HERPETOLOGICAL NATURAL HISTORY

VOL. 9 2002 NO. 1

Herpetological Natural History, 9(1), 2002, pages 1–14.

A REVIEW OF 30 YEARS OF ECOLOGICAL RESEARCH ON THE SHEDAO PITVIPER, *GLOYDIUS SHEDAOENSIS*

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Abstract. Although it remains virtually unknown to western scientists, an insular population of pitvipers in northeastern China has attracted intensive study for > 30 yr. The small (< 1 km^2) island of Shedao lies on a migratory pathway for passerines, and the regular spring and autumn migrations of these birds support a remarkably dense population of endemic pitvipers (*Gloydius shedaoensis*). Adult pitvipers of both sexes average 60–70 cm snout–vent length and prey almost entirely on birds. Juvenile snakes feed less often than adults, and consume invertebrates as well as birds. Reproductive output is high, perhaps because the assured food supply after parturition each year minimizes energy-based "survival costs of reproduction." Offspring size is large, presumably as an adaptation to the paucity of small prey items on the island. The snakes ambush birds from trees and shrubs as well as from the ground; arboreal ambush sites are more frequent in juveniles than adults. Snakes are inactive for most of the year apart from brief (6-wk) periods of bird migration in spring and autumn. Even in peak periods, only one-third of snakes are active each day. The snakes display high philopatry and high energy-assimilation efficiency. Research on *G. shedaoensis* has stimulated major conservation initiatives to eliminate illegal collecting, reduce fire frequency, increase water availability, reduce the numbers of introduced weeds and rats, revegetate areas affected by landslides, and sometimes directly supplement food supplies for the snakes. Since these management strategies commenced, the numbers of pitvipers have increased substantially and the age structure of the population has shifted.

Key Words. China; Conservation; Foraging; *Gloydius shedaoensis*; Reproduction; Viperidae.

Studies of snake ecology have increased dramatically in number over recent decades (Shine and Bonnet 2000). Although this increase has involved an expansion of the geographic and taxonomic range of study, most research has continued to focus on a relatively small number of taxa in a relatively small proportion of the world. For example, North American garter snakes (*Thamnophis* spp.) and rattlesnakes (*Crotalus* spp.) and European vipers (*Vipera* spp.) continue to be the subjects of a high proportion of all studies. Thus, much of the expansion of research on snake ecology has involved more work on already-studied taxa and areas. Based on the contents of recent issues of herpetological or ecological journals, or reviews of snake ecology (Seigel and Collins 1993), one could imagine that there have been virtually no detailed studies on the ecology of the snake fauna over large parts of the world.

This apparent neglect may tell us as much about the lack of communication between scientists writing in different languages, as about the actual distribution of research effort. In this paper we review the results of a prolonged and ambitious research program on the pitviper *Gloydius shedaoensis* (Fig. 1), a program arguably rivaling even Henry S. Fitch's herculean efforts (Fitch 1999) in some respects. The Shedao research program is surely one of the most ambitious conservation-oriented ecological studies ever conducted on snakes. Remarkably, the species involved is one that most professional herpetologists have never even heard of, let alone seen. Because it occurs in China, and most publications about it are in Chinese-language journals, the research carried out on this taxon has attracted very little attention from researchers who publish in western-language (English, French, etc.) journals.

In an attempt to bring the Chinese research to the attention of western scientists, we review major results of studies on this system. This is not a straightforward task. Previous English-language publications on this system (Huang 1989; Li 1995) generally provide conclusions but not actual data nor statistical analyses. For the raw data, we have gone to the original publications. In cases where sufficient detail is available, we have carried out statistical tests on appropriate hypotheses (all such tests in this paper are our own, rather than reporting of prior analyses). Most of the Chinese papers do not include such tests, and often they provide only average values (albeit, often with accompanying SDs). It was not always feasible to retrieve original data because numerous workers have been involved, many of whom are now retired or deceased. We also mention major results that were simply reported as conclusions in the original studies. Because Chinese workers have tended to measure traits other than those traditionally quantified by western workers (again reflecting the lack of international communication), we supplement this review with original data from our recent collaborative studies.

Figure 1. The Shedao pitviper, *Gloydius shedaoensis*, in a typical arboreal foraging pose.

MATERIALS AND METHODS

Study Area

Shedao (literally, "snake island") lies approximately 13 km (7 nautical miles) off the coast of the Liaodong Peninsula in northeastern China, in the Bohai Sea (38°57' N, 120°59' E). The island is 0.73 km^2 in overall size, and is very steep-sided. The highest peak on the island is 215 m above sea level.

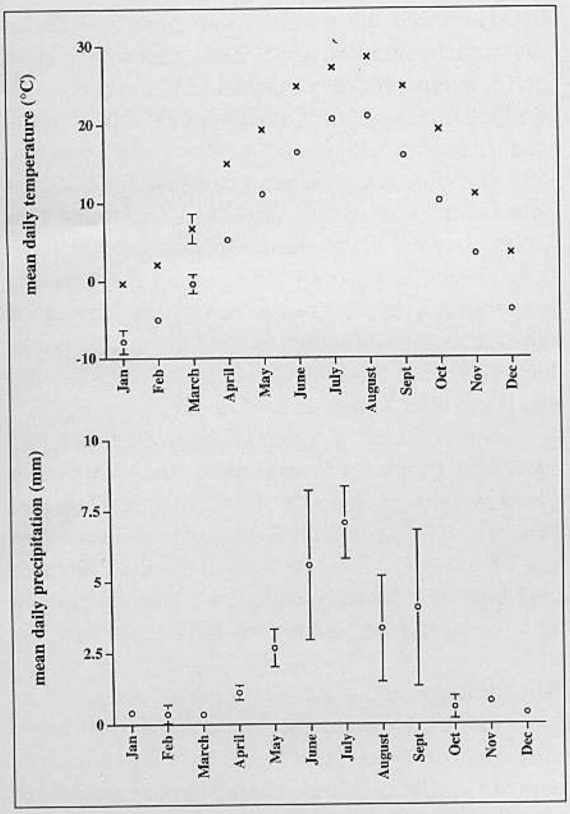

Figure 2. Weather records from Shedao, based on a meteorological station set up on the island. The graphs show mean minima and maxima (upper graph) and mean values and standard deviations for daily records (lower graph) over the years 1990–97.

Several ephemeral watercourses run in shallow valleys on the southeastern side of the island, but there is no permanent water except for that provided by human activities (see below). The island is formed by sedimentary rocks that have been deeply folded and fractured, creating many crevices that provide retreat sites for snakes. The island was formed by uplift about one million years ago, but was connected to the mainland (Liaodong Peninsula) intermittently during Pleistocene sea-level fluctuations (Li 1993; Zhao 1980).

The climate on Shedao is highly seasonal, with an annual mean temperature of about 10°C. Winters are severely cold. During the snakes' main activity periods (May and September), air temperature typically ranges from 10–20°C (Fig. 2). Rain falls primarily in summer (June–August). The island is frequently exposed to strong winds, typically from the southeast from March–July but switching to the north in September. Despite its small size, cool climate and lack of standing water, the island supports 209 species of plants. Except for very steep areas, most parts of the island are covered by shrubs or trees. The species comprise plants typical of Northern China. Surveys have revealed 143 invertebrate taxa on Shedao, primarily arthropods. Apart from Shedao pitvipers, the only vertebrates living permanently on the island are one microchiropteran bat (*Pipistrellus abramus*), the introduced brown rat (*Rattus norvegicus*), and seabirds (black-tailed gull *Larus crassirostris*; Chinese egret *Egretta eulophotes*; northern white-rumped swift *Apus pacificus*).

Each year the island is visited by large numbers of migratory birds (at least 84 species total, 50 of them passerines: Snake Island Survey Team 1973, 1974, 1976; Shine et al. unpubl. data). The migration occurs in two discrete seasons, in spring (mid-April to the end of May) and autumn (late August until the end of October). Most of these transient birds probably remain on the island for only a few days (Snake Island Survey Team 1974, 1976). The peak of the bird-migration periods occurs before (in spring) and after (in autumn) the major snake-activity periods, presumably because thermal conditions restrict snake foraging more than bird migration.

History of Ecological Research

Although the island and its snakes must have been known to local people (fishermen frequently visit the island in small boats in calm weather), the first scientific reports of the extraordinary density of pitvipers on Shedao date from the Japanese occupation of Manchuria (Hasegawa 1932; Koba 1933, 1938; Mori 1932). Although based on only a single day's data collection on the island, Koba's 1938 paper provides a long (20-page), detailed, and well-illustrated account on topics such as the snakes' morphology, diet, and feeding behavior.

Chinese scientists began significant research on Shedao in the 1950s, although most papers were brief and many were semi-popular (Wu 1957, 1958, 1961). The initial stimulus for the work was scientific curiosity but with increasing understanding of this remarkable system the emphasis began to shift towards research on conservation issues. Several major papers were published in the 1970s under collective authorship of the "Snake Island Survey Team," including a semi-popular synthesis of major results in 1976. The research was broadly-based, and included extensive surveys and analysis of the island's flora and fauna, not simply the snakes (e.g., Huang 1979). For example, avian migration patterns attracted detailed study.

Taxonomy

Early publications refer to the snake as *Agkistrodon halys*, but Zhao described it as a separate species in 1979 (Zhao 1979) based on morphological traits. Zhao recognized two disjunct populations of *Agkistrodon shedaoensis*, one on Shedao Island and one in mountainous areas of the mainland (Quianshan Mountain. 90 km S Shenyang; Long-panshan Mountain, 100 km N Dalian). A subsequent paper by Zhao (1980) examined the taxonomic distinctiveness of the island snakes in much more detail using a wide array of data including electrophoretic analysis of venoms, venom toxicity, immunodiffusion, and scalation counts (see also Chen et al. 1984). Zhao (1980) also interpreted the biogeographic history of the taxon. The distinctiveness of *G. shedaoensis* was further demonstrated by Jiang and Zhao (1980), who compared *G. shedaoensis* with mainland pitvipers in terms of ecological traits such as habitat use, food habits, daily activity cycles, seasonal activity patterns, tolerance to low temperatures, and reproductive biology (dates of parturition, litter sizes, offspring sizes).

Since those studies, most authorities have treated *G. shedaoensis* as a separate species (see Literature Cited). However, Ji et al. (1989) treated *G. shedaoensis* as a subspecies of *G. saxatilis*, based on similarity of coloration and scalation. Electrophoresis of 23 presumptive loci failed to distinguish between *G. saxatilis* and *G. shedaoensis*, although this technique differentiated all other taxa investigated (Murphy et al. 1993). Genetic studies indicate that the two *G. shedaoensis* populations are very similar to each other, but distinct from *G. saxatilis* (Shan et al. 1993). The overall conclusion from this work seems to be that *G. shedaoensis* is indeed a distinctive taxon, albeit closely related to *G. saxatilis*. Recent changes to the understanding of higher-level phylogenetic relationships within pitvipers have led to division of "*Agkistrodon*," with the Asian species now allocated to *Gloydius* (Gloyd and Conant 1990; Parkinson et al. 1997).

RESULTS AND DISCUSSION

Venom Composition, Toxicity, and Yield

The venom of *G. shedaoensis* contains no detectable neurotoxins, and hence is less toxic than the venoms of most other Asian pitvipers (Zhang 1989; Zhang and Hsu 1985; Zhao 1980; Zhao et al. 1979). Interperitoneally injected LD_{50}s in mice averaged 0.81 mg/kg (Zhang and Hsu 1985). In comparison, LD_{50}s averaged 0.38 for *G. intermedius*, 0.33–0.63 for *G. ussuriensis*, 0.49–0.88 for *G. brevicaudus*, and 0.83 for *G. saxatilis* (Zhang and Hsu 1985). A more recent study supports most of these conclusions (Chen et al. 1992). Chinese scientists envenomated by *G. shedaoensis* have developed massive local swelling but few or no systemic symptoms (LS, pers. obs.). Hospitalization for up to 2 mo can occur after a very severe bite (LS, pers. obs.).

Fangs of adult *G. shedaoensis* average 7.4 mm in length (range: 4.5–10.0 mm) and the venom gland weighs an average of 163 mg (50–310 mg: Wu 1977*a*). A single bite yields approximately 96.5 mg of venom (27.5–156.6 mg). A snake requires about 10–15 d to fully replenish its venom supply after emptying the glands (Wu 1977*a*).

Morphology

Gloydius shedaoensis is a relatively large species, with a maximum recorded body length of 99 cm (Li 1995). Adults average about 60–70 cm total length, compared to < 60 cm for most other Chinese species of *Gloydius* (Zhao 1980). General body shape is similar to that of congeneric taxa (Gloyd and Conant 1990). The dorsal scales are strongly keeled, and the overall color of the dorsum ranges from dark gray to pale pinkish-gray. Irregular light-colored blotches break up the animal's outline, such that the snakes are well camouflaged, both in arboreal and terrestrial situations.

Early studies provided data from dissection of snakes to quantify relative masses of medicinally important components of the body such as fat stores, gall bladders and venom glands, as well as the gonads (Wu 1977*a*). This work documented higher fat reserves in adult females than in adult males (Wu 1977*a*). Li (1995) provided an English-language review of scalation, body size, color and skeletal morphology.

Males and females attain similar adult body sizes (Table 1). Analysis of our own data on SVLs of adult snakes confirms that mean adult body sizes are very similar in the two sexes (unpaired t_{143} = 1.14, P = 0.25). Body sizes at maturity are known with confidence only for females; the smallest female of 79 animals recorded to give birth was 54 cm long (Sun et al. 2002).

TABLE 1. Body sizes and sexual size dimorphism of Shedao pitvipers, *Gloydius shedaoensis*. Table shows values for total body length, except that the last row shows snout–vent length and is based only on adult snakes (estimated at > 50 cm SVL). All measurements in cm.

Males			Females			Reference
n	range	mean (SD)	*n*	range	mean (SD)	
9	48.0–78.4		4	69.7–84.0		Koba (1938)
87	61.2–82.0		78	60.0–79.0		Snake Island Survey Team (1973)
19	53.3–73.0	64.4	28	50.4–78.2	69.3	Zhao (1980)
41	54.5–80.0	70.2	41	51.2–76.1	68.3	Ji et al. (1989)
64	51.0–69.0	59.8 (4.5)	81	50.0–74.0	60.7 (5.0)	Shine et al., unpubl. data

Life History

Chinese researchers have classified snakes as "juvenile," "adult," or "old adult" based on body size, color, scale rugosity, and the presence and number of white spots on a snake's head and body (Li et al. 1990; Snake Island Survey Team 1979). These "white spots" are unpigmented scales. Although long-term mark-recapture programs have been a central feature of research on snake ecology in western countries and in Japan (Fitch 1999; Fukada 1992), they have not been employed in China. Such a study has recently commenced on Shedao, to clarify growth trajectories and age structure of the Shedao pitviper population (Sun, unpubl. data).

Demography has been well-studied, with several short-term mark-recapture censuses to quantify both absolute numbers of snakes and population composition in terms of sex ratio and age structure. Females generally outnumber males in these counts (53% of 1638 snakes in Li et al. 1990 against a null of 50%, $\chi^2 = 4.52$, $df = 1$, $P < 0.05$). The proportion of the population composed of juvenile snakes has decreased through time because heavy commercial harvesting removed many adult snakes during the earliest years of study (Huang 1990). With the cessation of harvesting in 1980, relative numbers of adults have increased. By comparing numbers of offspring born to the rate of population recovery, Huang (1990) estimated an annual survival rate for neonatal snakes of approximately 56%.

Seasonal Activity Patterns

The snakes hibernate through the colder months of the year, emerging in mid-April during the first bird-migration period (Huang 1989; Li et al. 1993; Snake Island Survey Team 1974, 1976). Juvenile snakes tend to emerge before adults, and adult females before adult males; such a pattern is quite unusual among snakes (Sun et al. 1993, 2001). Even at the peak of the bird abundance, only about one-third of snakes in the population are active on any given day (Sun et al. 1990). This estimate was derived by paint-marking snakes within large field enclosures, followed by visual censuses to determine the proportion of marked snakes active at different times. During summer the snakes are largely inactive, and remain hidden except after rain showers (Li 1995). The autumn bird-migration period engenders a similar level of activity to the spring migration, with the snakes disappearing to their hibernation sites in late October. Detailed analyses reveal subtle seasonal shifts in habitat use; for example, the proportion of snakes recorded in grass versus trees varies among months. The snakes use both habitat types fairly equally in midsummer (when there are no birds to eat), but tend to be found more often in trees during the bird-migration periods of spring and autumn (Snake Island Survey Team 1974; Yang 1986). Such shifts may, however, reflect seasonal biases in observability (due to vegetation growth in summer) rather than (or as well as) actual changes in snake behavior.

Because parturition is highly seasonal, the age structure of the population shows regular seasonal fluctuations. Neonates are most abundant in late autumn, soon after birth (Snake Island Survey Team 1974).

Diel Activity Patterns

Within the main seasons of activity, the snakes also display regular diel patterns of movement. They typically spend the night on the ground, often under rocks or grass. They climb to their ambush sites early in the morning, stay there for a few hours, then retreat to the ground in the late morning (Sun 1990; Shine et al. 2002*a*). They return to the trees in the late afternoon, descending at dusk. Some animals remain at their foraging sites overnight, and others move about actively after dark.

Home ranges of individual snakes include an overnight retreat site (on or under the ground) plus one or more foraging sites. These are typically close together (Sun 1990). Individual snakes usually return to the same foraging site over long periods of time. If displaced (even to the extent of being removed from the island and released in the sea nearby), they rapidly return to their original capture site (Sun 1990). Snakes displaced 500 m from their usual home ranges returned within a week (Sun 1990).

Although thermoregulatory biology has played a central role in the study of snake ecology, it has attracted little direct interest from Chinese researchers. However, they have noted that diel shifts in ambush-site selection (especially, the tendency to spend the middle of the day on the ground rather than in the trees) may be driven by thermal cues (e.g., Li 1995). Also, the snakes' retreat to deep burrows for the winter is presumably forced by the fact that the ground freezes to depths of up to 1 m (Sun 1990). Burrows used during winter typically have leaf litter blocking the entrance, thus providing additional insulation against severely low air temperatures (Sun 1990). Hibernating snakes typically display body temperatures between 2 and 5°C (Li et al. 1993). Thermal factors may also explain why the snakes do not commence foraging until after the peak of the bird-migration period in spring, and cease foraging prior to the end of the bird-migration period in autumn (Shine et al. 2002*b*).

Reproductive Biology

Reproduction by Shedao pitvipers has attracted substantial study over a long period of time. Seasonal cycles based on sizes and histological examination of the testes and ovaries were reported by Yang (1983), who inferred from these data that most mating occurred from August to October. Testes are largest during midsummer (June–July; Yang 1983). Sperm are produced from April to July, and testes and epididymes of adult males contain mature spermatozoa from July–October. Ovulation occurs in June, with parturition from late August to mid-October (Sun et al. 1993, 1994, 2002). Most births occur during September (Sun et al. 1993).

Many papers report litter sizes, mostly from dissections of gravid females (e.g., Huang 1989; Snake Island Survey Team 1974; Wu 1977*a*). More extensive data came from a study in which near-term females were captured and maintained in captivity until they gave birth (Sun et al. 1993, 1994, 2002). Stillborn offspring are rare (5.3% of neonates were stillborn: Sun et al. 1993). The proportion of reproductive animals in samples of adult females averages around 25%, suggesting a 4-yr reproductive cycle (Sun et al. 1994). For example, Li et al. (1990) reported that 72 of 323 adult-size females were gravid during summer (23%). Of 64 females with lengths > 900 mm, only ten were gravid (15.6%). The authors suggest that this may represent a significant decline in reproductive frequency with increasing body size (and thus, perhaps with age) but statistical analysis does not support this inference ($\chi^2 = 1.60$, $df = 1$, $P = 0.25$). The proportion of reproductive animals may vary in response to year-to-year variation in food supply; certainly, females are in higher body condition in some years than in others (Sun et al. 1993, 2002).

Studies on reproductive output show that female *G. shedaoensis* produce a remarkably heavy litter relative to maternal mass and produce very large offspring (Sun et al. 2002). In both respects, they differ substantially from related taxa (including the mainland population of *G. shedaoensis*; Li pers. comm. 2000). The very high relative clutch mass (0.80 vs. < 0.50 litter mass as percent female postpartum body mass for most other pitvipers) may reflect the fact that some components of the costs of reproduction (post-parturition mortality?) are low on Shedao. Because parturition occurs just before the autumn bird migration, post-partum females face little risk of dying from starvation before they can obtain food (Sun et al. 2002). The large offspring size on Shedao (14 vs. < 7 g in other *Gloydius*) plausibly reflects the scarcity of small prey on the island. Neonatal *G. shedaoensis* that are too small to ingest passerines must feed on invertebrates, thus enforcing strong selection for larger size at birth (Sun et al. 2002).

There are few published data on behaviors associated with reproduction, because courtship, male-male combat and copulation are rarely observed on the island (LS, pers. obs.). Copulation can occur in both arboreal and terrestrial locations (Li 1995), and may be relatively brief (18-min duration: Snake Island Survey Team 1974, 1976).

Figure 3. A Shedao pitviper, *Gloydius shedaoensis*, swallowing a bird.

Food Habits

Adult Shedao pitvipers feed almost exclusively on birds. Of 81 prey items recorded in adult snakes by the Snake Island Survey Team (1974), 80 were birds and the other was a rat (*Rattus norvegicus*). Analyses of stomach contents have documented predation on 24 species of birds, all of them passerines except for two species of quail (*Coturnix coturnix, Turnix tanki*). Warblers and buntings are probably the most important prey groups (Shine unpubl. data). Gape-limitation is important, with some birds being killed but then rejected because they are too large to swallow (e.g., doves). Shedao pitvipers are able to swallow prey items that weigh as much as the snake itself (Li 1995; Fig. 3). Juvenile snakes take small birds, but also feed upon invertebrates. Of 12 prey items from juvenile snakes, seven were birds, four were centipedes (*Otostigmus politus*), and one was an isopod (*Metoponorthus pruinosus*: Snake Island Survey Team 1974). Researchers have seen pitvipers approaching the nests of seagulls (presumably to feed on chicks), but the snakes were attacked by the adult birds (LS, pers. obs.).

Shedao pitvipers require 3–7 d (depending on the size of the prey and weather conditions) to fully digest their prey (Li et al. 1990), but they do not cease foraging during this period. Some snakes in ambush poses contain freshly-ingested birds. For example, one sample of adult snakes included ten snakes with empty stomachs, 59 snakes with a single bird in each, nine snakes each containing two birds, and one with three birds (Snake Island Survey Team 1974). Of 16 juvenile snakes, six had empty stomachs, eight contained single prey, and two contained two prey items each (bird plus centipede; centipede plus isopod: Snake Island Survey Team 1974). In other studies, the proportion of snakes containing prey in autumn averaged about 20% in adults and 10% in juveniles (Li 1995; Li et al. 1990). Adult females typically contain food more often than do adult males (26% vs. 22% in Li et al. 1990). Statistical analysis of the raw data used for these conclusions reveals that the difference in proportions with food between adults and juveniles is significant ($\chi^2 = 9.03$, $df = 1$, $P < 0.003$)

Figure 4. A Shedao pitviper, *Gloydius shedaoensis*, in typical terrestrial foraging pose.

whereas that between males and females is not ($\chi^2 = 1.05$, $df = 1$, $P = 0.31$). The lower rate of feeding in juvenile snakes may result from gape-limitation: juvenile snakes are unable to ingest most bird species in the area (Li et al. 1990).

Foraging Behavior

Snakes catch birds from ambush, and foraging snakes display distinctive postures and patterns of habitat selection. Although some birds are taken from the ground, many are captured on arboreal perches. Snakes lie with the head facing outwards along a branch approximately 1 m above the ground; the forebody is formed into a concertina shape to permit a rapid strike when a bird alights in front of the pitviper (Fig. 4). The incidence of arboreality changes with the size of the snake: approximately 90% of juvenile snakes are found above the ground, whereas this is true for only 63% of adults (no raw data available; Li 1995). This difference may be partly attributable to the lower visibility of small snakes on the ground compared to in a tree (Sun et al. 2001; Shine and Sun 2002). The height above ground to which the snakes climb to adopt their ambush posture also differs between age groups (adults typically climb to 1–1.5 m, juveniles to 0.5–1 m) and also varies with the time of day (higher in the morning than the afternoon) (Li 1995; no raw data available).

Although most prey are undoubtedly taken from ambush sites, Shedao pitvipers will also eat dead birds or those trapped in mist nets (Sun 1990). Thus, they can forage actively as well as ambush their prey. Because small snakes often strike and kill birds that are too large for them to swallow, an actively foraging snake may well encounter a dead bird on the ground. The invertebrates taken by juvenile pitvipers are presumably taken at night by active foraging; it is common to see small snakes moving about at this time (RS, pers. obs.).

Some birds taken from arboreal perches are retained after the initial strike, whereas others are struck and released (RS, pers. obs.). In some cases, the snake falls off its perch either at the time of the strike (as it throws its body forward) or later, as it struggles with a bird that it has seized. In other cases it retains its hold on the branch and may swallow the bird without leaving the tree.

Snakes also ambush birds from terrestrial sites. These usually involve a tightly coiled posture, often with the head facing towards an exposed open area such as a rock. Commonly a snake will lie with only its head visible, and the rest of the body hidden under leaf litter (Sun 1990). Surveys suggest that approximately two-thirds of snakes use arboreal rather than terrestrial foraging sites (Snake Island Survey Team 1974), but this estimate may be sensitive to differential observability of snakes in the two environments.

Studies on 17 captive snakes have quantified the efficiency with which the snakes can turn bird biomass into snake biomass (Wu 1977*a*,*b*). These snakes ranged in mass from 53.5–188 g prior to the experiment. They ingested 15.0–62.5 g of mice, and gained 2.0–36.0 g in body mass. The mass gained as a proportion of mass ingested averaged 33.4%, and ranged from 7.0–72.7%. Regression analysis revealed no significant relationship between assimilation efficiency (mass gained/mass ingested) and absolute body mass ($n = 17$, $r = -0.13$, $P = 0.61$).

CONSERVATION ISSUES

Research by Chinese scientists identified a number of potential or actual threats to the Shedao pitviper population (reviewed by Huang 1989 and Tang 1990). These can be classified into two major types: threats that involve human activities, and "natural" processes.

Effects of Human Activities

Commercial exploitation. Prior to the commencement of research, the Shedao pitviper population was heavily exploited for commercial purposes (Tang 1990). The snakes were killed to make snake wine or snake powder, or to feed to domestic pigs. Snake venom was used for medicine. Research to document this threat involved a comparison of population estimates from earlier workers to assess snake numbers through time. Although the data were imprecise, they suggested a strong decline from the 1930s (approximately 100,000 snakes: Koba 1933, 1938) to the 1950s (50,000 snakes) and continuing through the 1970s (20,000 snakes) to the early 1980s (10,000 snakes) (Tang 1990). Regular mark-recapture studies (using short-term paint-marking) were instituted, to provide more robust estimates of actual snake densities.

Introduction of feral plants and animals. The leguminous vine *Pueraria lobata* is the most important threat in this category. It is a strangling creeper that eliminates or overgrows native woody vegetation (Zhao et al. 1990). Its slender branches do not provide suitable ambush sites for the snakes. Surveys showed that snake abundance was lower in plots covered by *Pueraria* than in control plots; and that the removal of *Pueraria* on these plots was followed by a significant increase in snake numbers (Zhao et al. 1990). This experiment involved three plots, each 12 x 12 m^2. One was covered by dense tangled *Pueraria* (typical of 2% of the island's surface area); one by *Pueriara* growing over other trees (typical of 10% of the island's surface area); and one was a control (*Pueriara*-free) plot. The first of these sites contained few snakes (mean = 0.3 snakes recorded per day), whereas the other two contained more animals (means of 5.3–6.0 snakes). Following removal of *Pueraria* in spring 1989 and replanting with native vegetation, the numbers of birds and snakes in the experimental plot increased substantially (to a mean of 11.7 snakes/day over a 7-d period). Unfortunately, *Pueraria* is difficult to kill because it is fast-growing and resistant to drought.

The other feral organism of potential concern is the brown rat (*Rattus norvegicus*); one of these animals was observed attacking a juvenile snake in the laboratory (Tang 1990). More importantly, the rats' activities may damage plants and soil cover on the island. However, rat numbers on the island are low (average capture rate < 5 rats per 100 trap-days: Li 1995), perhaps because the snakes readily feed on these rodents. Thus, rats may at times provide a significant prey resource.

Fire. Several fires prior to 1980 destroyed vegetation over significant areas of the island (Tang 1990).

Threats Due to Natural Processes

Research has identified a series of potential sources of mortality which might reduce the rate of population recovery.

Food and water supply. Experiments with artificial hibernacula suggested that > 40% of neonatal snakes die during winter, possibly due to low energy reserves prior to hibernation (Wu 1977*a*,*b*). Laboratory experiments show that neonatal pitvipers can survive for very long periods without food, as long as they have access to water. In experimental studies, seven neonates survived an average of 148 d (range = 30–392 d) under these conditions (Wu 1977*a*). Another eight neonates survived an average of 274 d (range 53–246 d) under similar circumstances (Wu 1977*a*). However, neonates kept without water died more quickly (mean = 78.2 d, range 34–107 d: Wu 1977*a*). Although there is no standing water naturally on the island, the snakes frequently drink dew on grass, or directly from the artificial pools now in place (Sun 1990). However, rainfall is rare during the main bird-migration periods in spring and autumn (Fig. 2).

Food may be limiting in some situations. It is common to see relatively emaciated snakes on the island (RS, pers. obs.), and the 4-yr delay between successive litters by a given female (see above) suggests that replenishment of energy stores is a slow process. Long-term observations suggest that the numbers of migrating passerines have declined over the years (Tang 1990). Because this decline is likely to reflect broadscale environmental degradation over the birds' summer or winter habitats, any solution must involve a massive spatial scale. Ultimately, the population density of pitvipers on Shedao will probably depend upon processes at work over a vastly greater area than the island itself.

Landslides. A typhoon in August 1985 caused 18 landslides, covering a total area of 4000 m^2 (Tang 1990). Plants were destroyed, soil was lost, and many snakes were killed.

Predation. Birds of prey are frequently seen on the island and have been recorded to eat neonatal pitvipers (Koba 1938; Tang 1990).

Disease. Ninety-six of 225 snakes examined on the island exhibited inflammation of the mouth, presumably due to injuries sustained during feeding (Tang 1990). In severe cases this may reduce the snake's ability to continue taking prey.

MANAGEMENT INITIATIVES

The research on Shedao pitvipers has been accompanied by a series of "hands-on" manipulations to address the problems listed above.

Effects of Human Activities

Commercial exploitation. The island of Shedao was declared a Nature Reserve in 1980. Protection was also afforded to a mountain (Laotieshan) on the mainland nearby that serves as a stopping-over point for migrating passerines on their way to Shedao. The mountain was protected to ensure food supply for the island snakes. A two-story six-room house was constructed on the island in 1986 to accommodate research teams. Researchers have been based on the island fulltime since the early 1980s. For example, one of the authors of this paper (SL) spends up to 200 d each year on the island, and has been doing so since 1982. No snakes are removed from the island, although venom is sometimes taken for medical research.

Faunal resources can also be conserved by making them valuable in economic or other terms. Venom from *G. shedaoensis* is used to treat a wide variety of medical conditions, including cerebral thrombosis, atrophic gastritis, tumors, and rheumatism (Tang 1990). A 100-bed hospital has been set up in Dalian in association with the Snake Island organization. Tourism also offers resources. Visitors are brought to the island during appropriate times of year, but are only allowed to remain on the island for < 30 min and are restricted to a small area near the boat-ramp. A small fee from these tourists helps to defray the cost of maintaining the facilities.

Unsurprisingly, the abundance of *G. shedaoensis* has stimulated researchers to use this species for a variety of projects. For example, recent work has measured electrocardiograms in the laboratory (Xu et al. 1987) and examined the distribution of trace elements within the snake's body (Xu et al. 1991).

Removal of feral plants and animals. There have been major attempts to eliminate the introduced weed *Pueraria* using herbicides, direct cutting, and replanting with native vegetation (Zhao et al. 1990). Rodent-trapping programs have been introduced also. Capture rates ranged from 3.8–5.8 rats per 100 trap-nights over a 4-yr period.

Fire. The control over visitor numbers (and the restriction of these people to a small area near the jetty) substantially reduces the risk of fires being lit by humans. The long-term effects of this reduced fire frequency remain unclear. The snakes select relatively open habitats for ambush-sites (Shine and Sun 2002), so that an increase in vegetation density may ultimately reduce the amount of optimal habitat. On the other hand, an intense fire at the wrong time of year could cause significant mortality of snakes. Thus, seasonal timing of fires is important in terms of the effect on snake populations.

Natural Sources of Mortality

Food and water supply. 800 water-basins were placed on the island during the 1980s, with water added or replaced every 10 d during drought conditions (Tang 1990). These are no longer used after the 1988 construction of four much larger concrete bowls (2 m wide, 2 m deep) to provide addi-

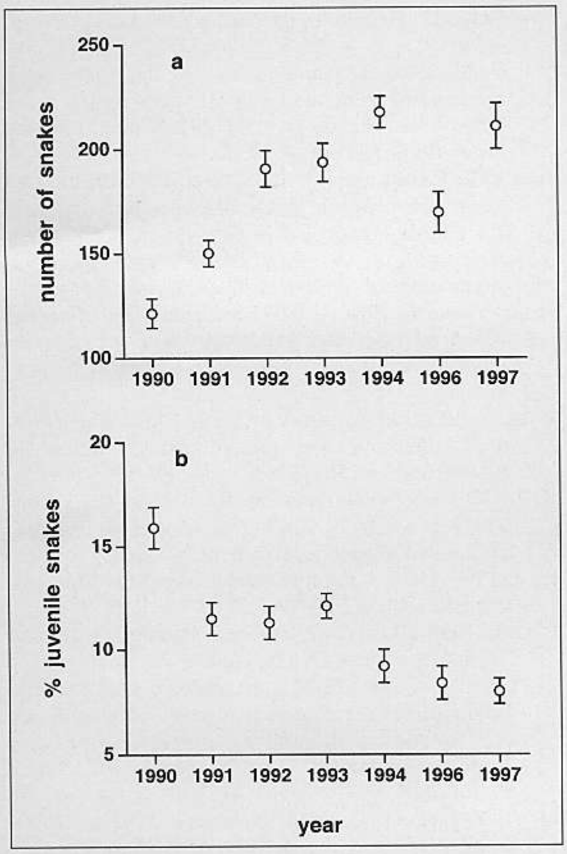

Figure 5. Overall trends in abundance and age structure of Shedao pitvipers, based on snakes recorded during regular census periods. See Sun et al. (2001) for details of survey methods. Bars show one standard error on either side of the mean.

tional drinking sites for snakes. These pools also enhance snake feeding rates by providing ideal ambush sites (Huang 1989). Beside one of these tanks, a 10-m deep well generates a constant water supply. Pumps and hoses allow water to be moved among bowls.

In 1986 and 1987, food supply was supplemented directly by bringing several hundred small birds (chicken, quail, etc.) from the mainland and offering them to the snakes. A less direct method to enhance feeding rates was trialed in 1992, by tying ears of rice to branches that were in use as foraging sites by snakes (Zhao et al. 1992). The rate of bird visitation and of snake abundance and feeding rate was monitored from 0700–0745 h over 3-day periods before and after this manipulation. Bird numbers increased from 60–125, snake numbers from approximately 47–87, and feeding rate per snake from approximately 10–20% (Zhao et al. 1992). Statistical analysis is rendered difficult, however, because of the lack of control plots monitored over the same time span. In another series of manipulations, twigs on many of the trees in Shedao have been pruned such that very slender branches (strong enough to support birds but not snakes) have been removed. This procedure reduces the number of available perching sites where the birds are safe from snake predation.

To address the high rate of neonatal mortality, a large (800 m^2) garden was built on the mainland. Neonates found active on the island late in autumn were brought back to this enclosure to hibernate, and then returned to the island the following spring. Construction of an artificial hibernaculum on the island allowed investigators to identify optimal thermal and hydric conditions during winter, and hence to mimic these in the mainland enclosure (Li and Diao 1993; Li et al. 1993).

Landslide. Areas affected by landslides have been replanted, in an attempt to stabilize the soil.

Predation. There has been no attempt to control birds of prey.

Disease. Mouth infections have been treated by capturing snakes and applying potassium permanganate and gentian violet.

Effectiveness of Conservation Initiatives

Periodic mark-recapture studies, using short-term paint-marking, indicate that the population of pitvipers on Shedao has been steadily increasing since the area was protected. From approximately 9000 snakes in 1982, the population grew to approximately 14,000 by 1989 (Huang 1984, 1990; Sun et al. 1994). It is currently estimated at approximately 18,000 (Sun unpubl. data).

Changes in population size and age structure over the last decade are also evident in data from regular census activities that do not involve marking the snakes. On most days throughout the spring and autumn bird-migration periods each year, scientists walk the same 540-m path and count snakes within a 3-m-wide transect (the path and 1-m widths on either side). The snake's sex and size class are also recorded. We have analyzed the raw data from these counts for the years 1990–97, excluding 1995 (Sun et al. 2001). Over this period total numbers of snakes averaged 40.6 per survey (0.31 per m): thus, the data set contains 37,980 records of sightings of snakes. Analysis clearly shows that snake numbers have increased through time, with a concurrent shift in the proportion of juvenile to adult animals (Fig. 5). The shift in age structure is characteristic of populations recovering from intense harvesting focussed on adult specimens (e.g., Caughley and Sinclair 1994; Webb 1995).

In summary, the pitviper population of Shedao not only has attracted intensive study over many years, but also has been a focus for the development and application of conservation initiatives. Those programs have been successful, and the Shedao studies may have much to tell western science about innovative approaches to issues of snake biology and conservation.

ACKNOWLEDGMENTS

We thank John Weigel for alerting Shine to the existence of Shedao; our wives and families for tolerating our absences on fieldwork on the island; M. Kearney for photographs; and the Australian Research Council for funding our studies.

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