 1990; Moore et al. 1999), including snakes (Moore et al. 2000), increase plasma levels of corticosterone and decrease plasma levels of testosterone in response to stress. In a lizard, Uller and Olsson (2006) showed that maternal steroids can influence the offspring:

corticosterone-treated individuals spent significantly longer time in a shelter after a simulated predator attack than did control offspring. King et al. (2002) showed that families responded (response distance) differently to testosterone manipulation in garter snakes. Also, King et al. (2004) showed that testosterone levels were different among families of garter snakes. Taken together, differences in FTR in both adult and neonatal mamushi between compromised and uncompromised habitats may reflect the differences in hormonal environment resulting from human disturbance. Yet, evidence of heritable variation in circulating testosterone levels suggest that the evolution of testosterone-affected traits, such as defensive behavior, might be mediated through genetic changes in levels of circulating hormones (King et al. 2004).

Though rapid evolution of antipredator behavior has not yet been documented in natural populations in the context of hunting or fishing, behavioral evolution can occur in such a situation. Walsh et al. (2006) demonstrated that an experimental fishing that targeted larger individuals of captive populations of Atlantic silverside over five generations (eggs collected from wild-caught individuals) resulted in evolution of the willingness to forage under the threat of predation (i.e., large-size harvested populations exhibited increased hiding time before resuming foraging than small-size harvested ones). Rapid behavioral evolution has been found in free-ranging populations that are under non-human predation pressure. O’Steen et al. (2002) showed that changes in predatory environments created phenotypic selection of escape ability of guppies and that the escape ability could evolve very rapidly in nature, within 26-36 generations. Kissecker and Blaustein (1997) showed that predator recognition and associated responses evolved in the red-legged frog (*Rana aurora*) in response to introduced bullfrogs (*R. catesbeiana*). An additional example comes from the selective breeding of foxes, where evolutionary changes have occurred in behavioral, as well as morphological and physiological traits, in about 40 years (Belyaev 1979; Trut 1999). The fox lost their behavior of fleeing from and biting humans. Finally, temperament traits (e.g., boldness) appear to be closely tied to antipredator behavior and have been shown to have fitness consequences and heritable variation (reviewed in McDougall et al. 2006).

Defensiveness

Differences in defensiveness between compromised and uncompromised populations were evident in both neonate and adult populations regardless of the sex, except in pregnant females. Both neonate and adult mamushi (males and nonpregnant females) belonging to compromised populations were less likely to turn to threatening displays and biting attempts compared to those from uncompromised populations. Only a small number of pregnant females were defensive regardless of site types, suggesting that pregnant females rely heavily on procrypsis and fleeing. Reproduction is known to affect antipredator behavior in garter snakes (e.g., Brown and Shine 2004). Females of other crotaline species have been documented to rely less on warning displays and more on procrypsis and escape when pregnant (Graves 1989). Such pregnancy-related changes may be a consequence of the increased physical and physiological burdens of pregnancy.

The question is whether such divergence of defensiveness between the site types involves genetic changes. Several lines of evidence suggest so. Defensiveness was variable among individuals, yet individuals were consistent in their defensiveness relative to the variation among individuals. Also, mortality was not random with respect to defensiveness; the more defensive the individuals, the greater their probability of being captured or killed. Thus, two conditions for selection to occur—individual variation and fitness differences—are present also in this trait in the mamushi populations. Two lines of evidence suggest the presence of heritability in defensiveness. First, the differences observed between adults of compromised and uncompromised populations were also evident in naïve (experience-free) neonatal snakes. Second, full-sib heritability for defensiveness measured at birth was high in both and compromised (0.88) and uncompromised (0.89) populations. Taken together, my study supports the hypothesis that the reduced propensity to turn to threatening displays and biting attempts in compromised populations reflects an evolutionary change in response to selective forces created by mamushi hunting.

Nonetheless, as discussed for FTR above, the observed differences between the site types could be produced via phenotypic plasticity and/or maternal environmental effects. Glaudas (2004) showed significant flexibility in the propensity to strike in crotaline species, where the propensity to strike declined significantly over days in response to repeated human handling. Bonnet et al. (2005) showed that tiger snakes (*Notechis scutatus occidentalis* [*ater*?]) living on the mainland with various predators attempted to flee more frequently and were prone to bite and strike compared to snakes on an island with no native, human, nor feral predators, and such tendency was experimentally partly reversible. Stress experienced mothers may be responsible for altering defensiveness of their offspring, which might carry on to adulthood (see discussion for FTR above). In addition, altered thermal conditions of individuals living in compromised habitats might have affected defensiveness. In pine snakes (*Pituophis* *melanoleucus*), Burger (1989) found that snakes incubated at low temperatures remained motionless until the experimenter picked them up, whereas those incubated at middle and high temperatures moved away rapidly in response to an approaching experimenter.

Response to repeated exposure to an approaching human

A pronounced difference was found in the response pattern to repeated human approaches between individuals from compromised and uncompromised populations. Individuals of uncompromised populations habituated to repeated human approaches, whereas those of compromised populations exhibited sensitization, i.e., increased FTR. A similar pattern of divergence between populations with differing predation pressures was documented in fish (Magurran and Girling 1986; Csányi 1985; Huntingford and Coulter 1989). My study also found that the response to repeated human approaches was variable among individuals, and yet individuals showed a single consistent level of FTR across years in both responsiveness and the rate of change over 8 days of daily trials. Although my study does not allow determining whether or not this trait is heritable, other studies on garter snakes (see Burghardt 2002 and reference therein) suggested that the way snakes process experience is under genetic control. Nevertheless, traits associated with fear and anxiety can be altered due to prenatal exposure to relatively high, stress-induced levels of corticosterone (Thompson 1957; Weinstock 2001); this might explain why mamushi populations differ in the response to repeated human approaches.

Latency to emerge from refuge

Individuals of compromised populations stayed longer in refuges after escaping from my approach than those of uncompromised populations. Uller and Olsson (2006) used this variable as a measure of fear in lizards, and found that corticosterone-treated animals stayed in refuges for a longer time after a simulated predator attack than did controls. It may be that compromised individuals have elevated corticosterone due to frequent, threatening confrontation with humans. Alternatively, based on a study of a fish-amphipod system, the observed divergence between the site types of my study may reflect genetic differences. Åbjörnsson et al. (2004) studied the original and the F1 generation of amphipods from ponds with and without predatory fish and showed that time in refuge is an inherited, adaptive trait to prevailing predator regimes. Also, the latency to restart foraging after a startle in birds has been shown to be heritable and responsive to selection (van Oers et al. 2004).

Microhabitat cover

Overall differences and similarities with respect to use of microhabitat among males and pregnant and nonpregnant females found in my study (irrespective of site type) were largely consistent with the findings reported for other snake species (e.g., Charland and Gregory 1995). Males and nonpregnant females were usually found in microhabitats that had high vegetation cover. They also frequented more open microhabitats, but only briefly, presumably to foster ecdysis and digestion processes. On the other hand, pregnant females generally frequented open, only sparely vegetated microhabitats that had rocks or fallen logs that served as refuges (i.e., basking spots).

Comparisons of compromised and uncompromised populations revealed that males and nonpregnant females living in compromised sites were found in more densely vegetated microhabitats than those in uncompromised sites, whereas pregnant females were found in open microhabitats regardless of site type. As discussed in the section for FTR above, males and nonpregnant females seem to avoid falling prey to humans by relying more on the use of densely vegetated cover, rather than substantially increasing FTR as exhibited by pregnant females. Abandoning insolated microhabitats (i.e., basking spots) seems not to be an option for pregnant females, probably because basking spots provide necessary conditions to carry out thermoregulation for normal embryogenesis.

What are the causal mechanisms that produced the differences in microhabitat use between compromised and uncompromised populations? Changes in microhabitat use can occur through plasticity without any genetic changes. Animals can respond to temporal variation in predation risk very quickly (Lima and Dill 1990), for example, by changing microhabitat use (Abramsky et al. 1996). In another crotaline species, pregnant female rattlesnakes living in disturbed (presumably not lethal) area of a park were less visible (due to vegetation or other structural cover) to humans than those in less disturbed areas of the park (Parent and Weatherhead 2000).

Although such modified microhabitat use has been observed in hunted non-reptile populations (reviewed in Knight and Cole 1995), the genetic basis of such modification in the context of human predation pressure has not been addressed or investigated. In nonhuman predation systems, literature surveys suggest that the trait of microhabitat use can be genetically based. Studies on non-snake taxa (Jaenike and Holt 1991; Rodriguez et al. 1992; Robinson and Rowland 2005; Nosil and Crespi 2006) supported a genetic basis of (micro)habitat selection. In fish, Iguchi (2001) and Lucas et al. (2004) showed that the frequency of cover use had a genetic basis and evolved in response to selection regimes imposed by captive rearing.

Although my study originally aimed to investigate such a possibility by studying experience-free neonates, data on neonates could not be obtained due to unexpected events (see Methods). My study, however, found that repeatability of this trait was significant (t = 0.50 and 0.67 for compromised and uncompromised populations, respectively). Such a significant repeatability estimate may set an upper limit for heritability of the trait because repeatability includes genetic and environmental sources of variation whereas heritability includes only genetic differences among individuals, or it may provide some insight on the strength of natural selection necessary to cause changes in the trait because of its relationship to heritability (see Dohn 2002 and references therein). However, some cautions are in order because repeatability estimates can be confounded with a number of other genetic and environmental causes of variation among individuals (Dohn 2002).

Movement and Activity

Though the movement data from my study are scanty (see Results), overall movement measures from uncompromised populations in my study agree with general trends commonly observed in other snake taxa (e.g., King and Duvall 1990; Graves and Duvall 1993; Johnson 2000). Pregnant female mamushi moved much less than males and nonpregnant females. Though preliminary, movements and activities appeared to be reduced in compromised versus uncompromised populations, especially in males. The longer time it took to reappear from a refuge after escaping from human approaches by snakes from compromised populations also supports that observation. In another crotaline species, Parent and Weatherhead (2000) documented results similar to my study, where eastern massasauga rattlesnakes (males and pregnant and nonpregnant females) reduced movement in response to human disturbance caused by park visitors within Killbear Provincial Park, Canada.

Other studies on different taxa suggest movements or activity patterns have genetic bases and can respond to selection imposed by predation pressures. In fish, frequency of cover use and swimming levels have a genetic basis and evolved in response to selection regimes (e.g., no predation) imposed by captive rearing (Iguchi 2001; Lucas et al. 2004). Relyea (2005), for example, demonstrated that larval wood frogs belonging to a predator (dragonfly nymph) environment had lower activity levels than those from a no-predator environment and that activity was highly heritable.

Reproduction

Overall, females of compromised populations produced more offspring and smaller offspring per litter. This agrees with the expectation drawn from life history theory that when mortality rates increase in one size class, then the optimal reproductive effort increases before that. Though this result can be interpreted as an evolutionary change, other factors, such as altered maternal condition (e.g., hormonal) might be responsible, as discussed elsewhere in this Discussion.

General Discussion and Conservation Implications

My study showed that hunting and killing have produced a strong phenotypic selection force that has generated population-wide changes in body size, antipredator behavior, microhabitat use, movements, and life history in the mamushi populations. These changes appear to be, in part, genetically based, and hence, evolutionary responses to intensive human predation pressures. Although males and pregnant and nonpregnant females all responded (phenotypically and/or genetically) to human predation, pregnant females did so in different ways in some traits compared to males or nonpregnant females. Also, no sex differences were apparent at birth. Therefore, the difference between pregnant females and other groups suggests that pregnancy might have a significant influence on their behavior of females.

Though not all traits measured in my study were tested vigorously for their heritabilities, these traits, based on other studies, may have the potential to evolve due to genetic correlations with other traits, if not their genetic basis itself (Walsh et al. 2006). For example, selection for increased FTR may select indirectly for individuals with lower activity levels. In my study, FTR and activity levels (number of moves per September) were negatively correlated in uncompromised populations ($r = -0.86$, $P < 0.001$) (no sufficient data to analyze for compromised ones). Clobert et al. (2000) showed that lizards with a low endurance at birth (heritable at least in garter snakes; Garland 1988) tended to have reduced activity and growth rate. Yamamoto and Reinhardt (2003) showed that artificial selection for fast growth in fish favored individuals that ignored predation risk and responded to food quickly. Genetic correlations between body size, development, and activity have been demonstrated in larval wood frogs (Relyea 2005). In a sunfish-salamander system, for example, Sih et al. (2003) showed that salamander larvae that were ‘geared up’ (maintained higher levels of exposure) more so than ‘geared down’ larvae, fed, grew, and developed rapidly, but were preyed upon by fish at higher rates.

It is now incontestable that commercial fishing causes rapid evolutionary changes in body size and life history traits in multiple species. Plus, a recently documented case on trophy hunting of mountain rams provides compelling evidence that targeting rams with large horns can cause reduction in horn size and body size as an evolutionary response within a few generations. An important conservation and management implication is that if such changes have a genetic basis, they can be slow or hard to reverse, even when selection forces caused by humans stop (Law 2001). Furthermore, a genetic-based change in one trait will inevitably cause changes in other correlated traits (e.g., Garland et al. 2002), which can negatively affect fitness. In fisheries, these consequences of genetic changes have been hypothesized as a mechanism for the collapse of fish populations and lack of recovery even after fishing pressures were relaxed or stopped (Walsh et al. 2006).

Although evolutionary consequences of such human predation pressures have received little attention, it seems that rapid evolutionary changes in hunted populations may be the rule instead of the exception in many exploited populations, given the “unnaturally” high adult mortality and the selective nature of much hunting (Harris et al. 2002; Festa-Bianchet 2003). For example, the increased frequency of tuskless elephants in many African populations may have occurred in response to selective ivory poaching (Festa-Bianchet 2003). Also, lowered aggressiveness of brown bears in Europe may have resulted from selection against aggressive individuals by humans who may have selectively killed aggressive individuals (Festa-Bianchet 2003). Moreover, hunting of moose has been suggested to act as a selective force and to cause changes in life-history traits (Ericsson et al. 2001).

Considering the current status of mamushi populations and habitats, I do not think hunting and killing alone can cause serious population decline or local extirpation in my study area. Mamushi habitats are still largely contiguous, unlike habitat in many other places of Japan. Nevertheless, some places where mamushi live are under rapid development, and by extension, suffer high human predation pressures. Under these conditions, phenotypic and/or genetic changes that were observed in my study can accelerate the process of population decline and increase the probability of local extirpation.

LITERATURE CITED

Aastrup, P. 2000. Responses of West Greenland caribou to the approach of humans on foot. Polar Research 19:83–90.

Åbjörnsson, K., L-A Hansson, and C. Brönmarka. 2004. Responses of prey from habitats with different predator regimes: local adaptation and heritability. *Ecology* 85:1859–1866.

Abramsky, Z., E. Strauss, A. Subach, B. P. Kotler, and A. Reichman. 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. Oecologia 105:313–319.

Aihara, T., S. Ito, S. Saito, T. Takahashi, K. Takamoto., and M. Yabuki. 1997. Taihaku no densetsu. Atarashii mori no miyako zukuri Taihaku kyogikai, Sendai, Miyagi, Japan.

Altmann, M. 1958. The flight distance in free-ranging big game. Journal of Wildlife Management 22:207–209.

Antoni, K.1995. The "separation of gods and buddhas" at Ōmiwa Jinja in Meiji Japan. Japanese Journal of Religious Studies 22: 39–60.

Arakawa, H. 1996. Ryu no kigen. Kinokuniya-shoten, Tokyo, Japan.

Arnold, S. J. 1994. Multivariate inheritance and evolution: a review of concepts. Pages 17–48 *in* C. R. P. Boake, editor. Quantitative Genetics Studies of the Evolution of Behavior. The University of Chicago Press, Chicago, Illinois, USA.

Arnold, S. J., and A. F. Bennett. 1984. Behavioral variation in natural populations. III. Antipredator displays in the garter snake *Thamnophis radix*. Animal Behaviour 32:1108-1118.

Ashley, M. V., M. F. Willson, O. R. W. Pergrams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionary enlightened management. Biological Conservation 111:115–123.

Association of Minakata Kumagusu Archives. 2006. Genpon honkoku, Minakata nisho: Matsumura Jinzou ate Minakata Kumagus genshokan. Wakayama, Japan.

Barot, S., M. Heino, L. O'Brien, and U. Dieckmann. 2004. Long-term trend in the maturation reaction norm of two cod stocks. Ecological Applications 14:1257–1271.

Barrow, E., and N. Pathak. 2005. Conserving "unprotected" protected areas – communities can and do conserve landscapes of all sorts. Pages 65–85 *in* J. Brown, N. Mitchell, and M. Beresford, editors. The protected landscape approach: linking nature, culture and community. IUCN World Commission on Protected Areas, Gland, Switzerland.

Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. Journal of Animal Ecology 50:733–743.

Behrend, D. F., R. A. Lubeck. 1968. Summer flight behavior of white-tailed deer in two Adirondack forests. Journal of Wildlife Management 32:615–618.

Bell, M. A., W. E. Aguirre, and N. J. Buck. 2004. Twelve years of contemporary armor evolution in a threespine stickleback population. Evolution 58:814–824.

Belyaev, D. K., and L. N. Trut. 1982. Accelerating evolution. Science in the USSR 5:24–29, 60–64.

Bernard, P. S. 2003. Ecological implications of water spirit beliefs in southern Africa: the needs to protect knowledge, nature, and resource rights. USDA Forest Service Proceedings RMRS-P-27:148–154.

Berteaux, D., D. Reale, A. G. McAdam, and S. Boutin. 2004. Keeping pace with fast climate change: can Artic life count on evolution? Integrative and Comparative Biology 44:140–151.

Blacker, C. 1983. Minakata Kumagusu: a neglected Japanese genius. Folklore 94:139–152.

Blumstein, D.T., A. Runyan, M. Seymour, A. Nicodemus, A. Ozgul, F. Ransler, S. Im, T. Stark, C. Zugmeyer, and J. C. Daniel. 2004. Locomotor ability and wariness in yellow-bellied marmots. Ethology 110:615–634.

Bonnet, X., F. Aubret, O. Lourdais, M. Ladyman, D. Bradshaw, S. Maumelat. 2005. Do ‘‘quiet'' places make animals placid? Island versus mainland Tiger snakes. Ethology 111:573–592.

Bonnet X., and G. Naulleau. 1994. A body condition index (BCI) in snakes to study reproduction. Comptes-rendus de l'Académie des Sciences. Série III: Sciences de la vie 317:34–41.

Borisov, V. M. 1978. The selective effect of fishing on the population structure of species with long life cycles. Journal of Ichthyology 18:896–904.

Bowers, B. B. 1992. Habituation of antipredator behaviors and responses to chemical prey in four species of garter snakes, *Thamnophis* (Serpentes: Colubridae). Dissertation, University of Tennessee, Knoxville, Tennessee, USA.

Brodie, E. D., III. 1993. Homogeneity of the genetic variance-covariance matrix for antipredator traits in two natural populations of the garter snake *Thamnophis ordinoides*. Evolution 47:844–854.

Brodie, E. D. III. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. Evolution 46:1284–1298.

Brodie E. D. III., and T. Garland Jr. 1993. Quantitative genetics of snake populations. Pages 315–362 *in* R. A. Seigel and J. T. Collins, editors. Snakes: ecology and behavior. McGraw-Hill, New York, New York, USA.

Brodie, E. D., III. 1989. Genetic covariances between morphology and antipredator behavior in natural populations of the garter snake *Thamnophis ordinoides*. Nature 342:542–543.

Brown, G. P., and R. Shine. 2004. Effects of reproduction on the antipredator tactics of snakes (*Tropidonophis mairii*, Colubridae). Behavioral Ecology and Sociobiology 56:257-262.

Burger, J. 1989. Incubation temperature has long-term effects on behavior of young pine snakes (*Pituophis melanoleucus*). Behavioral and Ecological Sociobiology 24: 201–207.

Burger, J., and M. Gochfeld. 1990. Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): variation as a function of human exposure. Journal of comparative psychology 104:388–394.

Burger, J., and M. Gochfeld. 1991. Human distance and birds: tolerance and response distances of resident and migrant species in India. Environmental Conservation 18:158–165.

Burghardt, G. M. 2002. Genetics, Plasticity, and the Evolution of Cognitive Processes. Pages *in* M. Bekoff, M. C. Allen, and G. M. Burghardt, editors. The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognition. MIT Press, Cambridge, Massachusetts, USA.

Burghardt, G. M., and Schwartz, J. M. 1999. Geographic variations on methodological themes in comparative ethology: a natricine snake perspective. Pages 69–94 *in* S. A. Foster and J. A. Endler, editors. Geographic variation in behavior: perspectives on evolutionary mechanisms. Oxford University Press, New York, New York, USA.

Callaway, R. M., W. M. Ridenour, T. Laboski, T. Weir, and J. M. Vivanco. 2005. Natural selection for resistance to the allelopathic effects of invasive plants. Journal of Ecology 93:576–583.

Clark, M. M., B. G. Galef, Jr. 1998. Perinatal influences on the reproductive behavior of adult rodents. Pages 261–271 *in* T. A. Mousseau and C. W. Fox, editors. Maternal effects as adaptations. Oxford University Press, New York, New York, USA.

Central Research Laboratories. 1999. Ecology and Artificial Propagation of the Mamushi. Central Research Laboratories, Yomeishu Seizo Co., Ltd., Nagano, Japan.

Charland, M. B., and P. T. Gregory. 1995. Movements and habitat use in gravid and nongravid female garter snakes (Colubridae: *Thamnophis*). Journal of Zoology, London 236:543–561.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge, UK.

Clobert, J., A. Oppliger, G. Sorci, B. Ernande, J. G. Swallow, T. Garland, Jr. 2000. Trade-offs in phenotypic traits: endurance at birth, growth, survival, predation and susceptibility to parasitism in a lizard, *Lacerta vivipara*. Functional Ecology 14: 675–684.

Colding, J., and C. Folke. 2001. Social taboos: "invisible" systems of local resource management and biological conservation. Ecological Applications 11:584–600.

Coltman, D. W., P. O'Donoghue, J. T. Jorgenson, J. T. Hogg, C. Strobeck, and M. Festa-Bianchet. 2003. Undesirable evolutionary consequences of trophy hunting. Nature 426:655–658.

Conant, R. 1992. Comments on the survival status of members of the *Agkistrodon* Complex. Pages 29–33 *in* P. D. Strimple and J. L. Strimple, editors. Contributions in Herpetology. Greater Cincinnati Herpetological Society, Cincinnati, Ohio, USA.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94–96

Coss, R. G. 1999. Effects of relaxed natural selection on the evolution of behavior. Pages 180-208 *in* S. A. Foster and J. A. Endler, editors. Geographic variation in behavior: perspectives on evolutionary mechanisms. Oxford University Press, New York, New York, USA.

Cousyn, C., L. De Meester, J. K. Colbourne, L. Brendonck, D. Verschuren, and F. Volckaert. 2001. Rapid, local adaptation of zooplankton behavior to changes in predation pressure in the absence of neutral genetic changes. Proceedings of the National Academy of Sciences (USA) 98:6256–6260.

Czaja, M. 1974. Gods of Myth and Stone: Phallicism in Japanese Folk Religion. Weatherhill, New York, New York, USA.

Csányi, V. 1985. Ethological analysis of predator avoidance by the paradise fish (*Macropodus opercularis* L.). I. Recognition and learning by predators. Behaviour 92:227–240.

Daniels, F. J. 1960. Snake and dragon lore of Japan. Folklore 71:145–164.

Darwin, C. 1859. On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life. John Murray, London, UK.

Dasmann, R. F., and R. D. Taber. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. Journal of Mammalogy 37:143–164.

de Boer, H. Y., L. van Breukelen, N. J. M. Hootsmans, and S. E. van Wieren. 2004. Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors. Wildlife Biology 10:35–41.

Delaney, D. K., T. G. Gurbb, P. Seibr, L. L. Pater, and M. H. Reiser. 1999. Effects of helicopter noise on Mexican spotted owls. Journal of Wildlife Management 63:60–76.

Diamond, J. 2005. Collapse: how societies choose to fail or survive. Penguin Books, London, UK.

Diego-Rasilla, F. J. 2003. Influence of predation pressure on the escape behaviour of *Podarcis muralis* lizards. Behavioural Processes 63:1–7.

Dill, L. M., and R. Houtman. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciuris carolinensis*). Canadian Journal of Zoology 67:233–235.

Dodd, C. K., Jr. 1987. Status, conservation, and management. Pages 478-513 *in* R. A. Seigel, J. T. Collins, and S. S. Novak, editors. Snakes: Ecology and Evolutionary Biology. McGraw-Hill, New York, USA.

Dohm, M. R. 2002. Repeatability estimates do not always set an upper limit to heritability. Functional Ecology 16:273–280.

Donadio, E., and S. W. Buskirk. 2006. Flight behavior in guanacos and vicuña as in areas with and without poaching in western Argentina. Biological Conservation 127:139-145.

Ducey, P. K., and E. D. Brodie, Jr, 1991. Evolution of antipredator behavior: individual and populational variation in a neotropical salamander. Herpetologica 47:89–95.

Dudden, A. 2005. Japanese colonial control in international terms. Japanese Studies 25:1–20.

Dufty, A. M., J. Clobert, and A. P. Møller. 2002. Hormones, developmental plasticity and adaptation. Trends in Ecology and Evolution 17:190–196.

Duvall, D., J. K. O'Leile, S. G. Heald, and S. J. Beaupre. 1996. Urban rattlesnake status and ecology. Arizona Game and Fish Department. Final Report.

Duvall, D., G. W. Schuett, S. J. Arnold. 1993. Ecology and evolution of snake mating systems. Pages 165-200 *in* R. A. Seigel and J. T. Collins, editors. Snakes: ecology and behavior. McGraw-Hill, New York, USA.

Duvall, D., M, B. King, and K. J. Gutzwiller. 1985. Behavioral ecology and ethology of the prairie rattlesnake. National Geographic Research 1:80–111.

Edmunds, M. 1974. Defence in Animals. Harlow, Longman, London, Great Britain.

Elsey, R. M, Joanen, T., McNease, L., Lance, V. 1990. Growth rate and plasma corticosterone levels in juvenile alligators maintained at different stocking densities. Journal of experimental zoology 255:30-36.

Endler, J. A. 1995. Multiple-trait coevolution and environmental gradients in guppies. Trends in Ecology and Evolution 10:2229.

Endler, J. A. 1986. Natural Selection in the Wild. Princeton University press, Princeton, New Jersey, USA.

Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. Ecology 82:1613–1620.

Falconer, D. S. 1981: Introduction to Quantitative Genetics. Second edition. Longman, New York, New York, USA.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics. Prentice Hall, Harlow, U.K.

Festa-Bianchet, M. 2003. Exploitive wildlife management as a selective pressure for the life-history evolution of large mammals. Pages 191–207 *in* M. Festa-Bianchet and

M. Apollonio, editors. Animal behavior and wildlife conservation. Island Press, Washington, D.C., USA.

Fincher, C. L., and D. Duvall. 1998. Intense hunting by humans may reduce rattling in rattlesnakes [Abstract]. American Zoologist 38:170.

Fuiman, L. A., and A. E. Magurran. 1994. Development of predator defences in fishes. Reviews in Fish Biology and Fisheries 4:145–183.

Fukada, H. 1989. Longevity of four species of Japanese snakes. Pages 414–432 *in* M. Matsui, T. Hikida, and R. C. Goris, editors. Current Herpetology in East Asia. Herpetological Society of Japan, Kyoto, Japan.

Garland, T., Jr., M. T. Morgan, J. G. Swallow, J. S. Rhodes, I. Girard, J. G. Belter, and P. A. Carter. 2002. Evolution of a small-muscle polymorphism in lines of house mice selected for high activity levels. Evolution 56:1267–1275.

Garland, T., Jr. 1994. Quantitative genetics of locomotor behavior and physiology in a garter snake. Pages 251-277 *in* C. R. P. Boake, editor. Quantitative Genetics Studies of the Evolution of Behavior. The University of Chicago Press, Chicago, Illinois, USA.

Garland, T., Jr. 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. Evolution 42:335–350.

Gibbons, J. W., and M. E. Dorcas. Defensive behavior of cottonmouths (*Agkistrodon piscivorus*) toward humans. Copeia 2002:195–198.

Glaudas, X. 2004: Do cottonmouths (*Agkistrodon piscivorus*) habituate to human confrontations? Southeastern Naturalist 3:129—138.

Gloyd, H. K., and R. Conant. 1990. Snakes of the *Agkistrodon* Complex. Society for the Study of Amphibians and Reptiles. Ithaca, New York, USA.

Goode, M. J., and D. Duvall. 1989. Body temperature and defensive behaviour of free-ranging prairie rattlesnakes, *Crotalus viridis viridis*. Animal Behaviour 38:360-362.

Goris, R. R., and N. Maeda. 2005. Guide to the Amphibians and Reptiles of Japan. Krieger Publishing Company, Malabar, Florida, USA.

Grant, B. C., and L. C. Wisenman. 2002. Recent history of melanism in American peppered moths. The Journal of Heredity 93:86–90.

Grant, P. R. and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. Science 296:707–711.

Grant, P. R. 1998. Evolution of Islands. Oxford University Press, New York, New York, USA.

Graves, B. M. 1989. Defensive behavior of female prairie rattlesnakes (*Crotalus viridis*) changes after parturition. Copeia 1989:791–194.

Graves, B. M., and D. Duvall. 1995. Aggregation of squamate reptiles associated with gestation oviposition, and parturition. Herpetological Monographs 9:102–119

Graves, B. M., and D. Duvall. 1993. Reproduction, rookery use and thermoregulation in free-ranging pregnant *Crotalus v. viridis*. Journal of Herpetology 27:33–40.

Green, A. J. 2001 Mass/length residuals: measures of body condition or generators of spurious results? Ecology 82:1473–1483.

Greene, H. W. 1999. Living with snakes. Pages xv–xix *in* G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka, editors. Problem snake management: the habu and brown treesnake. Cornell University Press, Ithaca, New York, USA.

Greene, H. W. 1997. Snakes: the evolution of mystery in nature. University of California Press, Berkeley, California, USA.

Guillette, L. J, Jr, D. A. Crain, A. A. Rooney, and D. B. Pickford. 1995a. Organization versus activation: the role of endocrine-disrupting contaminants (EDCs) during embryonic development in wildlife. Environmental Health Perspectives 103 (Supplement 7) 157–164.

Guillette, L. J., Jr., A. Cree, and A. A. Rooney. 1995b. Biology of stress: Interactions with reproduction, immunology, and intermediary metabolism. Pages 32–81 *in* C. Warwick, F. L. Frye, and J. B. Murphy, editors. Health and Welfare of Captive Reptiles. Chapman & Hall, London, UK.

Hairston, N. G., S. P. Ellner, M. A. Geber, T. Yoshida, and J. A. Fox. 2005. Rapid evolution and the convergence of ecological and evolutionary time. Ecology Letters 8:1114–1127.

Hairston, N. G. Jr., W. Lampert, C. E. Cáceres, C. L. Holtmeier, L. J. Weider, U. Gaedke, J. M. Fischer, J. A. Fox, and D. M. Post. 1999. Rapid evolution revealed by dormant eggs. Nature 401:446.

Hairston, N. G., and T. A. Dillon. 1990. Fluctuating selection and response in a population of freshwater copepods. Evolution 44:1796–1805.

Harris, R. B, W. A. Wall, and F. W. Allendorf. 2002. Genetic consequences of hunting: what do we know and what should we do? Wildlife Society Bulletin 30:634–643.

Harris, J. D. 1943. Habituatory response decrement in intact organisms. Psychological Bulletin 40:385–422.

Hattori, S. 2002. Present State and Problem of Habu Snake (*Trimeresurus flavoviridis*). South Pacific Studies (Minami taiheiyou kaiiki chousa kenkyu houkoku) Occasional Papers 36:15–21.

Herzog, H. A. Jr. 1990: Experimental modification of defensive behaviors in garter snakes *Thamnophis sirtalis*. Journal of Comparative Psychology 104:334–339.

Herzog, H. A. Jr., B. B. Bowers, and G. M. Burghardt. 1992. Development of antipredator responses in snakes: V. Species differences in ontogenetic trajectories. Developmental Psychobiology 25:199–211.

Herzog, H. A. Jr., and G. M. Burghardt. 1988: Development of antipredator responses in snakes: III. Stability of individual and litter differences over the first year of life. Ethology 77:250–258.

Hikida, T. 2002. Natural history of the reptiles (Hachurui no shinka). University of Tokyo Press, Tokyo, Japan.

Hosmer, D.W. and Lemeshow, S. 2000. Applied logistic regression. Second edition. Wiley and Sons, New York, New York, USA.

Hutchings, J. A. 2005. Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 62:824–832.

Hutchings, J. A. 2000. Numerical assessment in the front seat, ecology and evolution in the back seat: time to change drivers in fisheries and aquatic sciences? Marine Ecology Progress Series 208:299–313.

Huntingford, F. A, P. J. Wright, and J. F. Tierney. 1994. Adaptive variation and antipredator behaviour in threespine stickleback. Pages 277–295 *in* M. A. Bell and S. A. Foster, editors. The evolutionary biology of the threespine stickleback. Oxford University Press, New York, New York, USA.

Huntingford, F. A., and R. M. Coulter. 1989. Habituation of predator inspection in the three-spined stickleback, *Gasterosteus aculeatus* L. Journal of Fish Biology 35:153–154.

Hutchings, J. 2000. Collapse and recovery of marine fishes. Nature 406:882–885.

Iguchi, K., N. Matsubara, and H. Hakoyama. 2001. Behavioural individuality assessed from two strains of cloned fish. Animal Behaviour 61:351–356.

Isogawa, K., and K. Kato. 1995. Mating season of the Japanese mamushi, *Agkistrodon blomhoffii blomhoffii* (Viperidae: Crotalinae), in southern Kyushu, Japan: relation with female ovarian development. Japanese Journal of Herpetology 16:42–48.

Jaenike, J., and R. D. Holt. 1991. Genetic variation for habitat preference – evidence and explanations. American Naturalist 137: S67–S90.

Johnson, G. 2000. Spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in a New York peatland. Journal of Herpetology. 34:186–192.

Kawanabe, H. 2003. Cultural association in an ancient lake: gods of water in Lake Biwa and the River Yodo basin, Japan. Hydrobiologia 500:213–216.

Kettlewell, H. B. D. 1973. The evolution of melanism. Clarendon Press, Oxford, U.K.

Kiesecker, J. M., and A. R. Blaustein. 1997. Population differences in responses of red-legged frogs (*Rana aurora*) to introduced bullfrogs (*Rana catesbeiana*). Ecology 78:1752–1760.

Knight, R. L. and D. N. Cole. 1995. Wildlife responses to recreationists. Pages 51-69 *in* R. L. Knight and K. J. Gutzwiller, editors. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, DC, USA.

King, R. B., J. H. Cline, and C. J. Hubbard. 2004. Heritable variation in testosterone levels in male garter snakes (*Thamnophis sirtalis*). Journal of Zoology, London 264:143–147.

King, R. B. 2002. Family, sex, and testosterone effects on garter snake behaviour. Animal Behaviour 64:345-359.

King, M. B., and D. Duvall. 1990. Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging, and sex differences. Animal Behaviour 39:924–935.

King, R. B., W. B. Milstead, H. L. Gibbs, M. R. Prosser, G. M. Burghardt, and G. F. McCracken. 2001. Application of microsatellite DNA markers to discriminate between maternal and genetic effects on scalation and behavior in multiply-sired garter snake litters. Canadian Journal of Zoology 79:121–128

Klauber, L. M. 1972. Rattlesnakes Their Habits, Life Histories, and Influence on Mankind. Second Edition. Volume 1. University of California Press, Berkeley, California, USA.

Klemens, M. W., and J. B. Thorbjarnarson. 1995. Reptiles as a food resource. Biodiversity and Conservation 4:281–298.

Kojima, Y. 1991. Hebi no uchushi. Tokyo Bijutsu, Tokyo, Japan.

Kurihara, A. 1963. Mamushi aiyou. Tokuma shoten, Tokyo, Japan.

Labra, A., and R. Leonard. 1999. Intraspecific variation in antipredator responses of three species of lizards (*Liolaemus*): possible effects of human presence. Journal of Herpetology 33:441–448.

Lance, V. A. 1990. Stress in reptiles. Pages 461–466 *in* E. A. Epple, C. G. Scones, and M. H. Stetson, editors. Prospects in comparative cndocrinology. Wiley–Liss, New York, New York, USA.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science 57:659–668.

Law, R. 1979. Optimal life-histories under age-specific predation. American Naturalist 114:399–417.

Law, R., and D. R. Grey. 1989. Evolution of yields from populations with age-specific cropping. Evolutionary Ecology 3:343–359.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Lillywhite, H. B. 1991. The biology and conservation of acrochordid snakes. Hamadryad 16:1–9.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Losos, J. B., Schoener, T. W., Langerhans, R. B., and Spiller, D. A. 2006. Rapid temporal reversal of predator-driven natural selection. Science 314:1111.

Lucas, M.D., Drew, R.E., Wheeler, P.A., Verrell, P.A., and Thorgaard, G.H. 2004. Behavioral differences among rainbow trout clonal lines. Behavior Genetics 34: 355–365.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey, USA.

Macer, D. R. J., and T. Boyle. 1995. Science and Christianity in Japan. Journal: Perspectives on Science and Christian Faith 47:255–259.

McClain, J. L. 2001. Japan: a modern history. W. W. Norton, New York, New York, USA.

Madsen, J. 1985. Impact of disturbance on field utilization of pink-footed geese in West Jutland, Denmark. Biological Conservation 33:53–63.

Madsen, T., and R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. Journal of Animal Ecoloty 69:952–958.

Madsen, T., B. Ujvari, R. Shine, M. Olsson, and J. Loman. 2006. Rain, rats and pythons: climate-driven population dynamics of predators and prey in tropical Australia. Austral Ecology 31:30-37.

Magurran, A. E., B. H. Seghers, G. R. Carvalho, and P. W. Shaw. 1992. Behavioral consequences of an artificial introduction of guppies (*Poecilia reticulata*) in North Trinidad: evidence for the evolution of antipredator behavior in the wild. Proceedings of the Royal Society of London Series B Biological Sciences 248:117–122.

Magurran, A. E. 1999. The causes and consequences of geographic variation in antipredator behaviour. Pages 139–163 *in* S. A. Foster and J. A. Endler, editors. Geographic variation in behaviour: perspectives on evolutionary mechanisms. Oxford University Press, New York, New York, USA.

Magurran, A. E., and S. L. Girling. 1986. Predator model recognition and response habituation in shoaling minnows. Animal Behaviour 34:510–518.

Maron, J. L., M. Vilà, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecological Monographs 74:261–280.

Matson, T. K, A. W. Goldizen, and D. A. Putland. 2005. Factors affecting vigilance and flight behaviour of impalas. South African Journal of Wildlife Research 35:1–11.

Matsutani, M. 2003. Gendai minwa ko. Volume 9: kodama, hebi, ko no seirei, sensou to ki. Chikuma Shobo, Tokyo, Japan.

Matsuyama, M. 1998. Habut koushou ni matsuwaru minzoku to sono minkan ryouhou: Tokukwase buraku wo chushin ni sita. Pages 367–404 *in* K. Tanigawa, editor. Habu no minzoku: Nihon minzoku bunka shiryou shusse. Volume 20. Sanichi Shobo, Tokyo, Japan.

McDougall, P. T., D. Réale, D. Sol, and S. M. Reader. 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. Animal Conservation 9:39–48.

Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. American Naturalist 113:531–550.

Mizuno, T., N. Fujii, M. Kanzaki, and T. Yamakura. 1999. Fractal nature of spatial patterns in Japanese evergreen oak forest trees. Vegetation Science 16:103–113.

Moore, I. T., M. P. Lemaster, and P. T. Mason. 2000. Behavioural and hormonal responses to capture stress in the male red-sided garter snake, *Thamnophis sirtalis parietalis*. Animal Behaviour 59:529–534.

Mori, A., and G. M. Burghardt. 2000. Does prey matter? Geographic variation in antipredator responses of hatchlings of a Japanese natricine snake, *Rhabdophis tigrinus*. Journal of Comparative Psychology 114:408–413.

Moriguchi, H., and S. Takenaka. 1984. Reptiles and amphibians of Kaminokuni, Hokkaido. Nippon Herpetological Journal 28:1–22.

Müllner, A., K. E. Linsenmair, and M. Wikelski. 2004. Exposure to ecotourism reduces survival and affects stress response in Hoatzin chicks (*Opisthocomus hoazin*). Biological Conservation 118:549–558.

Nago, H. 2001. Akawan no yonooshi, Yui, Okinawa, Japan.

Naito, M. 1978. Kikikaki Tono monogatari. Shin-Jinbutsuoraisha, Tokyo, Japan.

Nakamura, K. 1998. Habu ni kansuru minzokugakutekikousatsu. Pages 405–415 *in* K. Tanigawa, editor. Habu no minzoku: Nihon minzoku bunka shiryou shusse. Volume 20. Sanichi Shobo, Tokyo, Japan.

Nakamura, M., and N. Furushou. 2004. Samukawa shuraku. Nakamura, M. and N. Furushou, Japan.

Nelson, K., and M. Soulé. 1987. Genetical conservation of exploited fishes. Pages 345–368 *in* N. Ryman and F. Utter, editors. Population Genetics and Fishery Management, Washington Sea Grant Program. University of Washington, Seattle, Washington, USA.

Nomoto, K. 2004. Kinbatsu denshou to irazu no mori. Pages 45–82 *in* M. Ueda, editor. Tankyu “chinju no mori”: shashougaku heno shoutai. Heibonsha, Tokyo, Japan.

Nosil, P., and B. J. Crespi. 2006. Ecological divergence promotes the evolution of cryptic reproductive isolation. Proceedings of the Royal Society of London Series B Biological Sciences 273:991–997.

Olsen, E. M., G. R. Lilly, M. Heino, M. J. Morgan, J. Brattey, and U. Dieckmann. 2005. Assessing changes in age and size at maturation in collapsing populations of

Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 62:811–823.

Olsen, E. M., M. Heino, G. R. Lilly, M. J. Morgan, J. Brattey, B. Ernande, and U. Dieckmann. 2004. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. Nature 428:932–935.

Omura, H. 2004. Trees, forests and religion in Japan. Mountain Research and Development 24:179–182.

Osemeobo, G. J. 1994. The role of folklore in environmental conservation: evidence from Edo state, Nigeria. International Journal of Sustainable Development and World Ecology 1:48-55.

O'Steen, S., A. J. Cullum, and A. F. Bennett. 2002. Rapid evolution of escape performance in Trinidad guppies (*Poecilia reticulata*). Evolution 56:776–784.

Ota, H., and H. Nakagawa. 1985. Notes on the specimens of reptiles deposited in Shiretoko Museum, Shari, eastern Hokkaido, Japan. Bulletin of Shiretoko Museum 7:1–6 (in Japanese with English summary).

Paik, N.-K., Min, M. S., Shim, J. H., Yang, S. Y. and Toriba, M. 1993. Isozyme analysis of the species of the genus *Agkistrodon* in far Eastern region. Snake 25:99–104.

Palumbi, S. R. 2001a. The Evolution Explosion: How Humans Cause Rapid Evolutionary Change. W. W. Norton, New York, New York, USA.

Palumbi, S. R. 2001b. Humans as the world's greatest evolutionary force. Science 293:1786–1790.

Parent, C., and P. J. Weatherhead. 2000. Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia 125:170–178.

Patten, M. A., D. H. Wolfe, E. Shochat, and S. K. Sherrod. 2005. Habitat fragmentation, rapid evolution, and population persistence. Evolutionary Ecology Research 7:235–249.

Phillips, B. L., and R. Shine. 2004. Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. Proceedings of the National Academy of Sciences 101:17150–17155.

Price, T., and D. Schluter. 1991. On the low heritability of life history traits. Evolution 45:853–861.

Ratner, S., and R. Lande. 2001. Demographic and evolutionary responses to selective harvesting in populations with discrete generations. Ecology 82:3093–3104.

Relyea, R. A. 2005. The heritability of inducible defenses in tadpoles. Journal of Evolutionary Biology 18:856–866.

Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112:183–198.

Reznick, D. N., F. H. Shaw, F. H. Rodd, and R. G. Shaw. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). Science 275:1934–1937.

Reznick, D. N., and H. Bryga. 1996. Life history evolution in guppies (*Poecilia reticulata*: Poeciliidae). V. Genetic basis of parallelism in life histories. American Naturalist 147:339–359.

Reznick, D. N, H. Bryga, and J. A. Endler. 1990. Experimentally-induced life history evolution in a natural population. Nature 346:357–59

Richardson, C. T., and C. K. Miller. 1997. Recommendations for protecting raptors from human disturbance: a review. Wildlife Society Bulletin 25:634–638.

Ricker, W. E. 1981. Changes in the average size and average age of Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 38:1636–1656.

Robison, B. D., and W. Rowland. 2005. A potential model system for studying the genetics of domestication: behavioral variation among wild and domesticated strains of zebra danio (*Danio rerio*). Canadian Journal of Fisheries and Aquatic Sciences 62:2046-2054.

Rodriguez, L., M. B. Sokolowski, and J. S. Shore. 1992. Habitat selection by *Drosophila melanogaster* larvae. Journal of Evolutionary Biology 5:61-70.

Romero, L. M., 2004. Physiological stress in ecology: lessons from biomedical research. Trends in Ecology and Evolution 19:249–255.

Rutter, C. 1902. Natural history of the quinnat salmon. A report of investigations in the Sacramento River, 1886–1901. Bulletin of the U.S. Fisheries Commission 22:65–141.

Sasaki, K, A. J. Place, and K. N. Gaylor. In Press. Attitudes toward rattlesnakes by the peoples of North America and its implications on rattlesnake conservation. Biology of the Rattlesnakes.

Sasaki, T. 2006. Yama no kami to nihonjin: yama no kami shinko kar saguru nihon no kisobunka. Yosensha, Tokyo, Japan.

Sasaki, K., and D. Duvall. 2003. Rainwater drinking by free-ranging Japanese pitvipers, *Gloydius blomhoffii*. Current Herpetology 22:43–44.

Sasamoto, S. 1994. Januke, ijin, kodama: rekishi saigai to denshou. Iwata Shoin, Tokyo, Japan.

Sato, H. 1952. Kindai shinsentan. Kangensha, Tokyo, Japan.

Sato, T. 1990. Tokachi no yasei: hebi II. Furusato Tokachi 15:16–17 (in Japanese).

Schaffer, W. M. 1974. Selection for optimal life histories : the effect of age structure. Ecology 55:291–303.

Schlaepfer, M. A., C. Hoover, and C. K. J. Dodd. 2005. Challenges in evaluating the impact of the trade in amphibians and reptiles on wild populations. BioScience 55:256–264.

Secor, S. M., and T. R. Nagy. 2003. Non-invasive measure of body composition of snakes using dual-energy x-ray absorptiometry. Comparative Biochemistry and Physiology Part A 136:379–389.

Seeley, R. H. 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. Proceedings of the National Academy of Sciences 83:6897–6901.

Senda, M. 1992. Japan’s traditional view of nature and interpretation of landscape. GeoJournal 26:129–134.

Sengoku, S. 1996. Aodaisho. Pages 84–86 *in* S. Sengoku, T. Hikida, M. Matsui, K. Nakaya, editors. The encyclopaedia of animals in Japan 5: amphibians, reptiles, chondrichthes. Heibonsha, Tokyo, Japan.

Shiki Elementary School. 1979. Furusato Shiki. Shiki Elementary School, Anjo, Aichi, Japan.

Sih, A., L. B. Kats, and E. F. Maurer. 2003 Behavioral correlations across situations and the evolution of ineffective antipredator behavior in a sunfish–salamander system. Animal Behaviour 65:29–44.

SPSS Inc. 2005. SPSS 14.0 for Windows. Release 14.0.0. SPSS, Inc., Chicago, Illinois, USA.

Stokes, K., and R. Law. 2000. Fishing as an evolutionary force. Marine Ecology-Progress Series 208:307–309.

Stoks, R., M. A. McPeek, and J. L. Mitchell. 2003. Evolution of prey behavior in response to changes in predation regime: damselflies in fish and dragonfly lakes. Evolution 57:574–85.

Strauss, R. E. 1990. Predation and life-history variation in *Poecilia reticulata* (Cyprinodontiformes: Poeciliidae). Environmental Biology of Fishes 27:121–130.

Strauss, S. Y., J. A. Lau, and S. P. Carroll. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? Ecology Letters 9:357–374.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.

Stergiou, K. I., 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. Fisheries Research 55:1–9.

Stokes, T. K., J. M. McGlade, and R. Law. 1993. The exploitation of evolving resources. Lecture Notes in Biomathematics No. 99. Springer-Verlag, Berlin, Germany.

Takara, T. 1998. Habu = Hanbida. Pages 103–208 *in* K. Tanigawa, editor. Habu no minzoku: Nihon minzoku bunka shiryou shusse. Volume 20. Sanichi Shobo, Tokyo, Japan.

Teyler, T. J. 1984. A Primer of Psychobiology: Brain and Behavior. Second edition. W. H. Freeman, New York, New York, USA.

Thompson, J. N., O. J. Reichman, P. J. Morin, G. A. Polis, M. E. Power, R. W. Sterner, C. A. Couch, L. Gough, R. Holt, D. U. Hooper, F. Keesing, C. R. Lovell, B. T. Milne, M. C. Molles, D. W. Roberts, S. Y. Strauss. 2001. Frontiers of ecology. Bioscience 51:15–24.

Thompson, J. N. 1999. The evolution of species interactions. Science 284:2116–2118.

Thompson, J. N. 1998. Rapid evolution as an ecological process. Trends in Ecology and Evolution 13:329–331.

Thompson, W. R. 1957. Influence of prenatal maternal anxiety on emotionality in young rats. Science 125:689–699.

Thorpe, W. H. 1963. Learning and Instinct in Animals. Harvard University Press, Cambridge, Massachusetts, USA.

Toriba, M. 1996. Mamushi, habu, beni-hebi, Pages 101–102 *in* S. Sengoku, T. Hikida, M. Matsui, K. Nakaya, editors. The encyclopaedia of animals in Japan 5: amphibians, reptiles, chondrichthes. Heibonsha, Tokyo, Japan.

Turchin, P. 2003. Evolution in population dynamics. Nature 424:257–258.

Trut, L. N. 1999. Early canid domestication: the farmfox experiment. American Scientist 87:160–169.

Uller, T., and M. Olsson. 2006. Direct Exposure to Corticosterone During Embryonic Development Influences Behaviour in an Ovoviviparous Lizard. Ethology 112:390–397.

Vallée, M., W. Mayo, F. Dellu, M. Le Moal, H. Simon, S. Maccari. 1997 Prenatal stress induces high anxiety and postnatal handling induces low anxiety in adult offspring: correlation with stress induced-corticosterone secretion. Journal of Neuroscience 17:2626–2636.

van Oers, K., P. J. Drent, P. de Goede, and A. J. van Noordwijk. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. Proceedings of the Royal Society of London Series B Biological Sciences 271:65–73.

Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory 1:1–30.

Vourc'h, G., J. Russell, and J-L, Martin. 2002. Linking deer browsing and terpene production among genetic identities in *Chamaecyparis nootkatensis* and *Thuja plicata* (Cupressaceae). The Journal of Heredity 93:370–376.

Walker, B. G., P. D. Boersma, J. C. Wingfield. 2005. Field endocrinology and conservation biology. Integrative and Comparative Biology 45:12–18.

Walker, B. L. 2004. Meiji modernization, scientific agriculture, and the destruction of Japan's Hokkaido wolf. Environmental History 9:248–274.

Walsh, M. R., S. B. Munch, S. Chiba, D. O. Conover. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. Ecology Letters 9:142–148.

Webb, J. K., G. P. Brown, and R. Shine. 2001. Body size, locomotor speed and antipredator behaviour in a tropical snake (*Tropidonophis mairii*, Colubridae): the influence of incubation environments and genetic factors. Functional Ecology 15:561–568.

Weinstock, M. 2001. Alterations induced by gestational stress in brain morphology and behaviour of the offspring. Progress in Neurobiology 65:427–451.

Wellborn, G. A. 1994. Size-biased predation and prey life histories: a comparative study of freshwater amphipod populations. Ecology 75: 2104–2117.

Yamamoto, T. and U. G. Reinhardt. 2003. Dominance and predator avoidance in domesticated and wild masu salmon *Oncorhynchus masou*. Fisheries Science 69:88–94.

Yanagita, K. 1935. Tono monogatari shui. Kyoudo Kenkyusha, Tokyo, Japan.

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, N. G. Hairston. 2003. Rapid evolution drives ecological dynamics in a predator-prey system. Nature 424:303–306.

Yoshida, C. 1980. Habu to ningen. Ryukyushinpo, Okinawa, Japan.

Yoshino, H. 2000. Hebi: nihon no hebi shinkou. Kodansha, Tokyo, Japan.

Yoshino, H. 2001. The snake cult in Japan. Pages 85–92 *in* Y. Yasuda, editor. Forest and civilisations. Lustre Press Pvy.Ltd. and Roli Books Pvt. Lt., New Delhi, India.

Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

Zhou, Z., and Z. Jiang. 2004. International trade status and crisis for snake species in China. Conservation Biology 18:1386–1394.

Table 1. *Selected summary statistics ($\bar{x}$ ± 1 SE and sample size in parentheses) for males and nonpregnant and pregnant female of adult mamushi in Hokkaido, Japan, studied between 1999 and 2002.

	Compromised populations			Uncompromised populations		
Dependent characters	Male	Nonpregnant	Pregnant	Male	Nonpregnant	Pregnant
SVL (cm)	48.2 ± 0.9 (22)	49.6 ± 0.7 (31)	51.4 ± 0.5 (37)	52.3 ± 0.7 (54)	52.6 ± 0.5 (71)	55.1 ± 0.5 (77)
BM (g)	114.2 ± 6.8 (21)	149.6 ± 5.4 (31)	187.1 ± 6.7 (37)	139.8 ± 4.1 (53)	170.6 ± 3.3 (70)	211.0 ± 4.4 (75)
FTR (cm)	69.4 ± 5.7 (21)	58.1 ± 4.5 (30)	54.9 ± 4.5 (33)	39.8 ± 2.9 (54)	26.8 ± 2.2 (66)	15.9 ± 2.0 (70)
Defensiveness	1.1 ± 0.1 (21)	1.2 ± 0.1 (30)	1.0 ± 0.0 (33)	2.0 ± 0.2 (53)	2.0 ± 0.2 (66)	1.3 ± 0.1 (69)
Emergence latency (min)	–	–	38 ± 9.7	–	–	7.4 ± 1.1
Percent of microhabitat cover	63.3 ± 5.6 (21)	45.3 ± 4.4 (31)	17.7 ± 2.0 (33)	32.5 ± 4.2 (53)	27.5 ± 2.9 (64)	17.4 ± 1.8 (73)

* Values in parentheses equal the number of snakes sampled per dependent variable; BM = body mass, SVL = snout-vent length. Body condition is a residual score derived from a general linear regression of log BM against log SVL. FTR (Flight threshold radius) is a measure of snake to predator proximity, where a snake shifts from immobility (static, cryptic) to fleeing (locomotive escape). Defensiveness indicates the rank of 3-unit behavioral sequences (e.g., flee → flee → flee; see text) in order of increasing defensiveness, with rank 1 being the least defensive and 8 being the most defensive. Emergence latency indicates the time taken (latency) for snakes to emerge from refuge after their escape from my approach. Percent of microhabitat cover indicates surface cover percentage for dense vegetation that potentially acts as concealment for snakes within a 80-cm circle surrounding a snake.

Table 2. Distances moved and the number of moves in males (M), pregnant (PF) and nonpregnant (NPF) females for radio-tracked mamushi in Hokkaido, Japan.

Sex		Total distance (Number of moves)				
M	ID Mo.	4053 (7/24-8/30)	4050_363.259 (8/14-10/27)	AM12 (9/11-12/14)	4450 (8/28-12/14)	4266_Chugai (8/21-9/10)
	Jun	-	-	-	-	-
	Jul	20 (4)	-	-	-	-
	Aug	46 (3)	17 (3)	-	-	15 (1)
	Sept	-	65 (5)	19 (3)	55 (5)	15 (1)
	Oct	-	220 (4)	15 (5)	6 (1)	-
NPF	ID Mo.	4150_Black (9/13-11/11)	4210 (9/11-10/15)	B1 (9/3-10/26)	024.376.021 (6/16-8/10)	5385 (8/21-10/26)
	Jun	-	-	-	10 (2)	-
	Jul	-	-	-	-	-
	Aug	-	-	-	25 (1)	0 (0)
	Sept	51 (1)	67 (2)	36 (2)	-	0 (0)
	Oct	136 (6)	28 (3)	0 (0)	-	160 (5)
PF	ID Mo.	024.256.017 (5/31-9/18)	023.532.334 (6/7-6/18)	A9 (7/5-7/17)	*024.264.851 (6/29-9/26)	*023.638.297 (6/26-10/17)
	Jun	0 (0)	0 (0)	-	-	0 (0)
	Jul	0 (0)	-	0 (0)	0 (0)	15 (1)
	Aug	0 (0)	-	-	0 (0)	0 (0)
	Sept	0 (0)	-	-	0 (0)	0 (0)
	Oct	0 (0)	-	-	-	25 (1)

Note: Values are in meters; number of movements is shown in parentheses.

* Pregnant female not radiotracked but frequently observed directly.

Table 2. Continued.

Sex	ID / Mo.	Total distance in m (number of episode)				
M	ID / Mo.	4480 (8/14-10/27)	4171 (9/9-9/13)	023.621.787 (9/1-10/6)		Mean
	Jun	-	-	-		-
	Jul	-	-	-		20 (4.0)
	Aug	10 (4)	-	-		22 (2.8)
	Sept	9 (4)	25 (1)	50 (1)		34 (2.9)
	Oct	0 (0)	-	-		60 (2.5)
NPF	ID / Mo.	4093 (6/9-6/26)	023.553.817 (5/30-6/18)	4194 (8/30-10/14)	FA (6/27-6/30)	Mean
	Jun	61 (4)	69 (4)	-	3 (2)	36 (3.0)
	Jul	-	-	-	-	-
	Aug	-	-	-	-	25 (1)
	Sept	-	-	19 (1)	-	43 (1.5)
	Oct	-	-	160 (5)	-	96 (3.8)
PF	ID / Mo.	*024.256.629 (5/29-10/11)	*023.871.623 (8/26-9/13)	*C1 (10/3-10/27)	C5-4450 (10/10-10/17)	Mean
	Jun	0 (0)	-	-	-	0 (0)
	Jul	0 (0)	-	-	-	3 (0.2)
	Aug	30 (1)	60 (1)	-	-	15 (0.4)
	Sept	0 (0)	0 (0)	-	-	0 (0)
	Oct	0 (0)	0 (0)	50 (1)	70 (1)	6 (0.3)

Figure 1. Photograph illustrating Japanese mamushi, ***Gloydius blomhoffii***, in Hokkaido.

Figure 2. Map of Japan, showing four major islands (Hokkaido, Honshu, Shikoku, and Kyushu) where Japanese mamushi (*Gloydius blomhoffii*) inhabit.

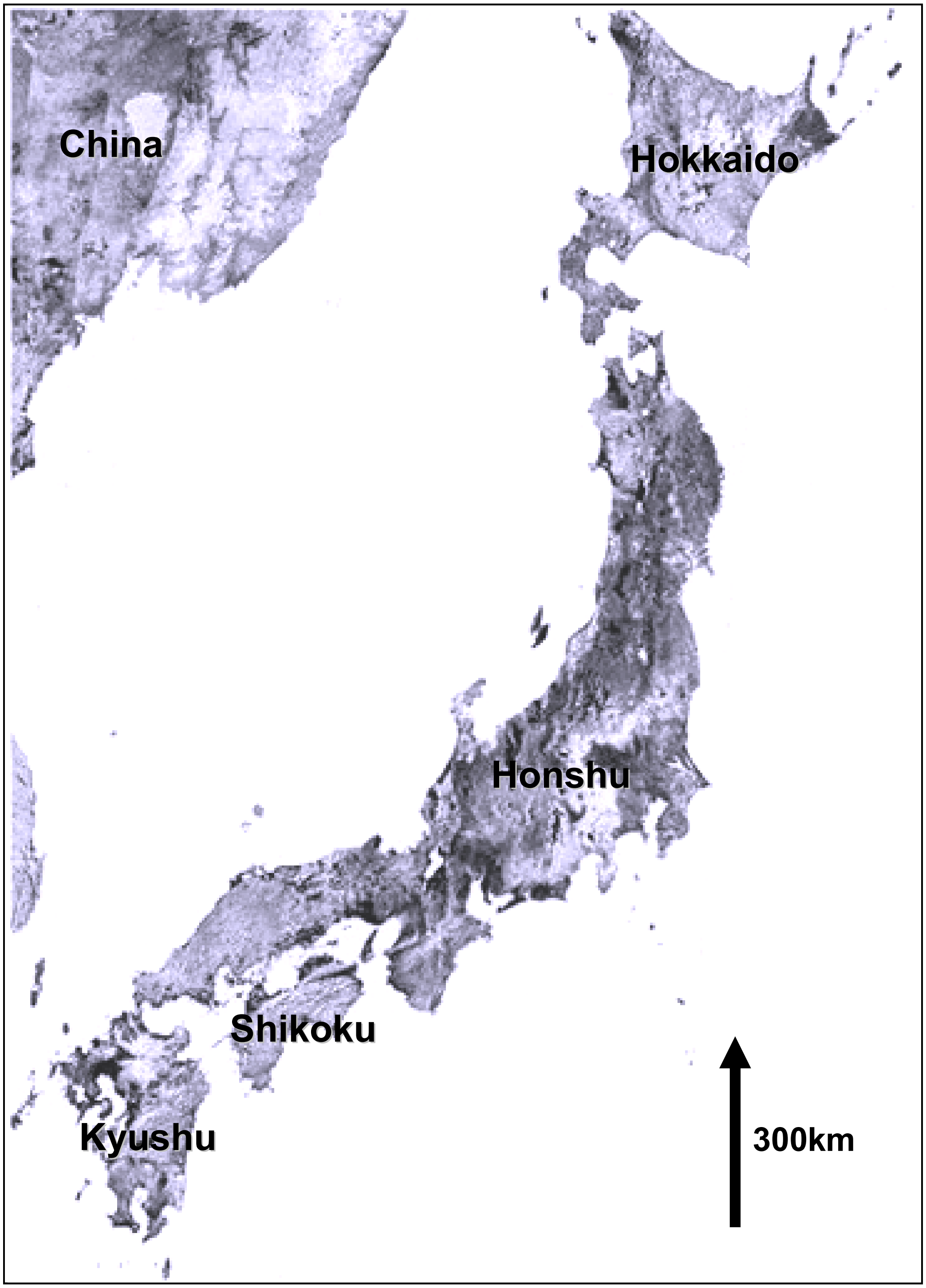


Figure 3. Number of males found during 1999-2002 and of shedding individuals (including those are about to shed or immediately after shedding). A horizontal bar indicates a duration when male aggregations were observed.

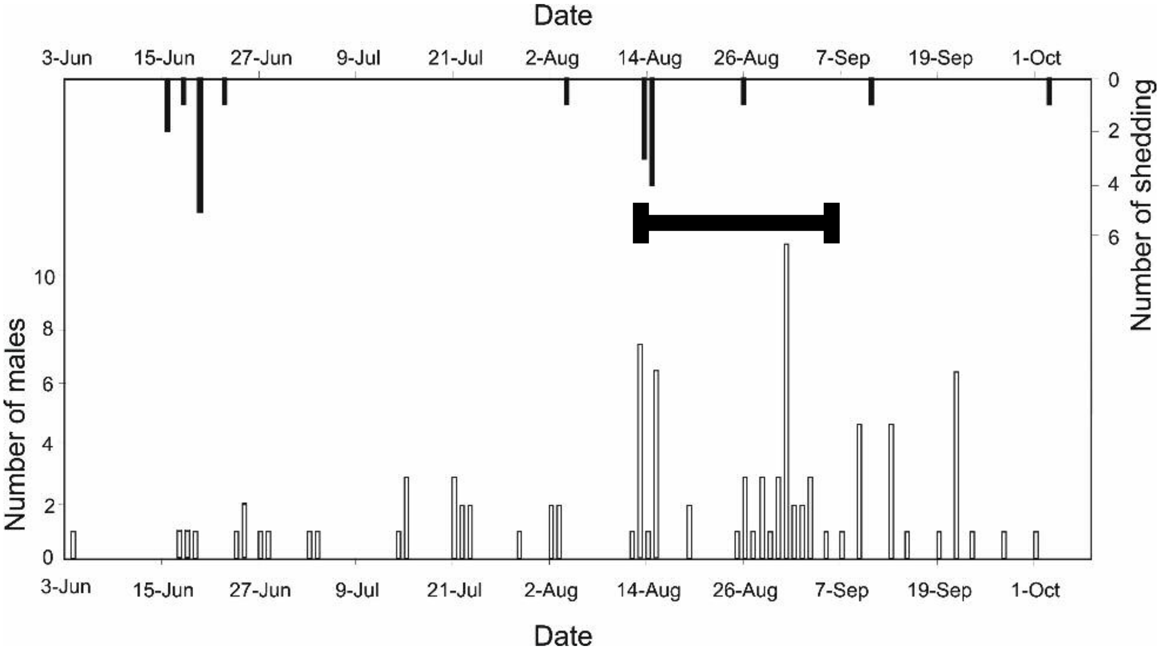


Figure 4. Distribution of compromised (triangles) and uncompromised (circles) populations in the study area. Numbers within symbols represent number of snakes (The actual number used for analyses varies depending on variables).

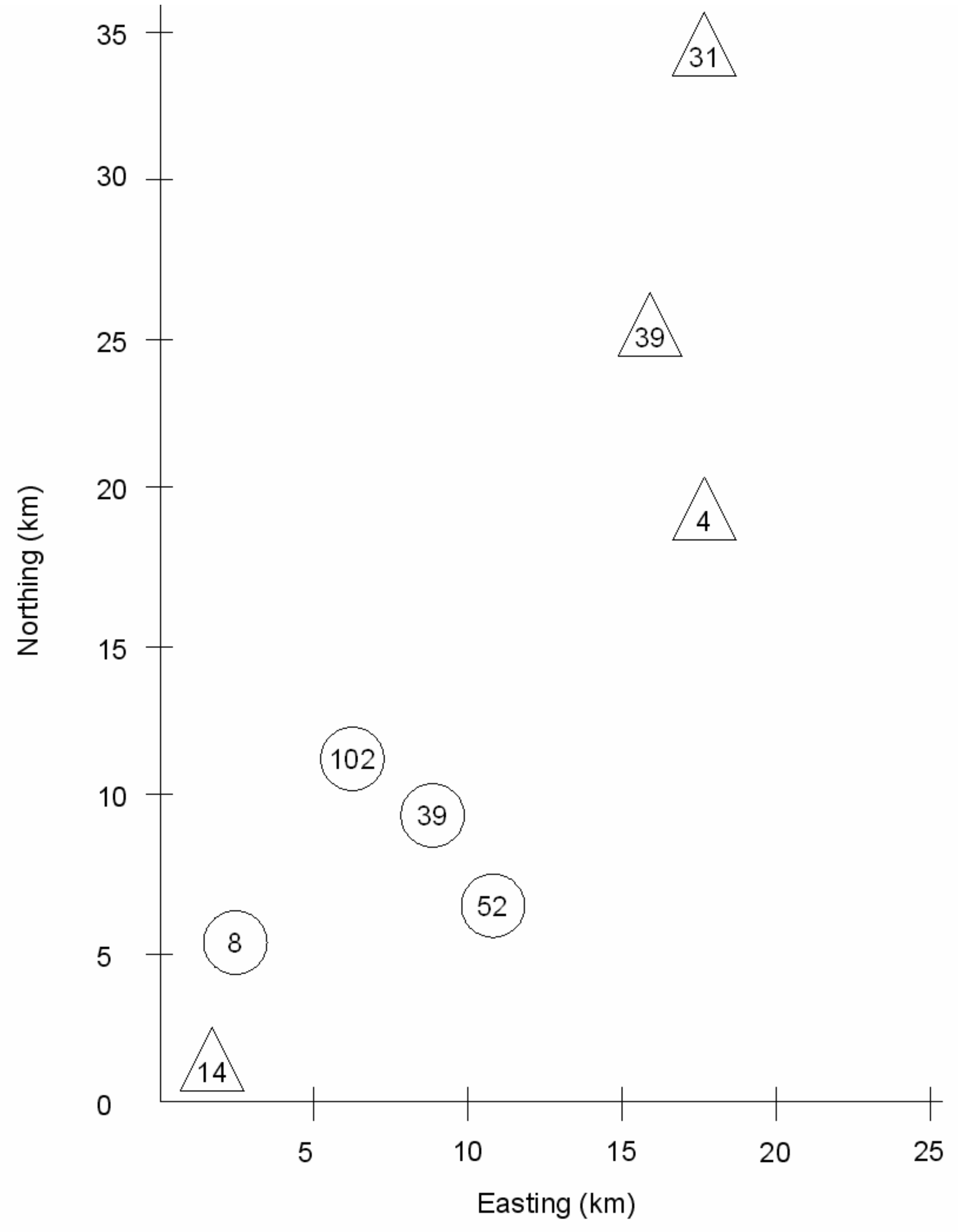


Figure 5. Examples of compromised (top) and uncompromised (bottom) sites.

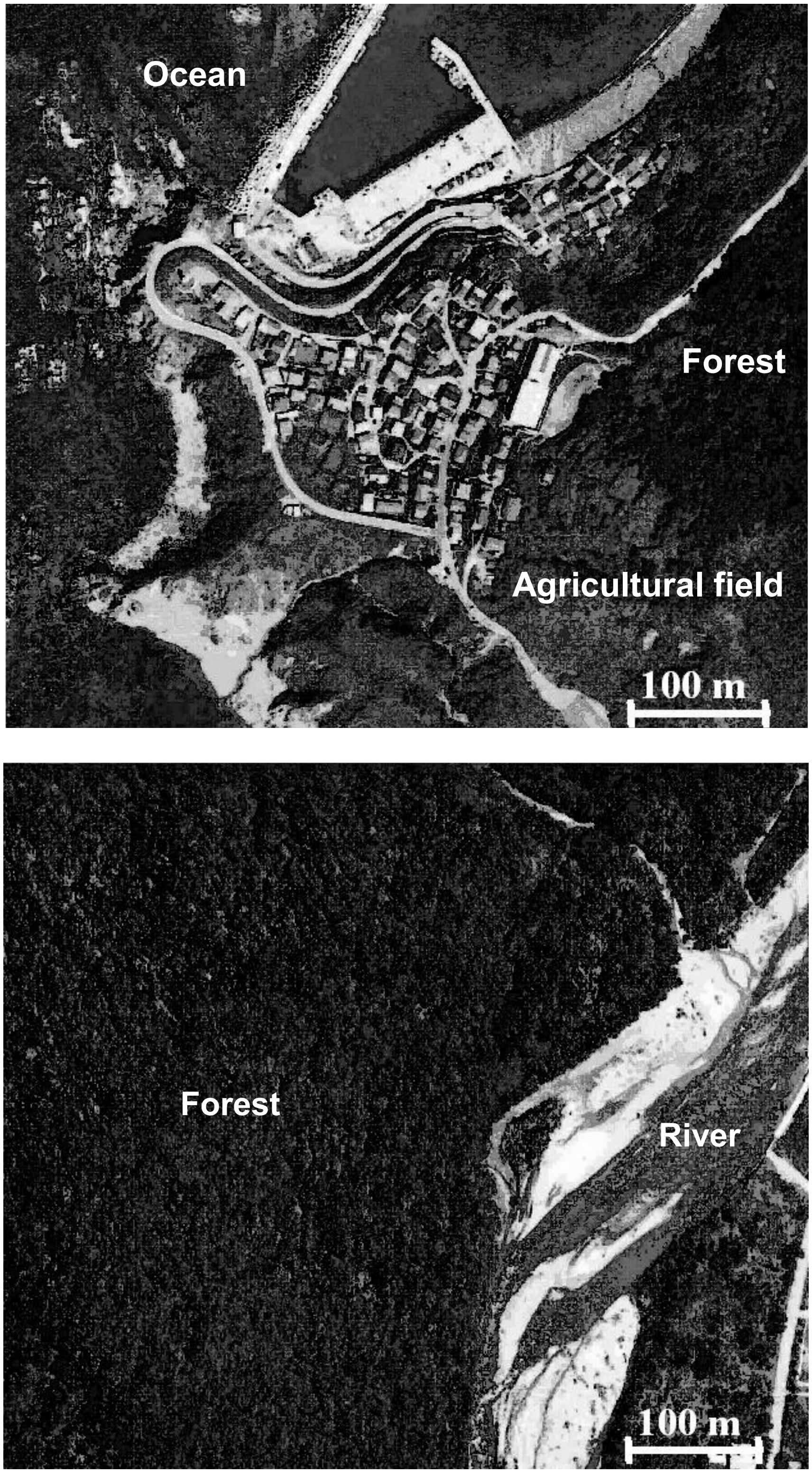


Figure 6. Logistic regression (with snout-vent length [SVL] as an explanatory variable) showing the observed proportions (circles) and the estimated probability (line) of mortality at the HMSC site (not assigned to either compromised or uncompromised; n = 42).

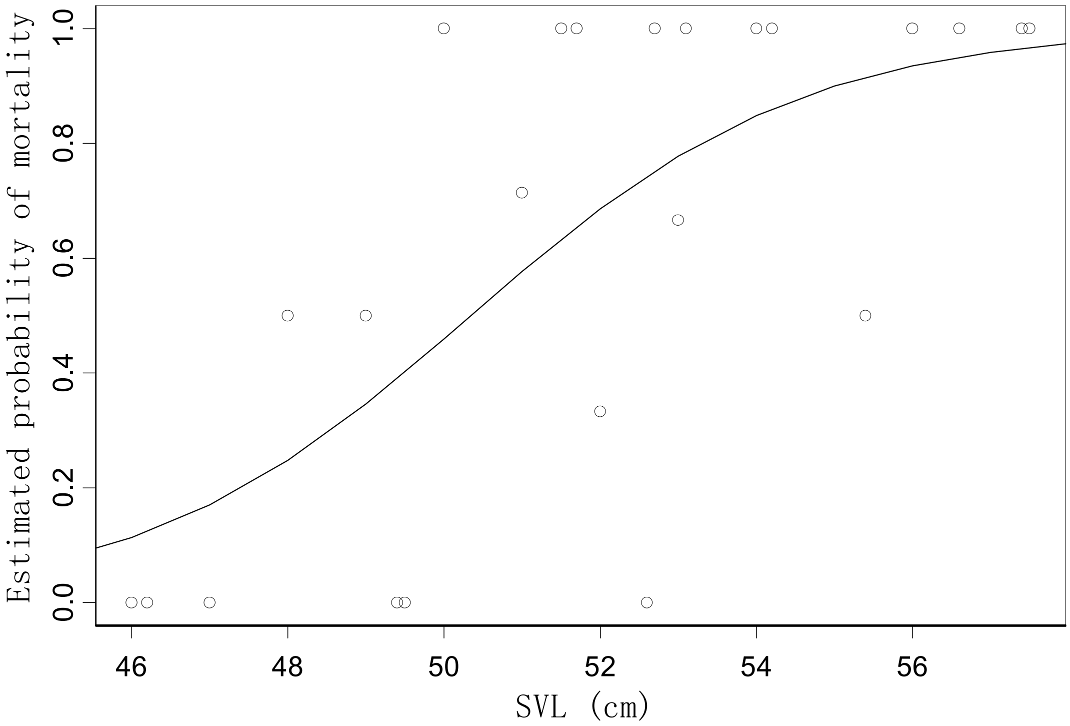


Figure 7. Adult snout-vent length (SVL) distribution in uncompromised (top panel; n = 202) and compromised (bottom panel; n = 90) populations.

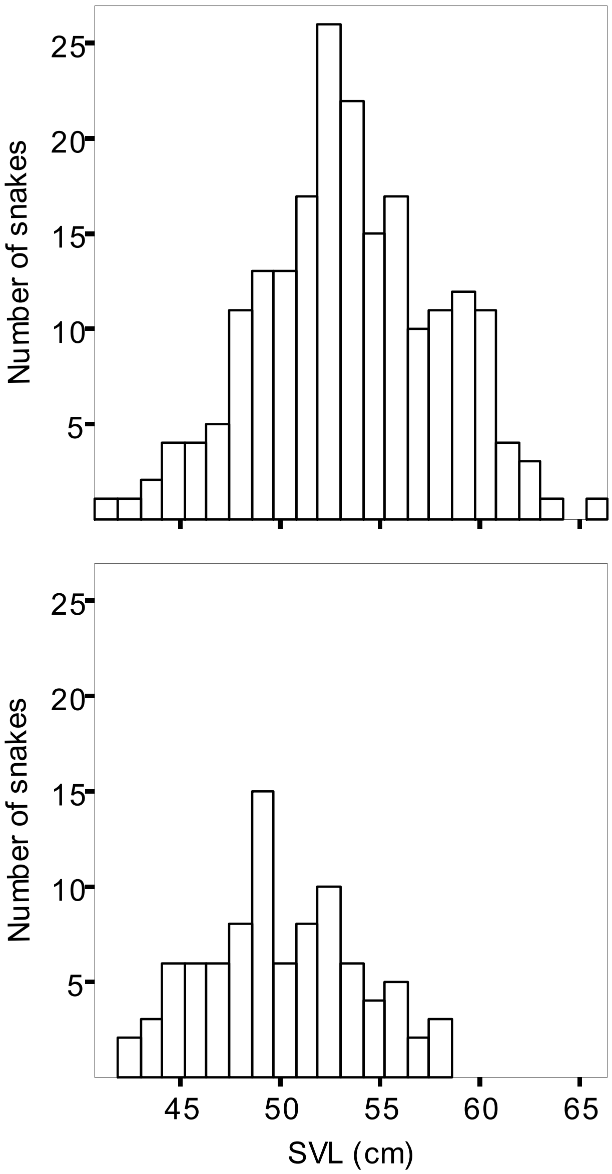


Figure 8. Snout-vent length (SVL) of nonpregnant and pregnant female and male adult mamushi in compromised (n = 90) and uncompromised (n = 202) populations. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values, excluding outliers (values > 1.5 times the interquartile range; denoted as open circles).

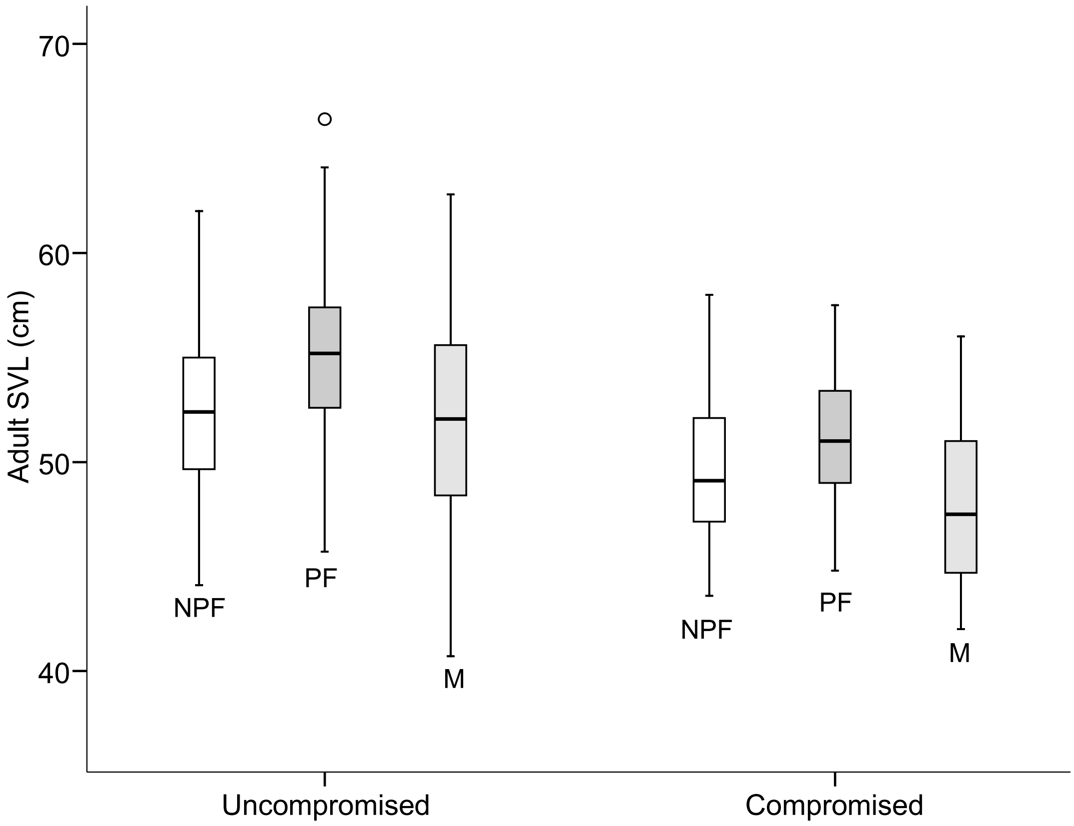


Figure 9. Neonatal snout-vent length (SVL) distribution in uncompromised (top panel; n = 108) and compromised (bottom panel; n = 74) populations.

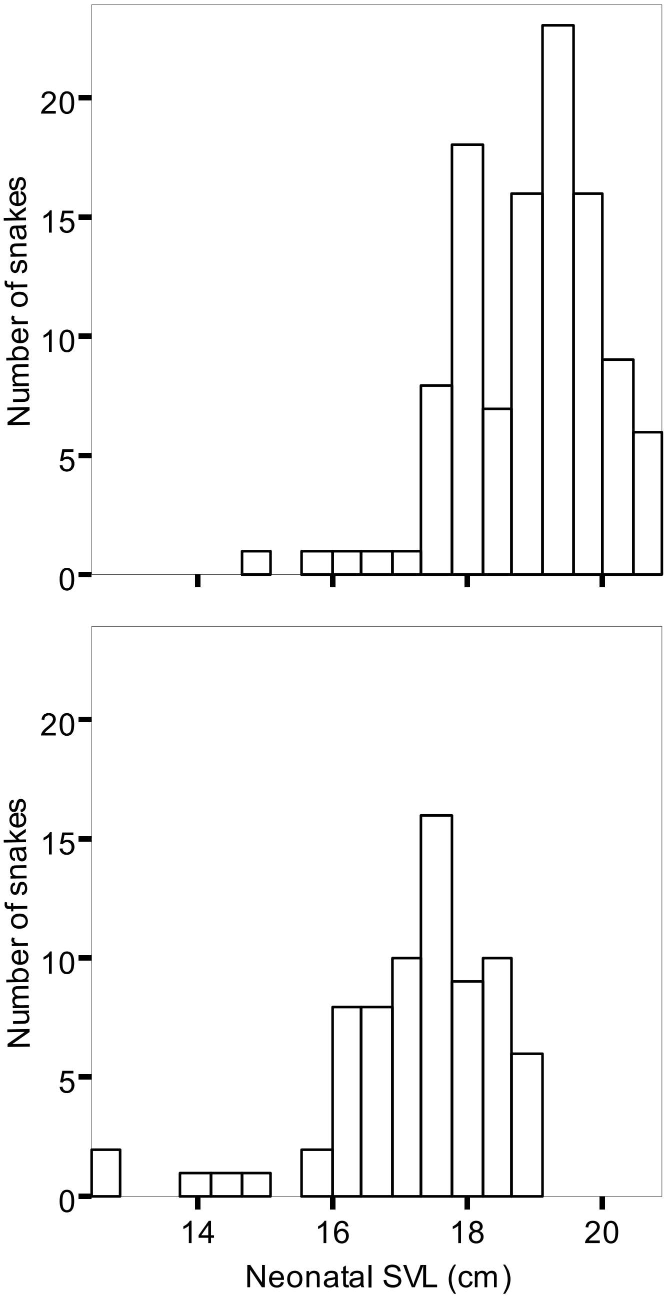


Figure 10. Snout-vent length (SVL) of neonate female and male mamushi in compromised (n =74) and uncompromised (n = 108) populations. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values, excluding outliers (values > 1.5 times the interquartile range; denoted as open circles).

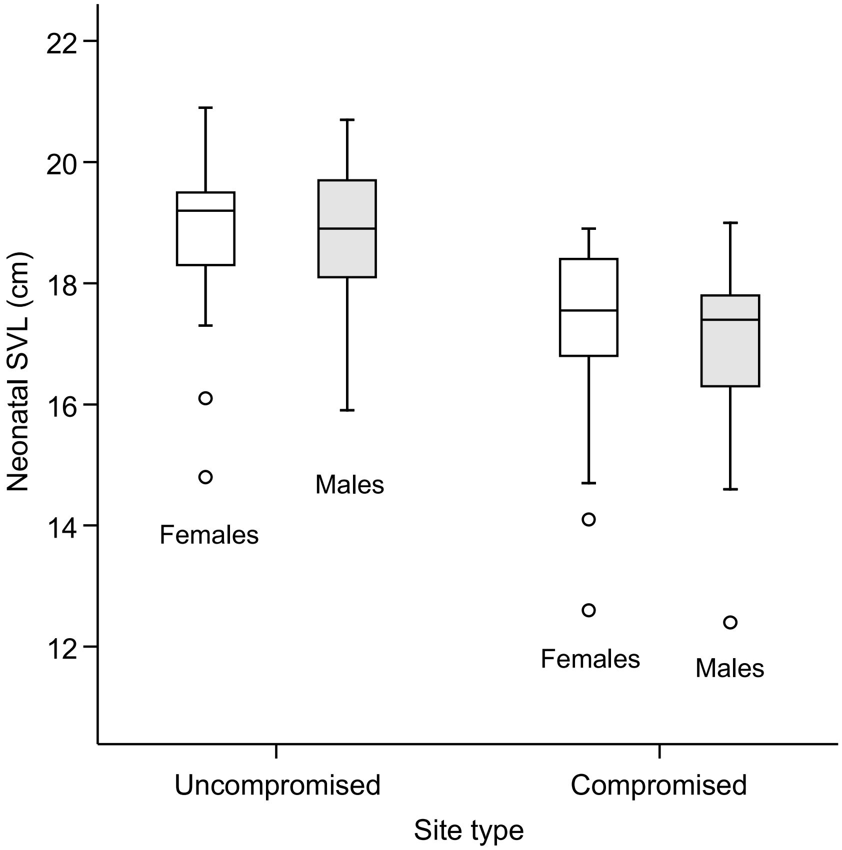


Figure 11. Neonatal snout-vent length (SVL) in relation to maternal SVL in mamushi in compromised (pluses) and uncompromised (circles) sites.

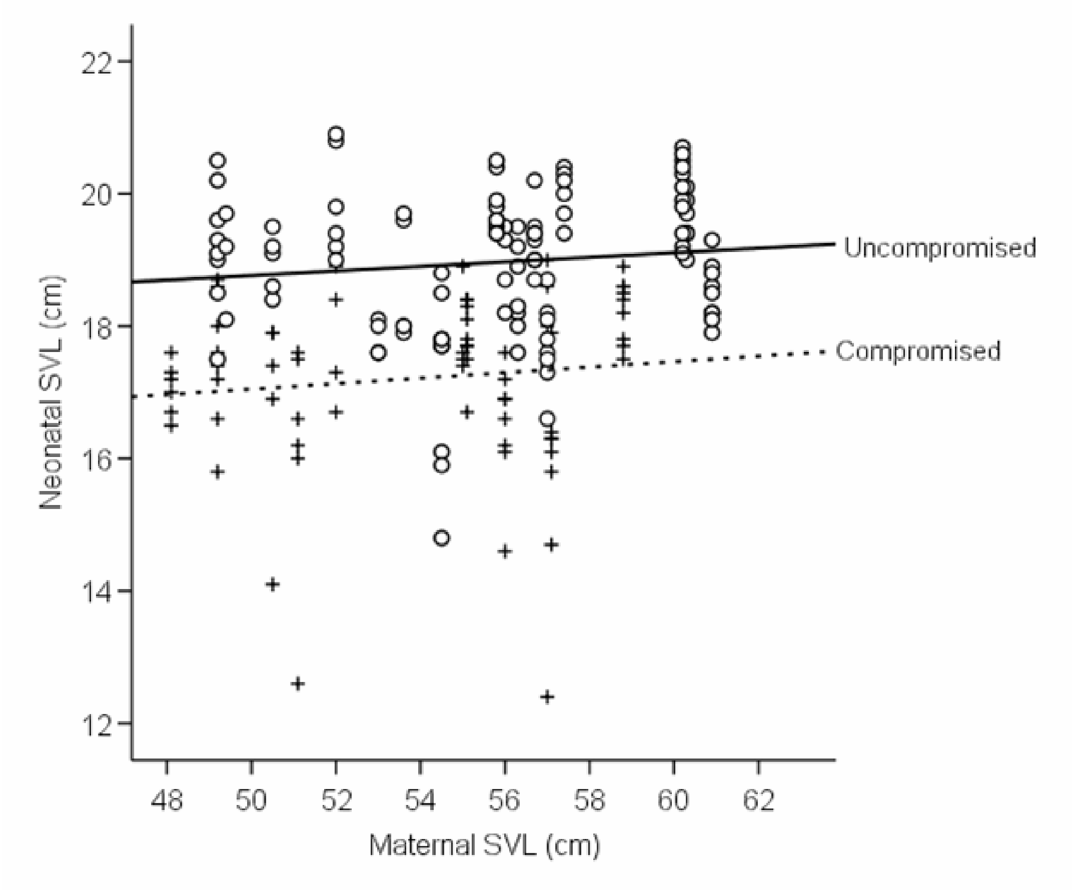


Figure 12. Logistic regression (with flight threshold radius [FTR] as an explanatory variable) showing the observed proportions (circles) and the estimated probability (line) of mortality at the HMSC site (not assigned to either compromised or uncompromised; n = 42).

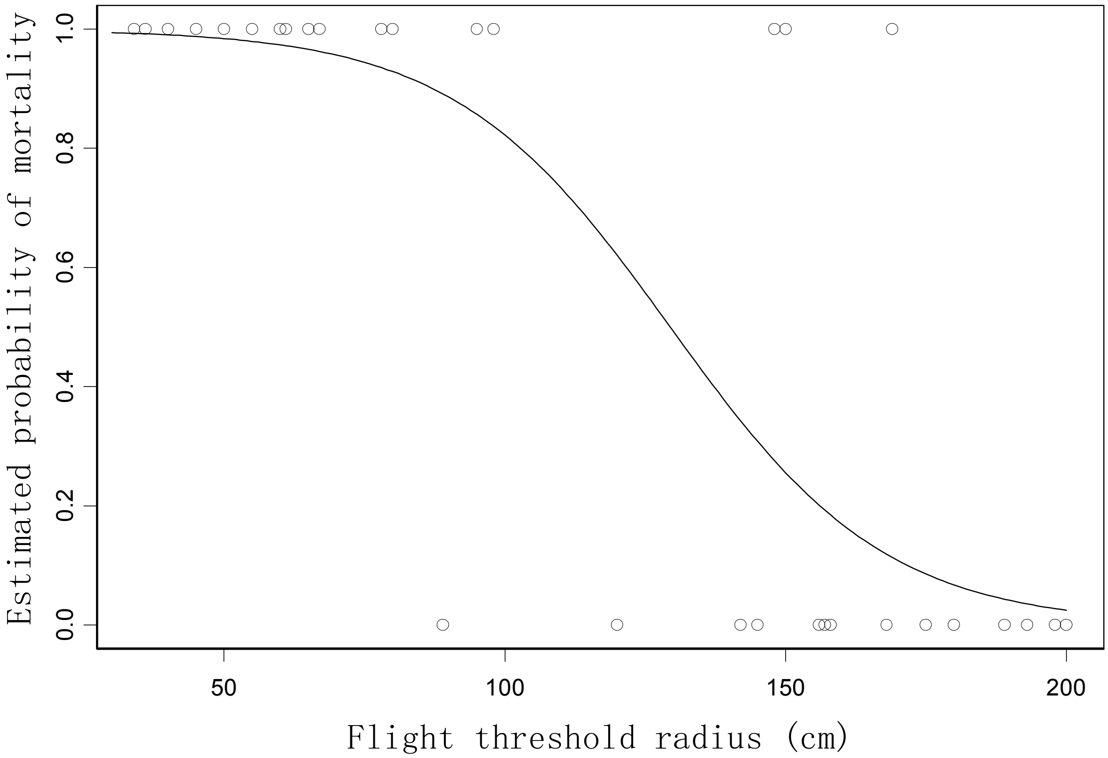


Figure 13. Flight threshold radius (FTR) of nonpregnant female (NPF), pregnant female (PF), and male (M) adult mamushi in compromised (n = 89) and uncompromised (n = 198) populations. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values, excluding outliers (values > 1.5 times the interquartile range; denoted as open circles) and extreme values (values > 3 times the interquartile range; denoted by asterisks).

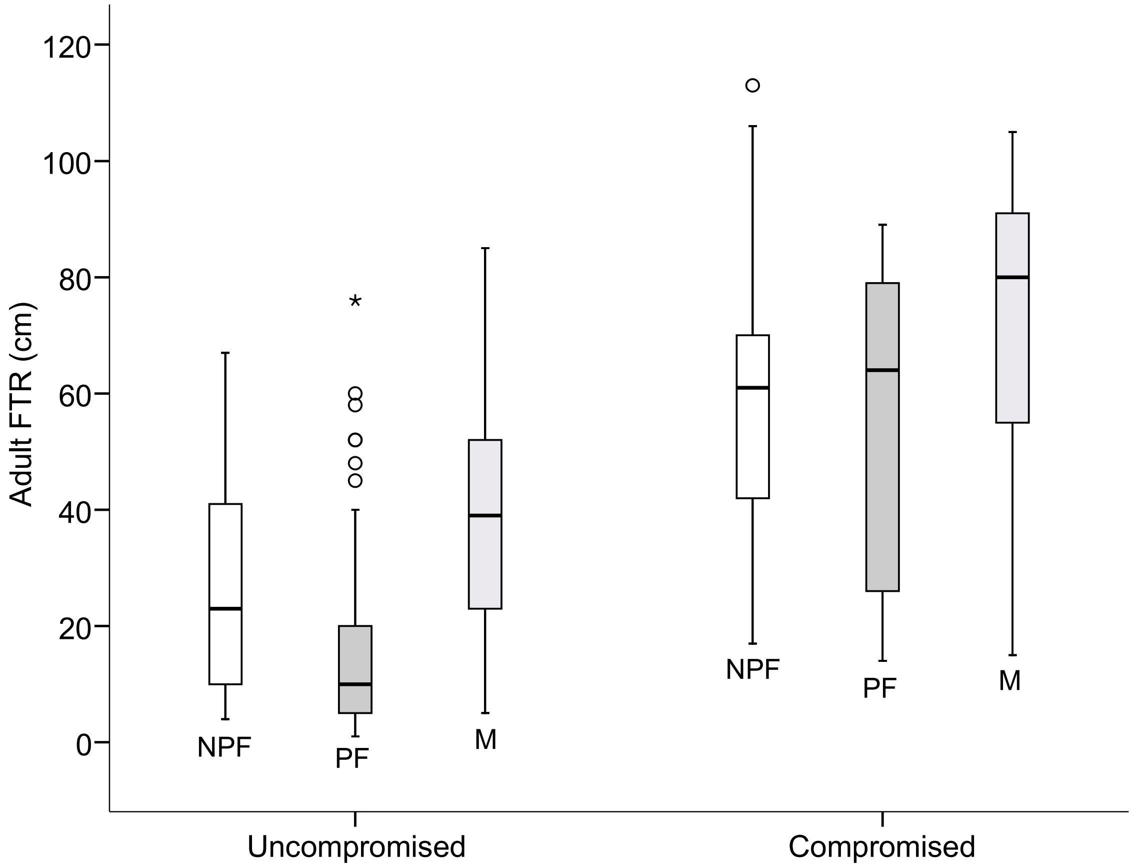


Figure 14. Flight threshold radius (FTR) of mamushi neonates born to wild-caught females from compromised (n = 24) and uncompromised (n = 20) populations. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values.

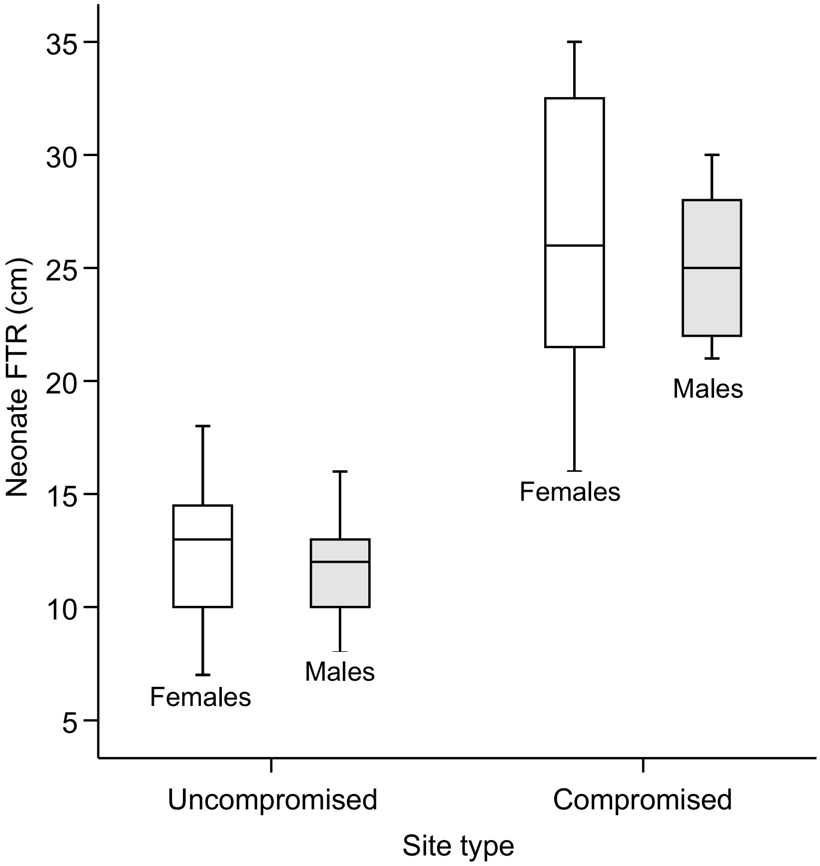


Figure 15. Logistic regression (with threatening defense rank as an explanatory variable) showing the observed proportions (circles) and the estimated probability (line) of mortality at the HMSC site (not assigned to either compromised or uncompromised; n = 42).

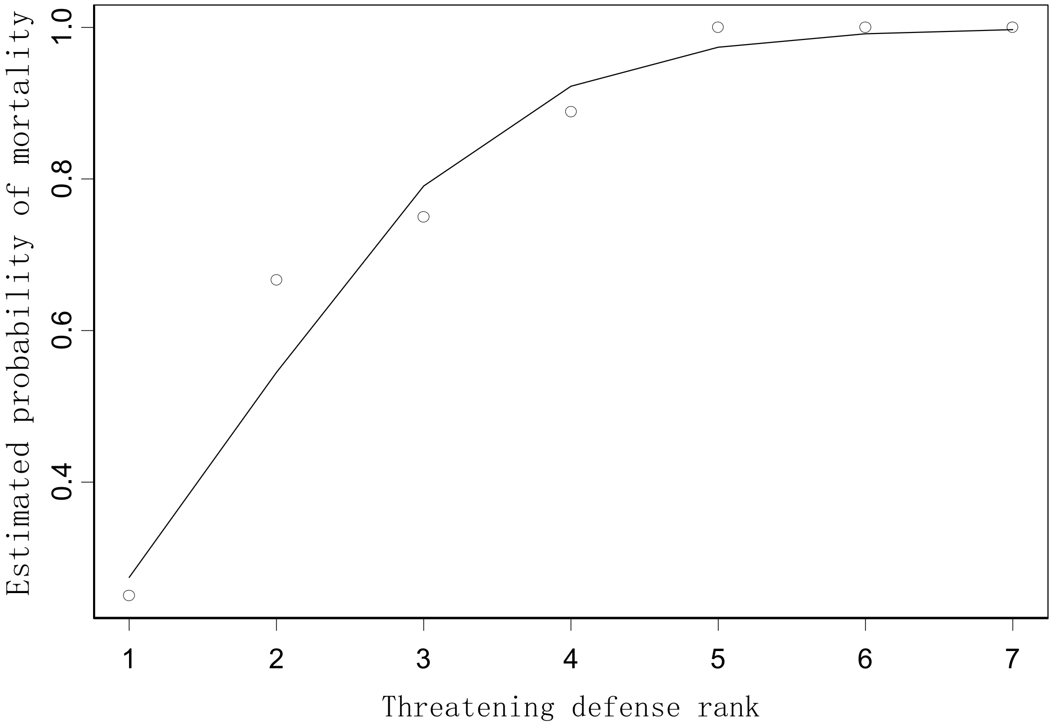


Figure 16. Defensiveness rank of nonpregnant female (NPF), pregnant female (PF), and male (M) adult mamushi in uncompromised (n = 188) and compromised (n = 83) sites. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values, excluding outliers (values > 1.5 times the interquartile range; denoted as open circles) and extreme values (values > 3 times the interquartile range; denoted by asterisks).

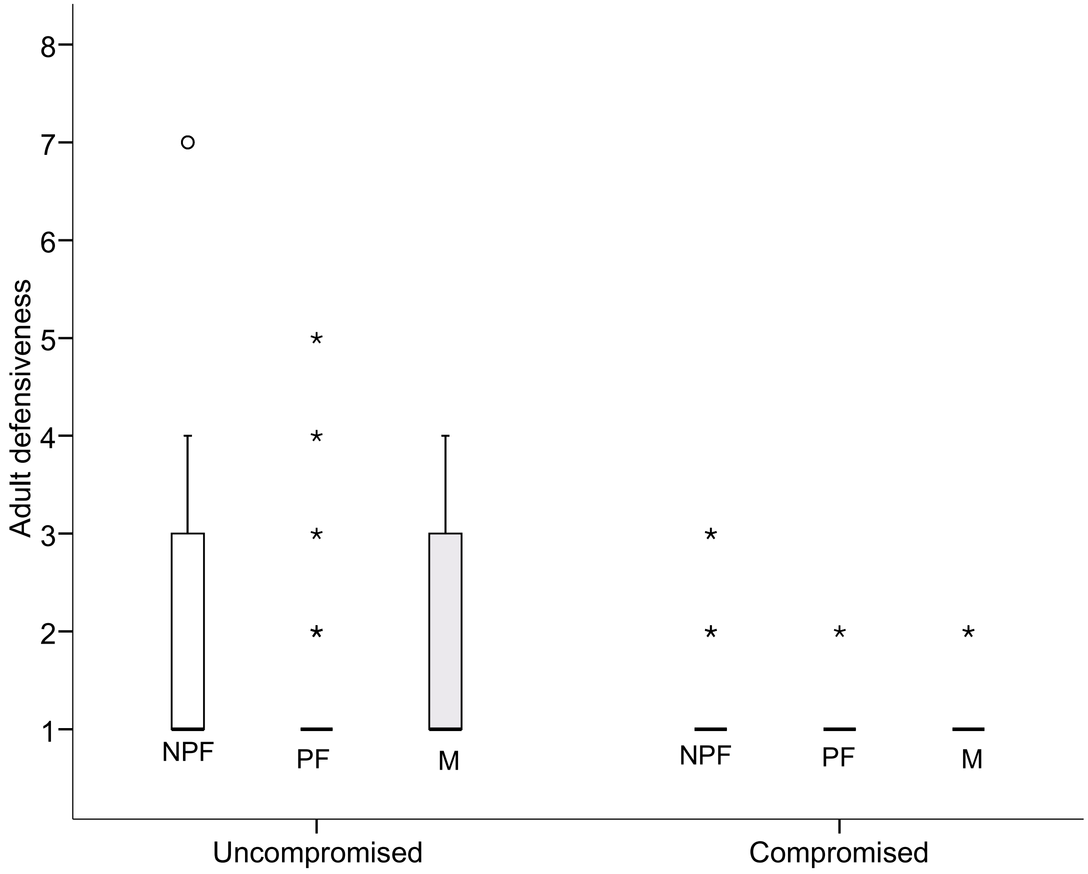


Figure 17. Defensiveness rank of mamushi neonates in uncompromised (n = 20) and compromised (n = 24) sites. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values, excluding outliers (values > 1.5 times the interquartile range; denoted as open circles) and extreme values (values > 3 times the interquartile range; denoted by asterisks).

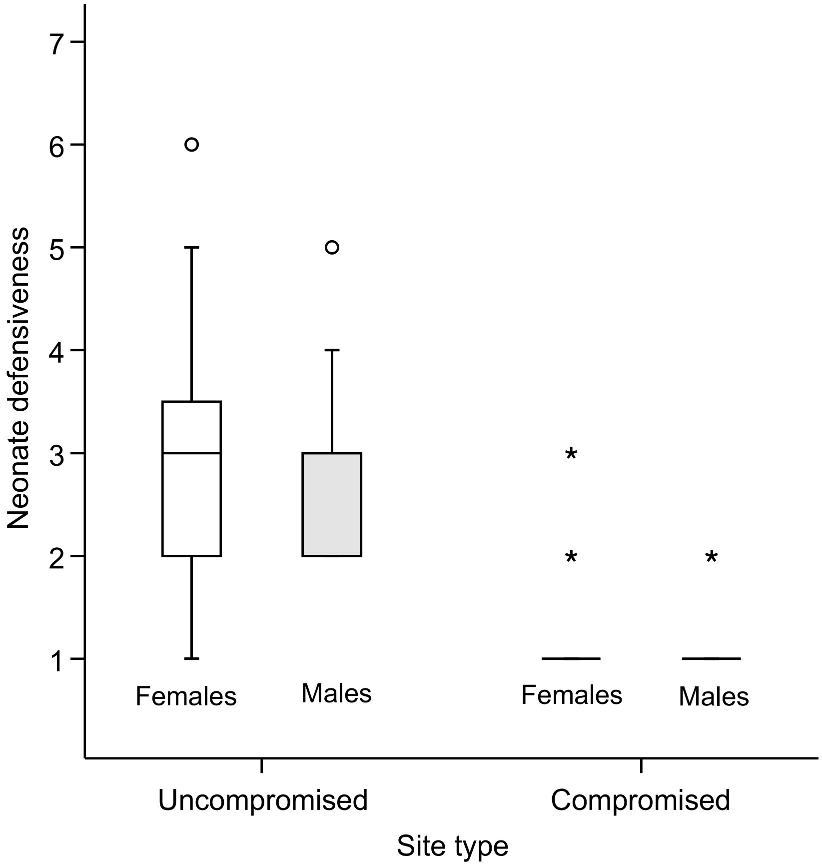


Figure 18. Changes in flight threshold radius (FTR) in response to repeated human approaches in uncompromised (top panel) and compromised (bottom panel) sites. Each line represents an adult individual that was tested daily over consecutive 8 days in 2001.

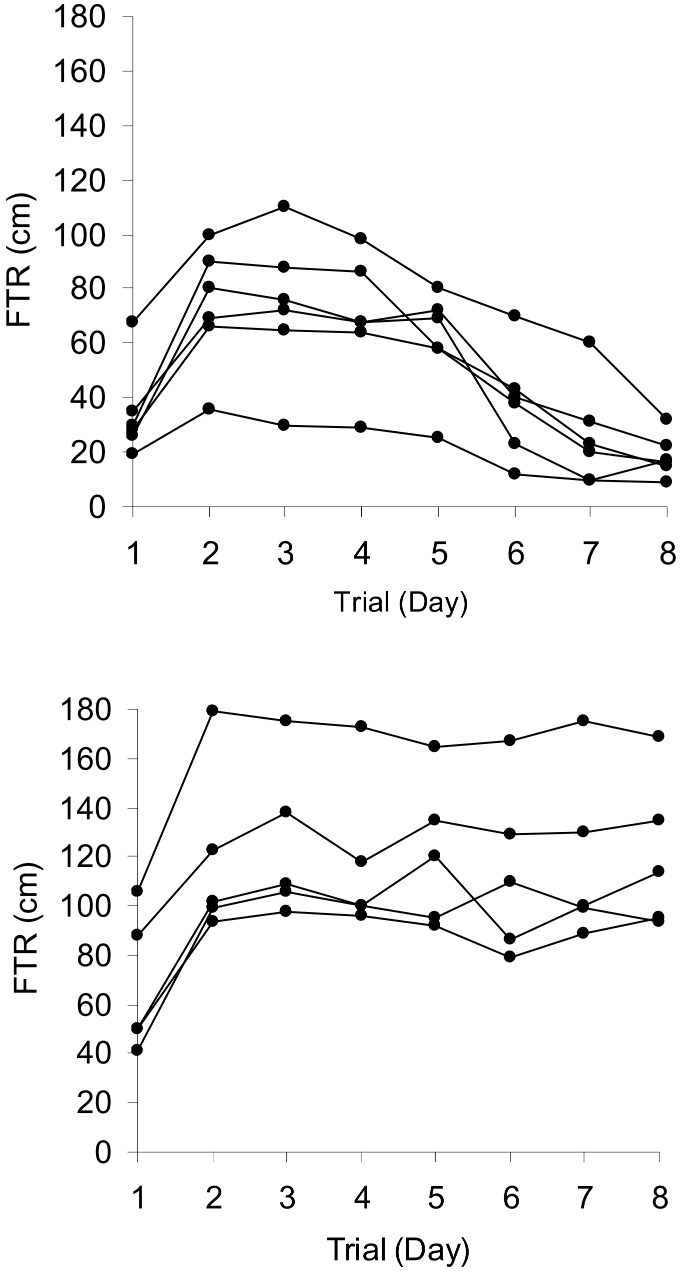


Figure 19. Responses to human approaches of three individual mamushi tested across years: 2001 (dotted lines) and 2002 (solid lines). Trials were conducted daily over 8 days.

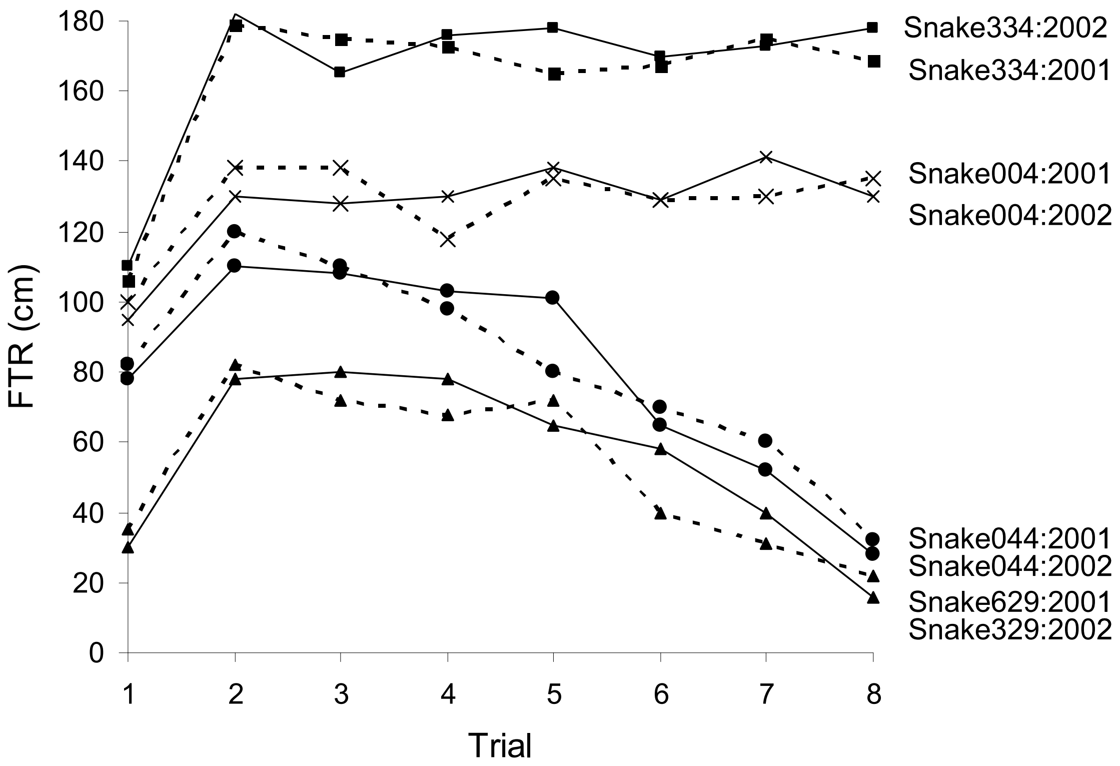


Figure 20. Latency to emerge from refuge in adult mamushi from compromised (n = 4) and uncompromised (n = 4) populations. Each box represents one individual tested 2-3 times. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values.

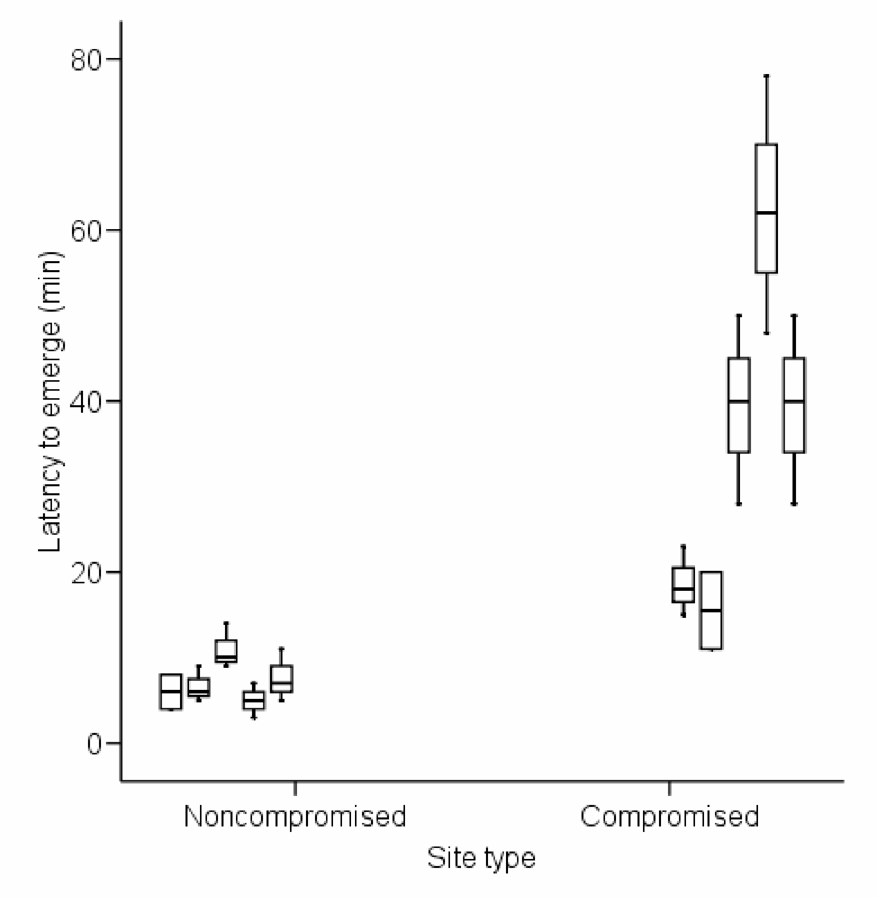


Figure 21. Microhabitat cover in which nonpregnant and pregnant female and male mamushi were found in compromised (n = 85) and uncompromised (n = 1 90) populations. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values, excluding outliers (values > 1.5 times the interquartile range; denoted as open circles).

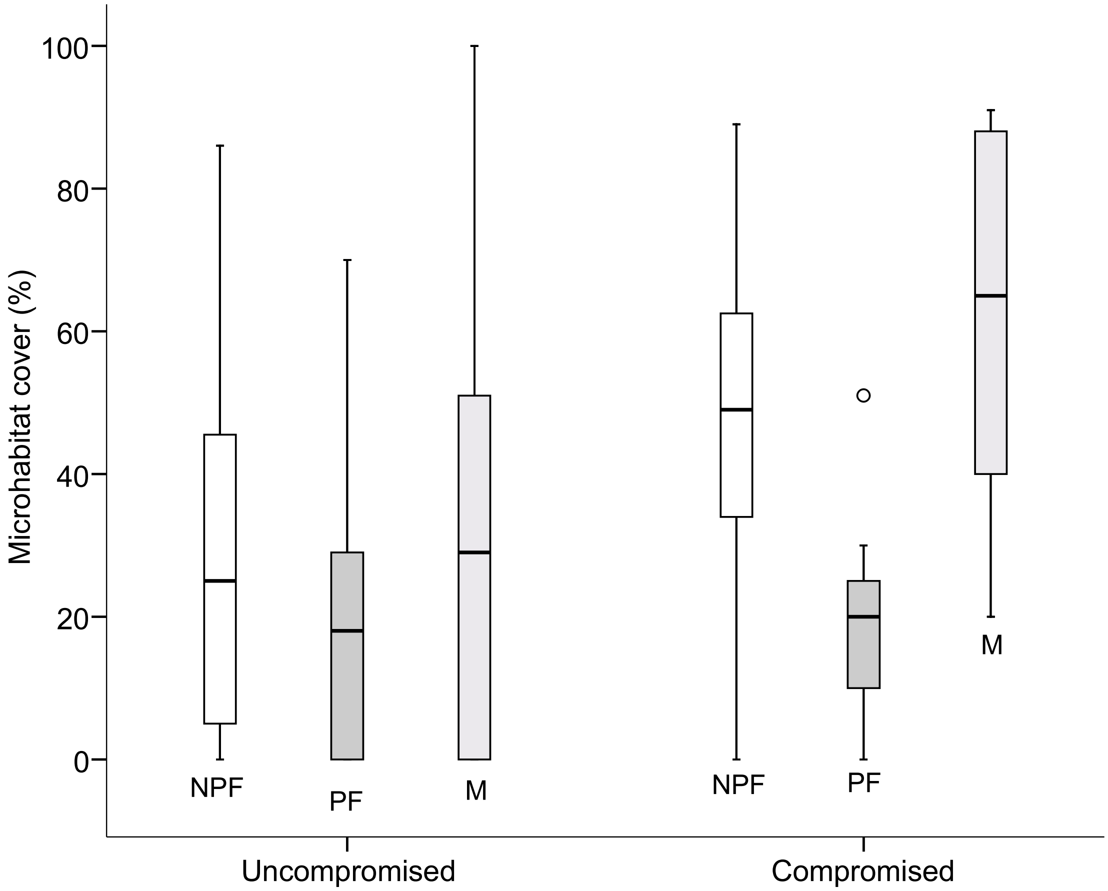


Figure 22. Total distance moved in September for adult mamushi of compromised (n = 2) and uncompromised (n = 7) populations. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values.

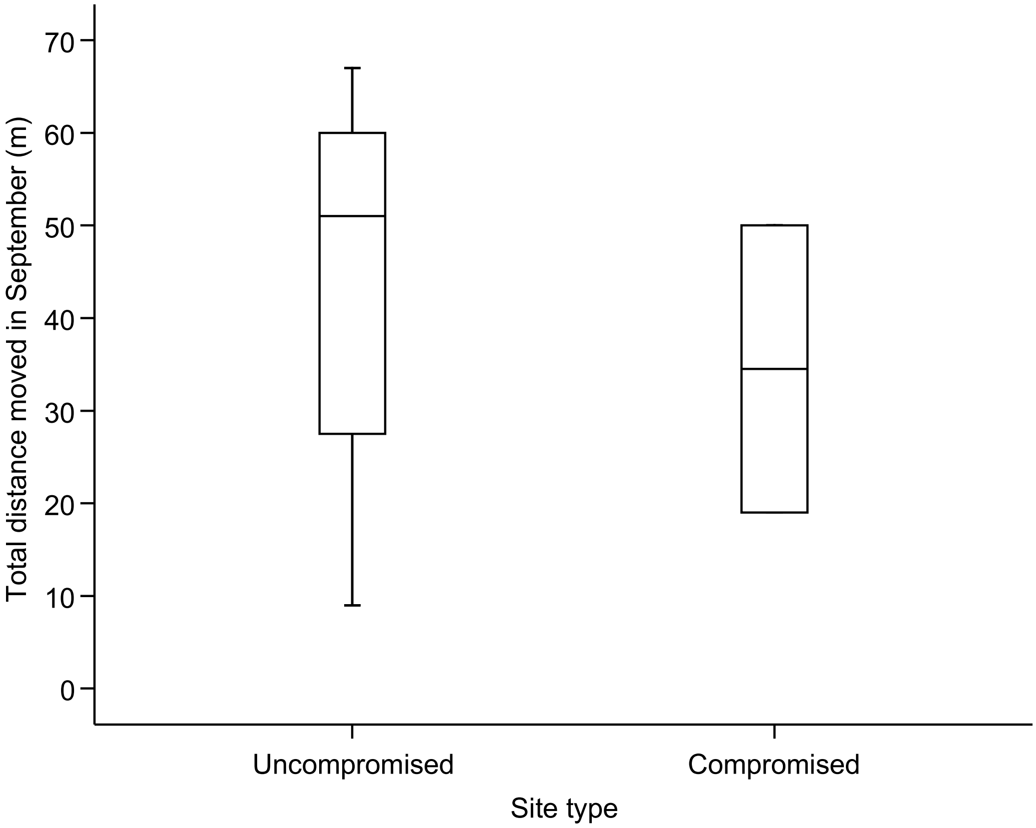


Figure 23. The number of movements in September for adult mamushi in compromised (n = 2) and uncompromised (n = 7) populations. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values.

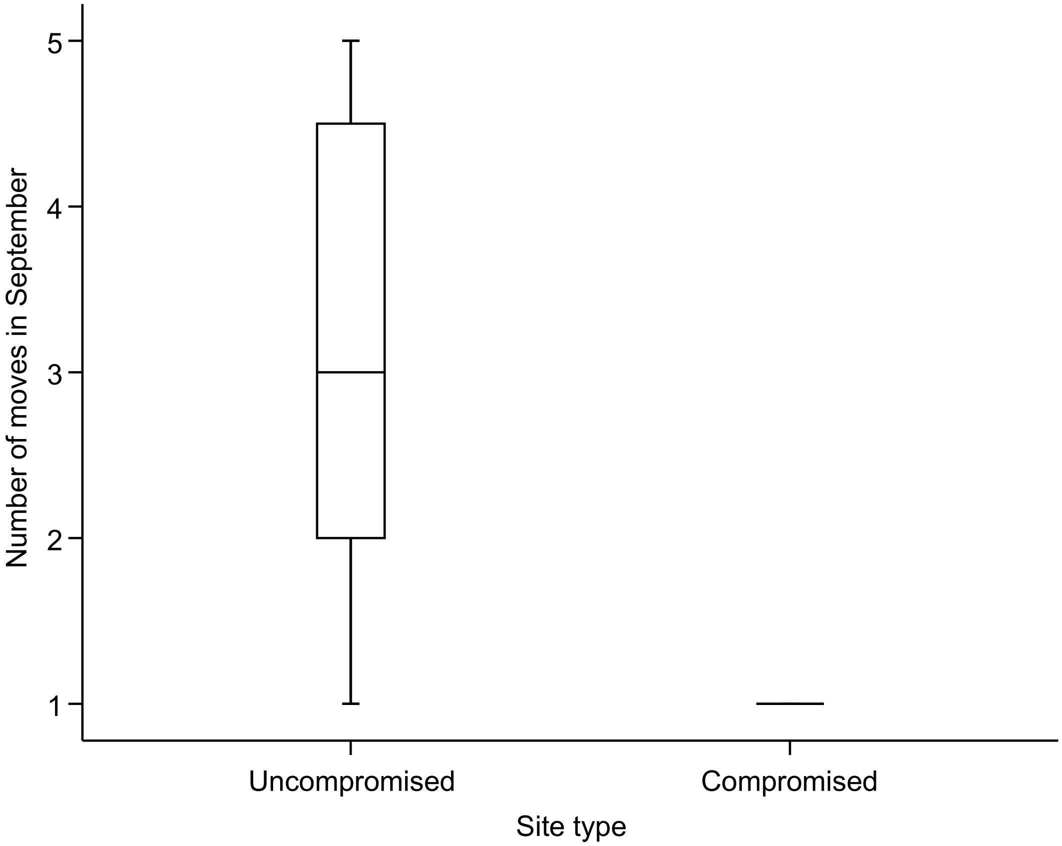


Figure 24. Timing of parturition of mamushi from compromised (n = 11) and uncompromised (n = 16) populations in Hokkaido, Japan, in 2001 and 2002. Boxplot represents median, 25th and 75th percentiles (interquartile range), and whiskers extend to the highest and lowest values.

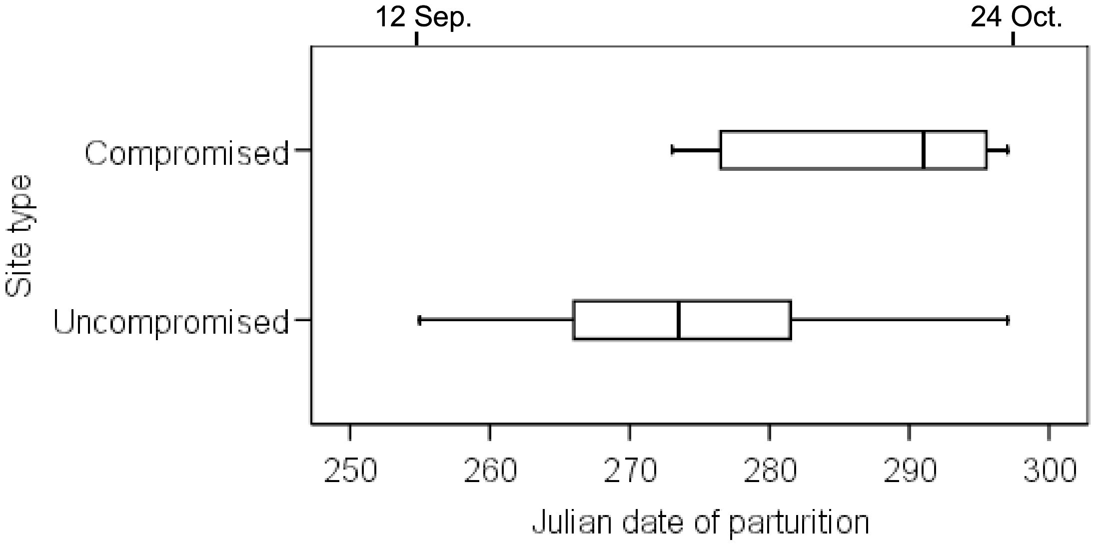


Figure 25. Number of offspring produced (i.e., litter size) in relation to maternal body size (snout-vent length, SVL). Open circles indicate snakes belonging to uncompromised population and closed circles indicate snakes belonging to compromised populations. The number below circles represents mean offspring SVL in cm. Mean offspring SVL is missing for one litter because of severe damage on offspring that were obtained from a road-killed mother.

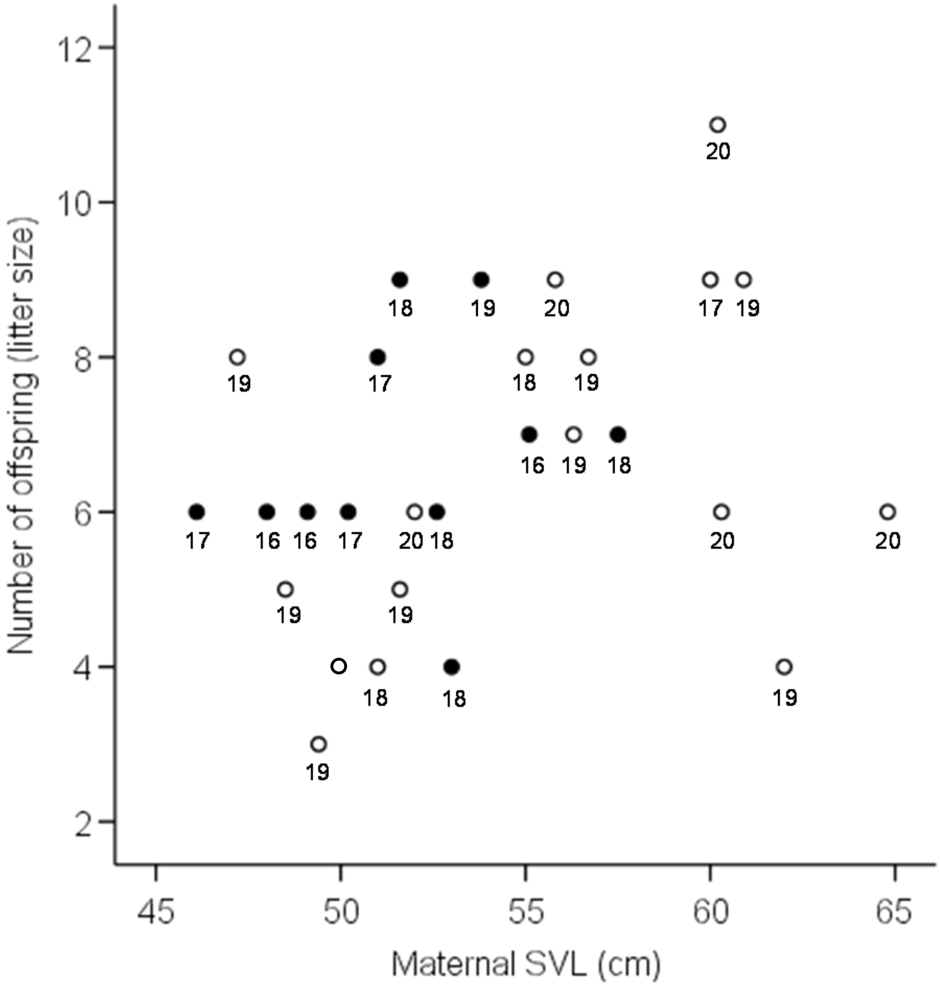


Figure 26. Body temperatures of non-radiotagged mamushi (n = 244) in association with air temperatures. Solid and open circles indicate pregnant and nonpregnant females, respectively. Crosses indicate males.

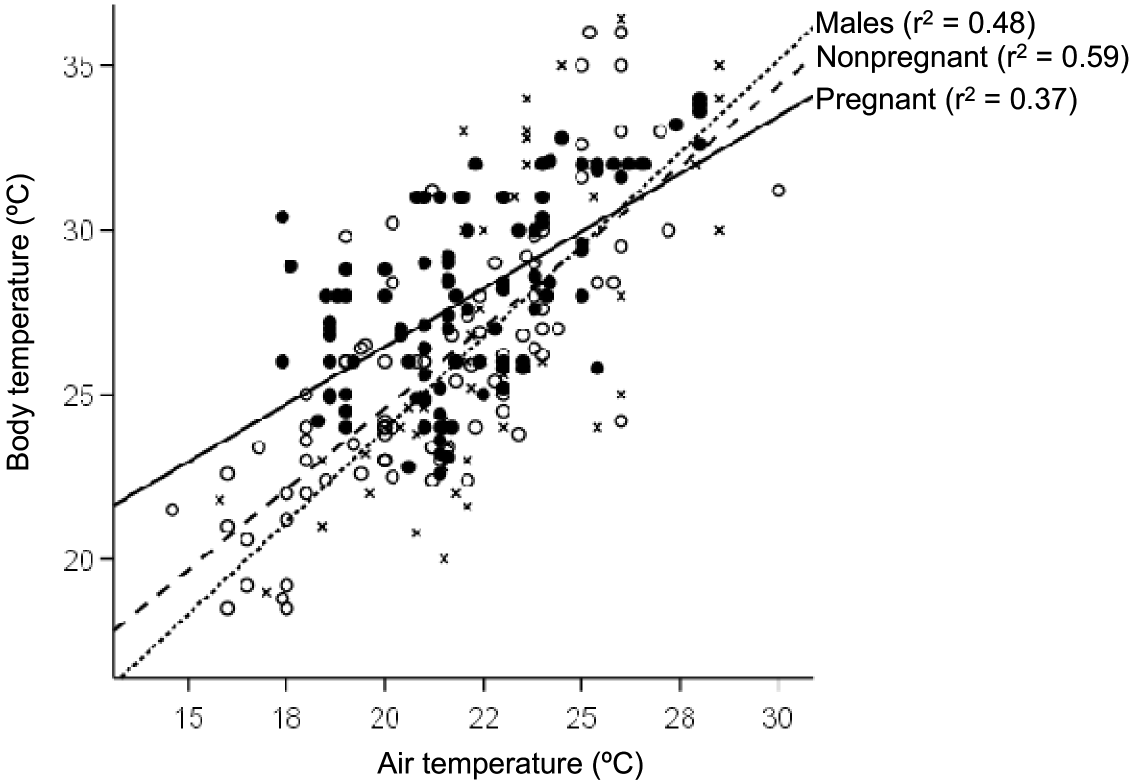
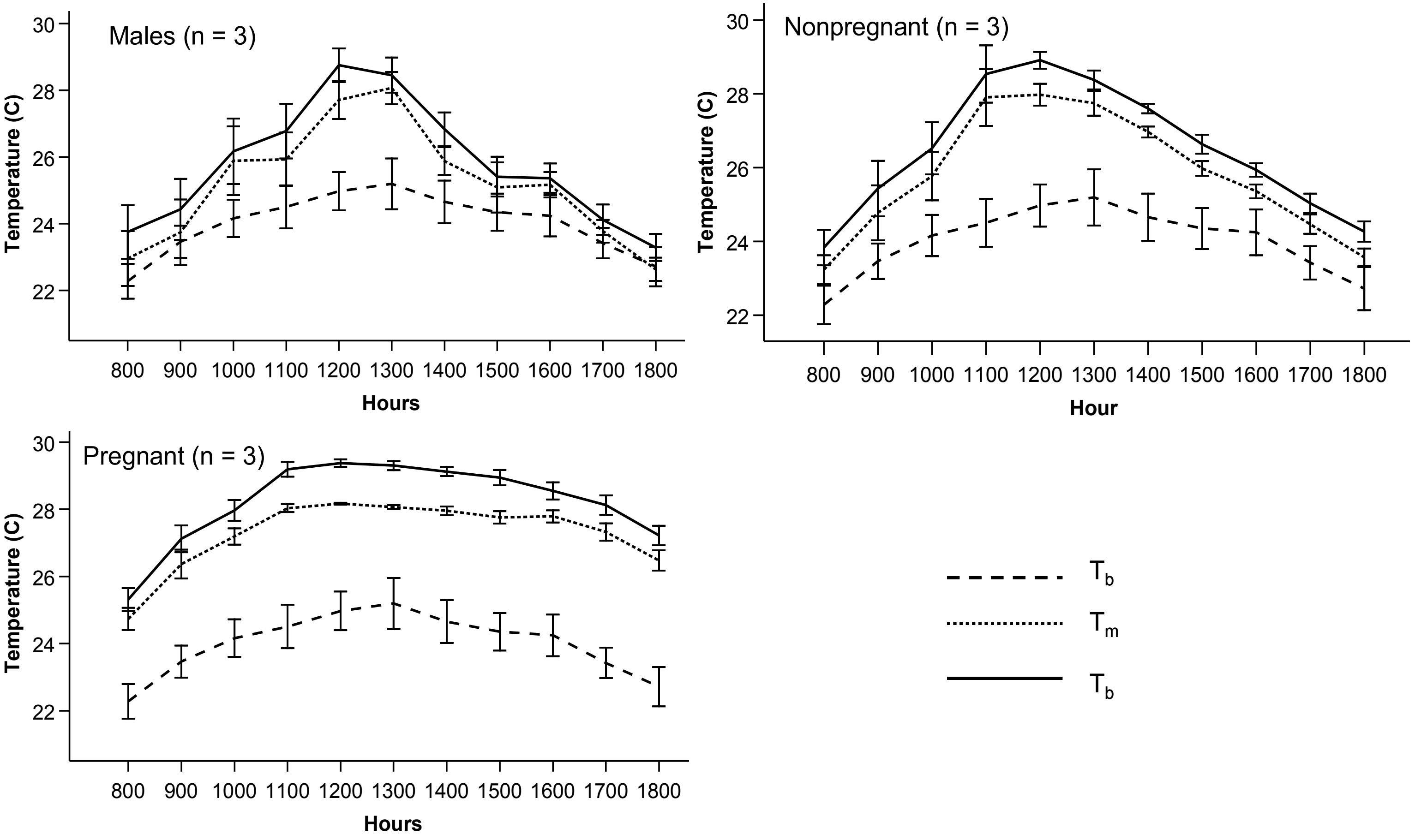


Figure 27. Air (T_a), microhabitat (T_m), and body temperatures (T_b) of radio-tracked mamushi recorded over a 3-day period (August 14, 18, and 21) in Hokkaido, Japan. Error bars = ± 1 standard error.



VITA

Kiyoshi Sasaki

Candidate for the Degree of

Doctor of Philosophy

Thesis: ECOLOGY, BEHAVIOR AND CONSERVATION OF THE JAPANESE MAMUSHI SNAKE, *GLOYDIUS BLOMHOFFII*: VARIATION IN COMPROMISED AND UNCOMPROMISED POPULATIONS

Major Field: Zoology

Biographical:

Personal Data: Born in Hokkaido, Japan, on May 4, 1973, the son of Yoshinori and Mitsuko Sasaki.

Education: Completed Intensive Chinese Language Program, Beijing Language Institute, China, in 1992; completed degree program in Martial Art, Beijing University of Physical Education, China in 1993; Northwest Indian College, 1996-1997; received Bachelor of Science degree in Zoology from Oklahoma State University, Stillwater, Oklahoma, in December 1999; completed the requirements for the Doctor of Philosophy degree with a major in Zoology at Oklahoma State University in December 2006.

Experience: Instructor, Tai Chi, Northwest Indian College (as Physical Education) and Lummi High School (Elective), 1997; instructor, Campus Recreation, Oklahoma State University (OSU), 1997-2006; animal caretaker, Department of Zoology, OSU, 1997-2005; teaching assistant, Department of Zoology, OSU, Fall 2005; graduate research assistant, Department of Botany, Spring 2006; instructor, dendroecology, Department of Botany, OSU, Spring 2006; graduate research assistant, Department of Zoology, Fall 2006.

Professional Memberships: Herpetological Society of Japan, Kansas Herpetological Society, Sino-Ecologists Association Overseas

Name: Kiyoshi Sasaki Date of Degree: December, 2006

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: ECOLOGY, BEHAVIOR AND CONSERVATION OF THE JAPANESE MAMUSHI SNAKE, *GLOYDIUS BLOMHOFFII*: VARIATION IN COMPROMISED AND UNCOMPROMISED POPULATIONS

Pages in Study: 125 Candidate for the Degree of Doctor of Philosophy

Major Field: Zoology

Scope and Method of Study: Japanese mamushi (mamushi, hereafter) have been impacted from killing and hunting by humans, and many populations in many places appear to be declining or are already extirpated. The purpose of this study was to investigate the effects of mamushi hunting on key morphological, behavioral, life history, and reproductive traits in the affected (i.e., compromised) populations, and to test a hypothesis that the changes in trait states in compromised versus uncompromised populations would be the result of response to selection imposed by mamushi hunting. My study has taken advantage of the existence of several local populations of mamushi in Hokkaido, Japan, that have been experiencing (i) regular hunting (compromised) and (ii) little or no hunting (uncompromised). It can be seen as a ‘natural experiment’ where uncompromised populations serve as a ‘before selection’ condition and compromised populations as an ‘after selection’ condition. This setting provided me with an opportunity to explore how fundamental ecological and evolutionary processes work, while simultaneously obtaining basic ecological, behavioral, and evolutionary data important in conservation and management of this species.

Findings and Conclusions: My study showed that hunting and killing have produced a strong phenotypic selection force that has generated population-wide changes in body size, antipredator behavior, microhabitat use, movements, and life history in the mamushi populations. These changes appear to be, in part, genetically based, and hence, evolutionary responses to intensive human predation pressures. An important conservation and management implication is that a genetic-based change can be slow or hard to reverse, even when selection forces caused by humans stop, and such a change in one trait will inevitably cause changes in other correlated traits, which can negatively affect fitness. Such a genetic-based change and potential correlated changes in fitness-associated traits can accelerate the process of population decline and increase the probability of local extirpation in harvested populations.

ADVISER’S APPROVAL: Stanley F. Fox