

NATURAL HISTORY OF PITVIPERS IN EASTERN AND SOUTHEASTERN ASIA

NIKOLAI ORLOV, NATALIA ANANJEVA, AND ROMAN KHALIKOV

ABSTRACT: We summarize our observations of 21 species and subspecies of pitvipers and the monotypic viperid, *Azemiops feae*, from the eastern Himalayas to eastern Tonkin, and from the Russian Far East to the Great Sunda Archipelago. We present data for species from the Russian Far East (Primorsky Territory, south of Amur Region and Khabarovsk Territory), Mongolia (Khalkhin-Gol River Valley, western foothills of Big Khingan), Vietnam (mountains of Tonkin and Annam), Eastern Nepal and India (Sikkim), and the Great Sunda Archipelago (highland regions of Southern Sumatra and western Java). Information on feeding behavior, ontogenetic dietary preferences, growth, and reproduction, from the wild and laboratory is discussed.

INTRODUCTION

The goal of this study was to better understand the ecology of rare and/or poorly known species of viperid snakes from different regions of eastern and southeastern Asia (Fig. 1). We investigated the taxa *Calloselasma*, *Deinagkistrodon*, *Gloydium*, *Ovophis*, *Protobothrops*, *Trimeresurus*, and *Tropidolaemus*, as well as the closely related Fea's Viper (*Azemiops feae*). The primary objective of our study, which was conducted from 1979 to 2000, was to document macro- and microhabitats, elevation, seasonal and daily activities, ambient temperature preferences, diet and feeding behavior, social behavior, and reproduction. We also collected information at different field stations with herpetological assemblages that contain several species of viperids, and we compared data for arboreal, semiterrestrial, and terrestrial taxa.

Azemiopinae Liem, Marx, and Rabb, 1971

Azemiops Boulenger, 1888

Monotypic genus.

Distribution: Northern Myanmar, China (southeast Xizang [= Tibet], Yunnan, Guangxi, Guizhou, Sichuan, Fujian, Zhejiang, Jiangxi, and Shaanxi provinces), and northern Vietnam (Vinh Phu, Bac Thai, Cao Bang, and Lang Son provinces) (Bourret, 1936; Smith, 1943; Klemmer, 1963; Green, 1992, 1997; Golay et al., 1993; Zhao and Adler, 1993; Orlov, 1995; 1997; 1998; Nguyen and Ho, 1996; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999).

Azemiops feae Boulenger, 1888

Type Locality: Kakhien (= Kakhien) Hills, Burma (= Myanmar).

Distribution: Same as for genus.

Natural History.—We observed this species in the mountains of northern Vietnam in Vinh Phu, Bac Thai, Cao Bang and Lang Son provinces at elevations from 600 to 1,100 m. This elevational range is similar to that reported for *A. feae* in China (610 to 1,372 m; Pope, 1935). In an effort to obtain natural history information on this poorly-known, cryptic species, we distributed a questionnaire and color photographs among local people (see Plate 3d). Hunters and foresters recognized this species and commented that it is seldom seen due to its secretive habits.

In northern Vietnam, *A. feae* occurs in bamboo and tree fern thickets in areas that are interspersed with well-lit clearings. Karst outcrops and numerous open and underground streams occur throughout this region, and the ground is typically covered with a deep layer of leaf-litter. *Azemiops* spends much of its life in the holes and crevices of the karst fields. Limited information on the natural diet of *A. feae* is available, but this taxon is known to consume rodents and shrews (Marx and Olechowski, 1970; Greene, 1992). We observed these prey species to be abundant in karst outcrops associated with swift mountain streams.

We encountered most *A. feae* before sunrise (3–4 am) from mid-May to early June, during weak rain, when the air temperature was 18–20°C. The snakes moved slowly, occasionally appearing on the surface, but soon after disappearing into the leaf-litter. Juveniles were found from 7 to 11 pm in October and November, also during weak rain, when the air temperature was 16–19°C.

In captivity, *A. feae* did not tolerate dry conditions. Animals required access to water and a moist, loose substrate, even when the relative humidity approached 100%. When this species is maintained under dry conditions, it loses mobility and the skin dehydrates and wrinkles. *Azemiops* feeds at low temperatures (16–17°C) and is capable of digesting food at 19–20°C. In the laboratory, individuals were main-

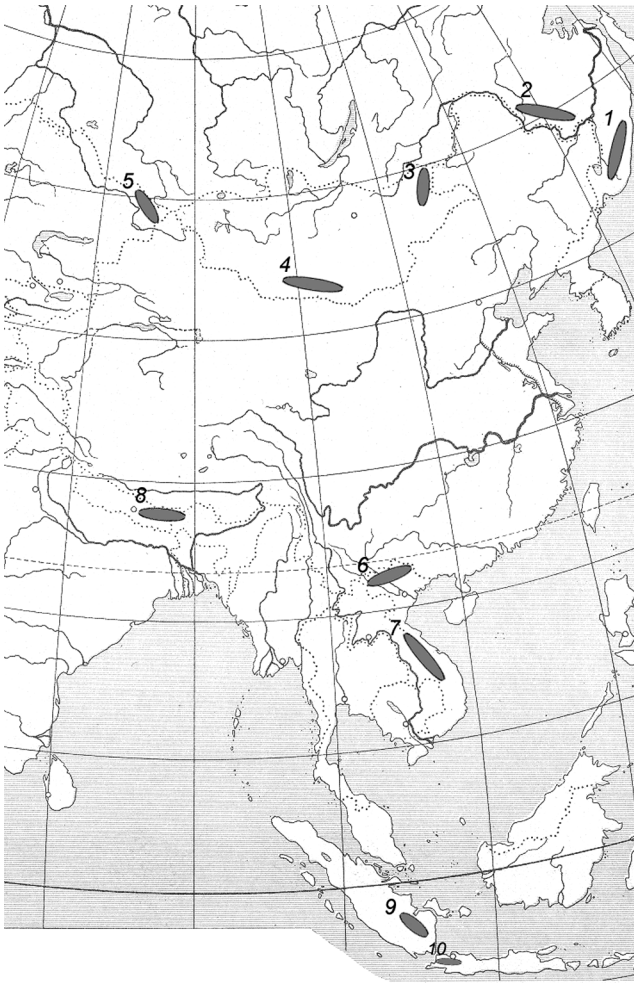


Fig. 1. Regions of investigation for pitvipers in this study. (1) Primorsky Territory (Sikhote Alin Mountains), Russia. (2) South of Amur Region and Khabarovsk Territory, Russia. (3) Khalkhin-Gol River Valley, Eastern Mongolia. (4) Transaltai Gobi, Southern Mongolia. (5) Eastern Kazakhstan. (6) Tonkin, North Vietnam. (7) Annam, Central Vietnam. (8) Eastern Himalayas, Nepal and Sikkim (India). (9) Southern Sumatra, Indonesia. (10) Western Java, Indonesia.

tained at 23–27°C (day) and 17–19°C (night). In a 5-year period a female *A. feae* grew in total length (TL) from 320 to 980 mm, and a male grew from 300 to 920 mm. Individuals this large have not been reported in nature. These snakes were maintained active from February until November and fed every 8–12 days on mice, newborn rats, geckos (*Hemidactylus* sp.), and pieces of chicken scented with rodents. During their active period each snake shed about every 45 days.

Azemiops feae differs from most terrestrial vipers in that it is non-aggressive and generally inactive. Its breeding behavior, however, is similar to that of other snake species in that males approach females in parallel motion, twitch sharply along their body, and

turn their tail and cloaca beneath the female's body. The female, in turn, responds by raising her tail, cloaca become juxtaposed, and the male inserts a single hemipenis. We have observed copulation several times, and it lasts ca. 10 min. In two cases clutches numbered five eggs and incubation was ca. 90 days.

Crotalinae Oppel, 1811

Gloydius Hoge and Romano-Hoge, 1981

Distribution: Sixteen species and subspecies occur in Palearctic Asia: from the southern Transcaucasus in the west to the Far East in the east, and from southern Siberia in the north to Tibet and the Himalayas in the south (Emelianov, 1929; Pope, 1935; Klemmer, 1963; Toriba, 1986; Gloyd and Conant, 1990; Golay et al., 1993; Zhao and Adler, 1993; Ananjeva et al., 1997, 1998; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999; Orlov and Barabanov, 1999). We present observations for three species that inhabit this region, and use the nomenclature presented by Orlov and Barabanov (1999).

Gloydius halys (Pallas, 1776)

Type Locality: [Neotype ZISP. 14784: Orlov and Barabanov, 1999] Borgayskaja steppe, 84 km W from Kjachta town, Burin-Khan Mountain (Burjatia, Russia).

Distribution: Five or six subspecies occupy a wide distributional range, from the Talysh and Alburz mountains in the west, across Central Asia and southern Siberia to the Zeya River and Big Khingan to the east, and to northern Shanxi and Hebei, China, to the southeast.

Gloydius halys halys (Pallas, 1776)

Type Locality: same as for species.

Distribution: *Gloydius h. halys* occurs from the Zeya River and Big Khingan to the east, through southern Siberia, Mongolia, and northwestern China to the west (up to longitude 74° N), in the mountains of Kyrgyzian Tian-Shan and Kazakh Melkosopohnik. In the southeast it penetrates the northern part of Xianyang (Yellow River), and to the south it is limited by the Alashan and Takla-Makan deserts; in the north this taxon borders the lower reaches of the Zeya River along the southern slope of the Yablonovyi, including the valley of the Selenga River and the coasts of Baikal to the Stanovoye Plateau, and through the Eastern Sayan Mountain and Altai to the eastern

Kazakhstan (Chernov, 1934; Terentiev and Chernov, 1949; Ananjeva et al., 1997; 1998; Orlov and Barabanov, 1999; see Plate 4a).

Natural History.—This eurytopic snake occurs at elevations from 200 to 3,500 m. It is abundant in mountain steppes (in eastern Kazakhstan, Altai, Mongolia, Transbaikal) and penetrates the forest zone of the Than Shan, Sayan, and Big Khingan mountains along rocky outcroppings, but does not occur in dense forest. It can be found on the rocky or steep clay banks of mountain rivers, and in moist meadows, but does not inhabit flat-bottomed valleys (numerous tributaries of Khalgin-Gol, Onon and Selenga rivers). *Gloydus h. halys* also occupies piedmont deserts, semideserts, and sand dunes (Zaissan Depression, Transaltai Gobi). These areas are characterized by a continental climate where summer temperatures exceed 30°C (40°C in piedmont deserts), and cold, severe winters. Hibernacula are generally located on south-facing slopes, in deep, underground chambers with tree and bush roots and other debris, and they are often associated with rodent burrows (e.g., *Microtus* spp. and *Rhombomys* spp.).

In the deserts of the Transaltai Gobi and Zaissan Depression, mating begins in early May, but in the mountains (Altai, Khangai and Khentei) mating does not take place until early June. In August and September we found neonates measuring 170–200 mm (TL). At higher elevations neonates hibernate soon after birth and do not feed until the following spring. *Gloydus h. halys* feeds primarily on small mammals and ground-nesting birds, and only occasionally consumes lizards. Snakes from Khangai are often found in *Microtus brandti* colonies where they feed almost exclusively on these rodents. In eastern Mongolia (Khalkhin-Gol River Valley, western foothills of Big Khingan) these pitvipers are often observed swimming, and they feed on frogs and fish (Ananjeva et al., 1997).

Gloydus intermedius (Strauch, 1868)

Type locality: [Terra typica restricta (hoc loco)] Malyi Khingan Mountain Range, Cape Tyr on the Amur River and Cape Kofel on the Ussuri River, Russian Far East.

Distribution: Northeastern China: eastern Manchuria; Korean Peninsula; Russian Far East: Primorsky Territory to the north along the Amur River to Nikolayevsk-na Amure, southern part of the Khabarovsk Territory, and extreme southern Amur Region westward to the Bureya River.

Natural History.—This mesophilic species inhabits forested regions in the Far East, including Ussuri taiga. It is abundant in the highlands of the Sikhote Alin Mountains in Ussuri, the Laso and Sikhote-Alin nature reserves, and along the coast of the Sea of Japan. In the latter area, *G. intermedius* inhabits a transition zone between forest and shore as far north as Soviet Gavan Town. The northern limit of distribution is near Nikolaevsk on the Amur River. In general, this species occupies broadleaf forest with Siberian Pine. In the Sikhote-Alin Mountains *G. intermedius* reaches the upper limit of pine-broadleaf forest (1,100–1,300 m). This region is characterized by a monsoon climate with warm, humid, nearly subtropical summers, and severe, cold winters. Hibernation sites are located in dry, deep (~ 4 m) underground chambers that are generally located on steep south-facing slopes.

Gloydus intermedius shares hibernation sites with *G. ussuriensis*, *Elaphe rufodorsata*, *E. dione*, *Amphiesma vibacari*, and *Rhabdophis tigrina lateralis*. North of the Primorsky Territory, *G. intermedius* will also hibernate with *Vipera sachalinensis* (Korotkov, 1978). In this region, the distribution and density of snakes is limited due to the availability of suitable hibernation sites.

Mating occurs from late August through September, and again in April and early May, when snakes emerge from hibernation. Like all members of the genus *Gloydus*, this taxon is viviparous. Births occur from September to early October, and neonates measured 190–250 mm (TL). *Gloydus intermedius* feeds primarily on rodents, occasionally on birds, and rarely on frogs (*Rana amurensis*, *R. chensinensis*). Juveniles are more likely to consume frogs than adults.

Gloydus ussuriensis (Emelianov, 1929)

Type Locality: [Terra typica restricta (hoc loco)] Russian Far East, Primorskiy Kray, Tetjukhe River Valley, Vladimiro-Monomakhovo village.

Distribution: Russian Far East: throughout the Primorsky Territory, north up to the mouth of Amur River, and south to the Khabarovsk Territory and Amursky Region; northeastern China: Manchuria; North Korea.

Natural History.—This mesophilic taxon inhabits riverbanks, swamps, rice fields, brushland, and grassland. In Sikhote-Alin it typically occupies forest edges and basks on rocky slopes. On the coast of the Sea of Japan it inhabits thickets of dogrose or heavy brush

bordering sand dunes and littoral. *Gloydus ussuriensis* occurs from sea-level to 1,300 m in elevation. This snake is often found sympatric with *G. intermedius* on rocky slopes and sandstone shoreline, but major differences in prey exist between the species: *G. ussuriensis* feeds mostly on frogs, rarely feeds on small mammals, and consumes fish; *G. intermedius*, in contrast, feeds mostly on mammals, rarely on frogs (although juveniles feed on frogs), and does not eat fish.

Gloydus ussuriensis congregates for hibernation from October to early November, sometimes communally with *G. intermedius*. Egress can last from late March until late May and largely depends on elevation and latitude. Mating occurs from April through May, and from September to early October females give birth from 4 to 11 offspring. Neonates measure 150–180 mm (TL) and feed on small frogs soon after they shed.

Deinagkistrodon Gloyd, 1979

Monotypic genus.

Distribution: Taiwan and central China from Zhejiang and Fujian west to Guizhou and southeastern Sichuan, and south to northern Vietnam and Laos. In northern Vietnam it occurs in the Fan Si Pan Mountains (Sa Pa District, Laocai Province), Tam Dao Mountains (Vinh Phu and Bac Thai provinces), and Mau Son (Lang Son Province).

Deinagkistrodon acutus (Günther, 1888)

Type Locality: Mountains north of Kiu Kiang (= Jiujiang Shi), Jiangxi Province, China.

Distribution: Same as for genus (Pope, 1935; Bourret, 1936; Smith, 1943; Deuve, 1970; Klemmer, 1963; Green, 1992; Golay et al., 1993; Zhao and Adler, 1993; Orlov, 1995, 1997, 1998; Nguyen and Ho, 1996; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999).

Natural History.—This species (see Plate 3f) lives in forested hills and mountains at elevations from 100 to 2,000 m. It inhabits rocky areas along streams, and we encountered it mostly during evenings or on cloudy or rainy days. On the Fan Si Pan (Sa Pa District, Lao Cai Province) and Tam Dao (Vinh Phu and Bac Thai Provinces) mountains, local people indicated that adult snakes are often found in association with rat colonies (*Rhizomys* sp.) and use their burrows as shelters and ambush sites. People in Vietnam and China frequently collect *D. acutus* for food and traditional medicine.

A female *D. acutus* ca. 1 m (TL) collected in late June in Mau Son (Lang Son Province), at an elevation of 600 m, produced 19 eggs. In captivity, *D. acutus* fed on frogs, small rats and other rodents. After a meal individuals have been observed in the same general area for nearly 20 days. Mating occurred in May, and oviposition (15–35 eggs) from July to September. Mating, however, was observed in September and October. Eggs averaged 15 g in mass, measured 45–55 x 25–30 mm, and contained well-developed embryos when oviposited. Females attended to and protected their clutches, and left the young snakes approximately 24–30 days after hatching. Neonates measured 215–240 mm (TL) and consumed mostly frogs but eventually fed on mice.

Calloselasma Cope, 1860

Monotypic genus.

Distribution: Indochina (Thailand; Malaysia; Laos; Cambodia; Vietnam); Indonesia (Java and small satellite islands).

Calloselasma rhodostoma (Boie, 1827)

Type Locality: Java (Indonesia).

Distribution: Same as for genus (Pope, 1935; Bourret, 1936; Smith, 1943; Klemmer, 1963; Deuve, 1970; Saint Girons, 1972; Golay et al., 1993; Nguyen and Ho, 1996; Orlov, 1997; 1998; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999).

Natural History.—We observed *C. rhodostoma* in the southern part of the Annam Mountains and the mountain plateau bordering Vietnam, Laos and Cambodia (Mountain Plateau Thai-Nguyen in the provinces of Kon Tum, Gia Lai and Dac Lac), at elevations from 300 to 800 m. This taxon occurs mostly in well-lit forests, particularly in dipterocarp forests where high grass and bamboo undergrowth grows on rocky, clay ground. In contrast to other pitvipers of the region, *C. rhodostoma* avoids steep slopes and excessively wet plots.

Calloselasma rhodostoma (Plate 3e) is typically terrestrial and active at night, and hunts for amphibians and small mammals in areas devoid of lush grasses. We recorded *C. rhodostoma* feeding on *Limnonectes limnocharis*, *Phrynoglossus martensi*, *Polypedates leucomystax*, *Rana nigrovittata*, rodents, and small birds.

Mating occurs from March to May and in utero development takes about two months. Females lay from 10 to 30 eggs and protect their clutches during

incubation. In captivity, incubation was from 35 to 40 days at 27–30°C. Neonates measured 155–175 mm (TL) and fed on frogs and newborn mice.

***Ovophis* Burger, 1981**

Distribution: Four species in Japan (Amami and Okinawa islands in the Ryukyu Archipelago); southern China, including Taiwan and Hainan; Vietnam; Laos; Cambodia; Thailand; Malaysia; Bangladesh; Myanmar; eastern India; Nepal; Bhutan; and Indonesia (Sumatra and Borneo) (Hoge and Romano-Hoge, 1981; Welch, 1988; Golay et al., 1993; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999).

***Ovophis monticola* (Günther, 1864)**

Type locality: Nepal and Sikkim.

Distribution: Southern and central China, including Hainan, Hong Kong, and Taiwan; Nepal; Bhutan; India; Bangladesh; Myanmar; Thailand; Vietnam; Cambodia; west Malaysia; and Indonesia (Sumatra). Four (or five) subspecies are recognized (Pope, 1935; Bourret, 1936; Smith, 1943; Klemmer, 1963; Taylor, 1965; Welch, 1988; Hoge and Romano-Hoge, 1981; Golay et al., 1993; Zhao and Adler, 1993; Orlov, 1995; Nguyen and Ho, 1996; David and Tong, 1997; Orlov, 1997, 1998; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999).

***Ovophis monticola monticola* (Günther, 1864)**

Type locality: Nepal and Sikkim.

Distribution: Xizang, Sichuan, Guizhou, and Yunnan Province, China; Bangladesh; Bhutan; Nepal; Arunachal Pradesh, Assam, Darjeeling (part of West Bengal) and Sikkim, India; and Myanmar.

Natural History.—We observed this taxon (see Plate 4e) in the middle tier of mountains of eastern Nepal (Mechi Province) and northeastern India (Sikkim) at elevations from 1,000 to 2,800 m. Snakes were found on rocky outcrops at the edge of oak and mixed humid forest and on the banks of mountain streams, as well as in agricultural fields, rock walls and other human structures near villages. As a rule, *O. m. monticola* lives in the vicinity of mountain rivers, streams, and wet slopes with underground springs. This species is mostly nocturnal, but in the mid-Himalayas we encountered snakes basking on cool, rainy, summer days. Pregnant females and individuals with full stomachs were observed to bask more frequently. At night *O. monticola* is active when temperatures are as low as 16–17°C. This species feeds primarily on rodents and rarely consumes

frogs. In captivity, newborn specimens preferred to eat mice. Mating occurred in late April and May, and from 5 to 11 eggs are deposited in July and August. Females protected their clutches, incubation was nearly 40 days, and neonates measured 180–200 mm (TL).

***Ovophis monticola convictus* (Stoliczka, 1870)**

Type locality: Western Hill of Penang, elevation ca. 2,400 feet (= Malaya Peninsula, Malaysia).

Distribution: Southern and central Vietnam; southern Laos; Cambodia; Thailand; west Malaysia (Malaya Peninsula); and Indonesia (Sumatra).

Natural History.—This snake is strongly terrestrial and nocturnal, and inhabits primary and closed-canopy rainforest at elevations from 400 to 2,000 m. It is often seen on the sandy banks of mountain streams, especially in areas that are covered with leaf-litter. This species feeds primarily on small mammals and seldom eats frogs.

In southern Annam (province of Gia Lai), at elevations from 700 to 900 m, mating occurs in March and April, and eggs are deposited in late June and July. Clutches of 4 to 18 eggs are deposited in holes or in leaf-litter and females often guard their eggs. A female of 690 mm (TL) laid 8 eggs, incubation lasted 44 days, and the neonates measured 178–185 mm (TL). In captivity, neonates usually fed on newborn mice after their first shed. In most of southern Annam, *O. m. convictus* is sympatric with *Trimeresurus albolabris*, *T. popeorum*, and *T. stejnegeri*, but this species occupies a different microhabitat.

***Ovophis tonkinensis* (Bourret, 1934)**

Type Locality: Chapa (= Sa Pa District, Lao Cai Province), Vietnam.

Distribution: Northern Vietnam (Lai Chau, Lao Cai, Ha Giang, Vinh Phu, Cao Bang, Bac Thai, Lang Son, Qang Ninh); China (Hainan Island, probably in southern Yunnan and Guangxi) (Bourret, 1936; Klemmer, 1963; Golay et al., 1993; Nguyen and Ho, 1996; Orlov, 1997, 1998; David and Ineich, 1999; McDiarmid et al., 1999).

Taxonomic Comments.—The taxonomic status of this species is controversial and *tonkinensis* may be a *nomen nudum*. Most authors consider *tonkinensis* a subspecies or junior synonym of *O. monticola* (for comparison, see Plate 4d, e). Its identity is in question because *Trimeresurus monticola meridionalis* R. Bourret, 1935 [= *O. monticola convictus* (Stoliczka, 1870)] was described from the same type locality (Chapa), consequently placing two species of *Ovophis*

in these mountains. We tentatively follow Hoge and Hoge-Romano (1981) and Toriba (in Golay et al., 1993) and recognize *O. tonkinensis*. The taxonomic status of *O. tonkinensis*, however, as well as studies on the distribution and relationships among members of “*Ovophis monticola*” complex, are in need of further investigation.

Natural History.—This montane species lives in rain and monsoon forests at elevations from 700 to 2,000 m. In northern Vietnam we observed this snake in the Tam Dao range (Vinh Phu Province) at elevations from 700 to 1,200 m, in the Fan Si Pan Mountains (Sa Pa, Lao Cai Province) from 1,400 to 1,900 m, and north of Cao Bang Province from 600 to 800 m. Snakes were found in leaf-litter and on piles of karst rocks on the banks of swift-moving streams, in areas where the open canopy exposed the ground to sunlight.

Young animals were located under rocks or brush during the day, and adults were found buried in leaf-litter. During evenings in March, at elevations from 900 to 1,100 m (Tam Dao), we encountered males and subadults active at temperatures of 13–15°C. Adult females were found on the surface on early evenings in March and early April at temperatures of 15–17°C. This is a slow-moving, nocturnal, terrestrial snake that we have never been observed to climb.

Ovophis tonkinensis appears to adjust well to disturbed areas and is often encountered in the vicinity of human structures near streams. In early June (Tam Dao) we found adult, pregnant females crossing paved roads in the evening 50–60 m from a stream, and subadults were located under rocks on forested mountain slopes at 100–150 m from a stream. Several adult females observed in early April were in ambush position, apparently seeking food to add mass for reproduction. Others, however, were seen moving about, but they appeared emaciated and did not have food in their stomachs. It was not clear if those individuals were ready to reproduce.

Most hunting females were observed on karst stream banks where they consumed amphibians (*Limnonectes kuhli*, *Rana maosonensis*, *Paa spinosa*, *Polypedates* cf. *leucomystax*), rodents (*Rattus* sp.), and insects (*Chimarrogales* sp.). Stomach contents for three females collected from 6 to 11 May, measuring 740, 620, and 560 mm (TL), contained 9, 17, and 6 frogs (*R. maosonensis*, *R. kuhli*, *P.* cf. *leucomystax*), respectively. This coincides with the time these amphibians congregate to reproduce (see Mori et al., this volume). In other seasons *O. tonkinensis* feeds mostly on small mammals.

We observed a male (430 mm TL) and female (770 mm TL) *O. tonkinensis* mating at night in early April when the air temperature was 17°C. The snakes were in leaf-litter on the forest floor, 6 m from a stream, in a sparse bamboo thicket with ferns and Araceae. Pregnant females were found from April to June at elevations from 700 to 1,200 m. We palpated the pregnant females and established that they contained from 5 to 9 eggs. In captivity, two females (610 and 670 mm TL) laid 5 and 7 elongated eggs on 29 June and 8 July, which were incubated at 28°C (day) and 25°C (night) and hatched in 42 and 38 days, respectively. Both females stayed with their clutches for several days. Seven hatchlings measured 195 to 210 mm (TL) (Orlov, 1997).

Protobothrops Hoge and Romano-Hoge, 1983

Distribution: Eight species in Japan (Ryukyu Archipelago: Okinawa, Amami, Takara-shima, Kotakara-shima); eastern India; Bhutan; Nepal; Myanmar; China (Yunnan, Henan, Shanxi, Shaanxi, Gansu, Sichuan, Guizhou, Hubei, Zhejiang, Jiangxi, Guangxi, Fujian, Guandong, Taiwan); Vietnam; and Bangladesh (Pope, 1935; Bourret, 1936; Klemmer, 1963; Hoge and Romano-Hoge, 1981; Golay et al., 1993; David and Ineich, 1999; McDiarmid et al., 1999; Orlov et al., 2001).

Protobothrops jerdonii Günther, 1875

Type Locality: Khassya (= Khasi Hills), Assam, India.

Distribution: Three subspecies (*P. j. jerdonii* Günther, 1875; *P. j. bourreti* Klemmer, 1963; *P. j. xanthomelas* Günther, 1889; see Plate 6d) occur in China, Vietnam, Myanmar, Assam, Sikkim, West Bengal (Darjeeling), Meghalaya, and Arunachal Pradesh, India; Buthan; and Nepal.

Protobothrops jerdonii bourreti (Klemmer, 1963)

Type Locality: Chapa (= Sa Pa, Lao Cai Prov.), Tonkin, Vietnam.

Taxonomic Comments.—*Trimeresurus jerdonii bourreti* K. Klemmer, 1963 nomen novum pro *Trimeresurus jerdonii meridionalis* R. Bourret, 1935, Bull. Gén. Instr. Publique, Hanoi, 1935 (7):14–15, non *Trimeresurus monticola meridionalis* R. Bourret, 1935, Bull. Gén. Instr. Publique, Hanoi, 1935 (7):13–14.

Distribution: Mountains in the provinces of Lai Chau and Lao Cai in northwestern Vietnam, and adjacent Yunnan Province, China (Orlov et al., 2001).

Natural History.—We studied this snake on Mount Fan Si Pan (Sa Pa, Lao Cai) at elevations from 1,500 to 2,000 m. This semiarborescent species was active mostly at night on bushes, large boulders, and rocky slopes on the banks of waterfall streams (Plate 6e). In March, when temperatures at night dropped between 7–11°C, *P. j. bourreti* was seen basking in the middle of the day. We observed an adult female with a rat in her stomach basking on a fallen trunk near a stream and a juvenile on a bush in the floodplain of the stream at an elevation of 1,900 m.

Protobothrops mucrosquamatus (Cantor, 1839)

Type Locality: Naga Hills, Assam, India.

Distribution: Northeastern India; Bangladesh; Myanmar; central and southern China (including Taiwan) and Vietnam southward to Gia Lai Province in the Central Highlands (Pope, 1935; Bourret, 1936; Smith, 1943; Klemmer, 1963; Golay et al., 1993; Zhao and Adler, 1993; Nguyen and Ho, 1996; Orlov, 1997, 1998; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999; Orlov et al., 2001).

Natural History.—This species (Plate 6c) is found at elevations from 150 to 1,500 m in habitats ranging from lowland bamboo thickets to highland rainforest, and it also occupies disturbed areas. In the Tam Dao range, *P. mucrosquamatus* is abundant at elevations from 700 to 1,000 m.

In the mountains of northern Vietnam, *P. mucrosquamatus* emerges from hibernation in early March. At that time, we observed males and subadults during the evening at a temperature of 13°C, but few females were seen until mid-April when the night temperatures had risen slightly (15–17°C). These snakes were encountered more frequently from late May to early June on evenings of light rain and temperatures ca. 20–22°C. Activity in Tam Dao subsides significantly by mid-November. In November, however, we encountered this species in rainforest in the northern Annam Mountains at elevations from 350 to 400 m.

At night we located *P. mucrosquamatus* on low bushes, fallen tree trunks, and rocky outcrops, but during the day individuals were generally under logs, in rock crevices, or in leaf-litter. In April and May, we discovered several *P. mucrosquamatus* basking about 0.5 m off the ground in bamboo thickets, but the majority of snakes were seen in late May and June on evenings without heavy rain and air temperatures ca. 20–22°C.

During spring in Tam Dao, *P. mucrosquamatus* feeds primarily on frogs. This coincides with the

time *Rana maosonensis*, *R. guentheri*, *Limnonectes limnocharis*, *Polypedates* cf. *leucomystax*, and other frogs congregate to reproduce. This species also feeds on rats, shrews, newborn squirrels, birds, and snakes. Orlov (1997) reports an observation of a *P. mucrosquamatus* feeding on an *Amphiesma*, which in turn was eating a *Rhacophorus* (= *Polypedates*); the *P. mucrosquamatus* swallowed both.

Snakes collected in April soon initiated copulation in captivity, and from late May to early June females appeared pregnant. A female measuring 920 mm (TL) laid a clutch of eight eggs on 22 June, which were incubated at 28°C (day) and 25°C (night), and four eggs hatched on 30 June. The neonates measured 215–220 mm (TL) and consumed young mice. They refused to feed on frogs, possibly because only non-native species were offered.

Trimeresurus Lacepede, 1804

Distribution: Thirty species in southern and central China, including Taiwan and Hainan; India; Sri Lanka; Nepal; Bhutan; Bangladesh; Laos; Vietnam; Cambodia; Thailand; Malaysia; Indonesia (except New Guinea), and the Philippine Islands (Bourret, 1936; Klemmer, 1963; Golay et al., 1993; David and Ineich, 1999; Hoge and Romano-Hoge, 1981).

Trimeresurus albolabris Gray, 1842

Type Locality: China.

Distribution: Nicobar Islands (India); Bangladesh; Myanmar; Thailand; Cambodia; Vietnam; Laos; southern China (Hong Kong Jiangxi, Fujian, Guangdong, Hainan, Guangxi, Guizhou and Yunnan Provinces); Malaysia (Western and Borneo); Indonesia (Kalimantan, Java, Sumatra, Sulawesi and Madura) (Pope, 1935; Bourret, 1936; Smith, 1943; Klemmer, 1963; Taylor, 1965; Kramer, 1977; Hoge and Romano-Hoge, 1981; Regenass and Kramer, 1981; Welch, 1988; Cox, 1991; Golay et al., 1993; Zhao and Adler, 1993; Das, 1994a, b, 1997; David and Vogel, 1996; Nguyen and Ho, 1996; Szyndlar and Nguyen, 1996; Orlov, 1995, 1997, 1998; Zhao and Yang, 1997; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999; Giannasi et al., 2001).

Taxonomic Comments.—*Trimeresurus albolabris* (Plate 5d) was comprised of three subspecies, but these forms have been elevated to specific status. Two of these taxa, *T. albolabris* and *T. septentrionalis* are considered here. The third species, *T. insularis* (Kramer, 1977) occurs in Indonesia (Lombok,

Sumbawa, Komodo, Sumba, Flores, Roti, Timor, and the Wetar Islands in the Lesser Sunda Archipelago; Mertens, 1930; Auffenberg, 1980; Hoge and Romano-Hoge, 1981; Regenass and Kramer, 1981; Welch, 1988; Golay et al., 1993; David and Ineich, 1999; McDiarmid et al., 1999; Giannasi et al., 2001). Several distinct populations may still comprise *T. albolabris*. In southern China and Indochina, at least three populations differ strongly in morphology and natural history, and a similar situation might exist in Java and Borneo.

Natural History.—This taxon is abundant in flat areas with dense grasses and trees at elevations from sea-level to 2,000 m. In Tam Dao, it is especially abundant at elevations from 400 to 800 m. Most snakes were encountered along the edge of primary forest, sparse bamboo thickets and fern thickets, and in the vicinity of human structures.

On evenings, from 7 to 11 pm, individuals were found from 0.5 to 1 m off the ground with their heads pointing down in a hunting posture. We found that they consumed mostly frogs (*Polypedates leucomystax*, *Rhacophorus appendicularis*, *Microhyla pulchra*, *Rana limnocharis*, *R. maosonensis*), but also small mammals and soricids. On evenings with heavy rain, *T. albolabris* often hunts for frogs on the ground. Under such conditions we found a female *T. albolabris*, measuring 590 mm (TL), that had consumed seven adult *P. leucomystax*. *Trimeresurus albolabris* was seldom located during the day, but several individuals were found in villages under palm roofs or resting on wooden beams in sheds at heights of 1–2 m. At night, these snakes did not travel far from where they were observed, and they remained close to the ground.

From late March to late May, mating occurs mostly at night in trees, bushes, or bamboo ca. 1–1.5 m above the ground. Additional males were found within 35 m of a breeding pair. This species is viviparous and produces from 4 to 14 young, which are born from late July to early August and measure 138 to 145 mm (TL). In captivity, neonates shed 1–2 days after birth. Neonates showed a feeding response to small jumping frogs, but no reaction to newborn mice unless they were scented with frogs.

Trimeresurus septentrionalis Kramer, 1977

Type locality: Nepal, 83° 55' 28" 15', 1500 m (Nähe Pokhara). Given as Hyangcha (Nepal) 83° 55' E. L. 28° 5' N. B. 1,500 m by Regenass and Kramer (1981:177).

Distribution: Himalayan region of northern India (Kashmir), Nepal, Buthan, Bangladesh, and Myanmar

(Kramer, 1977; Golay et al., 1993; David and Ineich, 1999; McDiarmid et al., 1999).

Natural History.—In central and eastern Nepal this taxon inhabits monsoon forests on mountain slopes at elevations from 900 to 3,000 m. No additional information is available for the natural history of this species.

Trimeresurus cornutus Smith, 1930

Type Locality: Fan-Si-Pan (= Mount Fan Si Pan), Chapa (= Sa Pa) Lao Cai Province, northern Vietnam, 2,000 m.

Distribution: Data on distribution is based on two specimens: holotype, BMNH, male, from Mount Fan Si Pan, Sa Pa District, northern Vietnam, and one female, from Tonkin, stored in Paris, MNHN (Smith, 1943; Klemmer, 1963; Golay et al., 1993; Orlov, 1995, 1998; David and Ineich, 1999; McDiarmid et al., 1999). There is also an unconfirmed report of a specimen from southern Vietnam from Bach Ma (Thua Thien-Hue Province; Campden-Main, 1970; Nguyen and Ho, 1996).

Natural History.—The holotype is from near Sa Pa at an elevation ca. 2,000 m. Hunters in Si Pa indicated that between 1996 and 1998, two *T. cornutus* were found on tree branches in polydominant forest on Mount Fan Si Pan at elevations from 1,400 to 2,000 m. Judging by the slender body structure of *T. cornutus* and from anecdotal information obtained from local people, this taxon appears to be a secretive, arboreal species that inhabits cool, mountain forests.

Trimeresurus erythrurus (Cantor, 1839)

Type Locality: “Delta Gangeticus” (delta of the Ganges River, west Bengal, eastern India).

Distribution: Myanmar; Bangladesh; eastern India (Shaw et al., 1939; Smith, 1943; Regenass and Kramer, 1981; Klemmer, 1963; Golay et al., 1993; David and Ineich, 1999; McDiarmid et al., 1999); Annapurna range in Himalayas (Shah, 1995). This species appears to be widely distributed in the Himalayan region of northern Nepal.

Natural History.—This arboreal species inhabits mountain forests in the eastern Himalayas at elevations from 1,000 to 2,000 m. It generally occurs along mountain streams on the slopes of monsoon forest, where there is bushy undergrowth, epiphytic plants, and lichens. Two females collected in July had five and nine developed embryos. In captivity, snakes mated from February to April, and neonates (14 in one litter) measuring 150–180 mm (TL) were born from

July to September. Newborn *T. erythrurus* feed on frogs and adults consume frogs and mice. In the eastern Himalayas and adjacent regions of Tibet, *T. erythrurus* is sympatric with *T. medoensis*, *T. septentrionalis*, *T. stejnegeri*, *Ovophis m. monticola*, and *Protobothrops j. jerdonii*.

Trimeresurus karanshahi Orlov and Helfenberger, 1977

Type Locality: Central Nepal, Bagmati Province, Godavari village, Phulchoki Mountain, 2,700 m.

Distribution: In addition to the type locality, this species is found in the Kaski District, Gandaki Province (central Nepal) at elevations from 2,500 to 2,600 m, and on the slopes of the Himalaya Shan mountain massifs, such as Gomolangma (Everest), Macalu, and Kanchenjunga at elevations from 3,000 to 3,500 m. This species apparently does not occur below 2,500 m, and wide intermountain plains separate the populations. *Trimeresurus karanshahi* exhibits a high degree of color and pattern polymorphism, and the taxonomic status, age and divergence of isolated populations will be studied in the future.

Natural History.—We encountered this semi-arboreal species (Plate 5c) in oak forests and bush thickets in mountains with large rocky slopes at elevations from 2,500 to 3,500 m. The rocks in this region are often covered with deciduous leaf-litter, and no permanent pools occur on the mountain slopes. Even in summer, temperatures at these elevations do not exceed 18°C during the day and they drop below 10°C at night. Heavy rainfall is a common occurrence, and the slopes are often covered in dense fog. We observed individuals basking on moss-covered rocks. Actively feeding individuals of both sexes were seen basking in July and August, and pregnant females were observed basking in August. In captivity, gestation was from seven to eight months. Due to climatic conditions, this species, at best, has a biennial reproductive cycle.

Trimeresurus macrops Kramer, 1977

Type Locality: Bangkok (Thailand).

Distribution: Thailand; Cambodia; and southern Vietnam (Minh Hai and Kieng Giang Provinces) (Regennass and Kramer, 1981; Cox, 1991; Gumprecht, 1998; McDiarmid et al. 1999).

Natural History.—This is an arboreal, viviparous species. According to Gumprecht (1998), this taxon consumes mainly frogs and lizards, and it attains a maximum elevation in Thailand of 1,670 m. Little information is available for *T. macrops* in southern

Vietnam, but local hunters have indicated that it occupies secondary forest, parks, and agricultural areas. Along the border of Cambodia *T. macrops* is sympatric with *T. popeorum* and *T. albolabris*, in hilly regions with bush covered, rocky outcrops. Individuals were obtained from local animal dealers who seldom provide locality data, but it is evident that the snakes were collected in the southern provinces of Vietnam and adjacent Cambodia. In captivity, *T. macrops* consumed frogs.

Trimeresurus popeorum Smith, 1937

Type Locality: No type locality was originally designated, but Taylor and Eibel (1958:1171) restricted the locality to the “Khasi Hills, Assam” (India).

Distribution: Sikkim, Assam, Western Bengal (India); Myanmar; Thailand; Laos; Vietnam; Cambodia; Malaysia; Singapore; Sumatra, Mentawai Archipelago; and Borneo (Indonesia and Malaysia) (Shaw et al., 1939; Smith, 1943; Klemmer, 1963; Golay et al., 1993; Zhao and Adler, 1993; Kramer, 1977; Orlov, 1997, 1998; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999).

Taxonomic Comments.—Three subspecies are recognized (see Regennass and Kramer, 1981), of which the nominate form *T. p. popeorum* occurs in Sikkim, Assam, western Bengal (India); Myanmar; Thailand; Laos; Vietnam; Cambodia; Malaysia; and Singapore. *Trimeresurus p. sabahi* occurs in Indonesia and Malaysia (Borneo). *Trimeresurus p. barati* is known from Indonesia (Mentawai Archipelago and Sumatra). The specific epithet is most commonly spelled *popeorum*. David and Vogel (1996) indicated that the emendation of the spelling from *popeiorum* to *popeorum* by Smith (1943) was unjustified. William W. Lamar (in litt.) has communicated to us, however, that that Smith (1943) was clearly correcting a copyist’s error, that such a change was allowed at the time, and that it was specifically allowed under the first published *International Code of Zoological Nomenclature*. While the 1985 and subsequent *Codes* prohibit this, they apply only to actions taken post-1985. Thus, the correct name is *popeorum*.

Natural History.—This species inhabits mountains and plains at elevations from 150 to 1,200 m, especially forested regions with streams, ponds, and swamps. In Tam Dao, we encountered *T. popeorum* on the banks of karst streams in primary forest at elevations from 900 to 1,200 m. At night snakes appeared to be actively hunting on tree branches and lianas over streams, as well as on the banks of small forest lakes

in swampy meadows, > 1.5 m above the ground. We observed *T. popeorum* swimming in streams, and during the day we discovered individuals hiding in small bushes near water.

In southern Vietnam we found *T. popeorum* on the Thai-Nguyen Mountain Plateau (Gia Lai and Dac Lac Provinces), and west of the town of Nhatrang (Khanh Hoa Province). In contrast to the northern population, southern animals did not climb high in trees, and their occurrence was not heavily associated with the banks of streams. Individuals were commonly seen along forest edges in bamboo thickets and clearings at elevations from 400 to 900 m.

We observed *T. popeorum* feeding from April to June, mostly on *Polypedates* and *Rhacophorus* (> 80% of stomach contents were *P. leucomystax*), and occasionally on *Rana maosonensis*, lizards, and small mammals. In southern Vietnam, west of the town of Nhatrang (Khanh Hoa Province), adult females and juveniles fed in October and November, whereas all the males we encountered had empty stomachs.

Mating occurs in trees and bushes, and one pair was observed copulating on the ground near water. Pregnant females were captured from late May to early June, and measured 540–730 mm (TL) and gave birth to 3–6 offspring from late July to mid-August. Neonates measured 170–195 mm (TL). Up to 10 offspring were born to captive females.

Trimeresurus puniceus (Kuhl, 1824)

Type Locality: “Java.”

Distribution: Southern Indochina; Sumatra, Java, Borneo, Mentawai Islands, Natuna Islands, and Simalur (Indonesia) (Klemmer, 1963; Hoge and Romano-Hoge, 1981; Golay et al., 1993; Zhao et al., 1998; David and Vogel, 1998; David and Ineich, 1999; McDiarmid et al., 1999).

Natural History.—This arboreal species is known to occur at elevations from 500 to 1,500 m (David and Vogel, 1996). We encountered *T. puniceus* in primary rainforest at elevations from 1,400 to 1,600 m in Jambi Province (South Sumatra) and the Bogor Region (West Java) on evenings in November and December (see Plate 5a, b). Individuals were found in closed-canopy rainforest, in hunting positions with their heads directed downward, on branches ca. 0.5 m above the ground. We collected five pregnant females that produced litters of 7–13 in captivity. The neonates measured 175–190 mm (TL) and fed on small frogs, but some also consumed newborn mice; adults preferred frogs and seldom fed on mice. In captivity

mating took place in late December and offspring were born in mid-June.

Trimeresurus stejnegeri Schmidt, 1925

Type Locality: Shaowu, Fukien (= Fujian) Province, China.

Distribution: Taiwan, Hainan, and the mainland of southern China, from eastern Sichuan to the south-eastern part of Gansu and east of Jiangsu Provinces; Vietnam; Laos; Cambodia; Thailand; Myanmar; Darjeeling (west Bengal), Sikkim and Assam, India; Bhutan; and eastern Nepal (Shaw et al., 1939; Smith, 1943; Klemmer, 1963; Golay et al., 1993; Zhao and Adler, 1993; Kramer, 1977; Orlov, 1997, 1998; Zhao et al., 1998; David and Ineich, 1999; McDiarmid et al., 1999).

Natural History.—This species inhabits mountains and hills at elevations from 400 to 2,500 m. It occurs in open areas, but is also found on rocky outcrops with dense lianas, mosses and ferns, as well as in rock walls and the sides of trails and fields. In Tam Dao, northern Vietnam, *T. stejnegeri* is frequently found at elevations from 700 to 1,100 m. Animals were observed on evenings in May and June, from 6 to 11 pm, when there was good weather. This species avoids dense brush and closed-canopy forest. It is typically found on trees and bamboo about 2 m above the ground, but was observed > 7 m in trees. This is the most abundant venomous snake in Vietnam (see Plate 5e, f).

Trimeresurus stejnegeri is active at different times, depending on the season. In late March it is active at temperatures of 12–13°C. Inactive males were observed near karst dens at 9°C. During the day, individuals often hid in empty karst niches or in cracks of vertical rocks covered with bush roots. The activity patterns displayed by *T. stejnegeri* are similar to those of *P. mucrosquamatus*.

This species feeds mostly on amphibians. In May and June, the diet consisted mostly of *Polypedates* and *Rhacophorus*, and to a lesser degree on ranids (*Rana maosonensis*, *R. limnocharis*, *R. guntheri*), but geckos (*Gekko sinensis*) and rodents were also consumed.

We observed *T. stejnegeri* mating from late April to early May. At this time males were moving on the ground, whereas adult females remained in the same location every night. In the southern highlands of Vietnam, males were active at night from March to December. Numerous adults of both sexes were observed from April to July, whereas juveniles were commonly seen in October and November. This

Table 1. Comparison of aspects of habitats, mode of reproduction, and prey in 20 species of Asian pitvipers and the monotypic *Azemiops feae*.

Taxon	N	Macrohabitat			Elevation (m)	Reproduction		Prey				
		Terrestrial	Arboreal	Semi-arboreal		Fossorial	Oviparous	Viviparous	Mammals	Frogs	Mixed	
<i>Azemiops feae</i>	12				+	+				+		
<i>Gloydius halys halys</i>	198	+					+			+		
<i>G. intermedius</i>	164	+					+					+ ¹
<i>G. ussuriensis</i>	170	+					+					+ ²
<i>Calloselasma rhodostoma</i>	46	+					+					+ ³
<i>Deinagkistrodon acutus</i>	7	+					+					+
<i>Ovophis monticola monticola</i>	52	+					+					+
<i>O. m. convictus</i>	18	+					+					+ ³
<i>O. tonkinensis</i>	27	+					+					+ ³
<i>Protobothrops jerdoni xamthomelas</i>	9					+		+				+ ¹
<i>P. j. bourreti</i>	22					+		+				+
<i>P. microsquamatus</i>	80					+		+				+ ⁴
<i>Trimeresurus albolabris</i>	193							+				+ ⁵
<i>T. septentrionalis</i>	6					+		+				+
<i>T. erythrurus</i>	16					+		+				+
<i>T. karanshahi</i>	6							+				+
<i>T. popeorum</i>	11					+		+				+ ⁵
<i>T. puniceus</i>	34							+				+
<i>T. stejnegeri</i>	203					+		+				+ ⁵
<i>T. macrops</i>	11					+		+				+ ⁵
<i>Tropidolaemus wagleri</i>	38					+		+				+ ⁶

¹Adults consume mostly mammals; juveniles consume anurans and mammals.²All age classes consume anurans; adults sometimes consume mammals.³Adults consume mostly mammals; juveniles sometimes consume frogs.⁴Adults consume mostly mammals; some individuals alter their diet to frogs during the amphibian breeding season.⁵Mostly consume anurans; adults sometimes consume mammals.⁶Adults consume mostly mammals; juveniles and males sometimes consume frogs.

species is viviparous, and depending on the region, gives birth to 3–7 young between July and September. In China, however, *T. stejnegeri* has been reported to give birth to as many as 15 young (Hu et al., 1987). In captivity, a female will frequently mate multiple times. In nature, on 8 and 11 April, a male was found near a pair in copulation. In captivity, four females gave birth on 16 and 24 August, and on 3 and 5 September. The neonates numbered from 3 to 7 and measured 155–175 mm (TL). Neonates consumed small frogs (*Rana* sp.) and geckos (*Hemidactylus* sp.) after their first shed.

Tropidolaemus Wagler, 1830

Distribution: Two species in Southern Thailand; Malaya Peninsula (Malaysia); Natuna Islands, Nias, Mentawai Islands, Sumatra, Bangka, Biliton, Borneo, Karimata Islands, Sulawesi, Sangihe Islands, and Buton (Indonesia); Balabac, Basilan, Jolo, Leyte, Luzon, Mindanao, Palawan, and Samar (Philippines); southern Vietnam; and Madura district, Tamil Nadu (southern India).

Tropidolaemus wagleri (Boie, 1827)

Type Locality: Java.

Distribution: Southern Thailand; Malaya Peninsula (Malaysia); Natuna Islands, Nias, Mentawai Islands, Sumatra, Bangka, Biliton, Borneo, Karimata Islands, Sulawesi, Sangihe Islands, and Buton (Indonesia); Balabac, Basilan, Jolo, Leyte, Luzon, Mindanao, Palawan, and Samar (Philippines) (Klemmer, 1963; Hoge and Romano-Hoge, 1981; Golay et al., 1993; Zhao et al., 1998; David and Vogel, 1996; David and Ineich, 1999; McDiarmid et al., 1999). Nguyen and Ho (1996) reported a specimen from Song Be Province, Vietnam. Hunters and dealers brought *T. wagleri* to Ho Chi Minh City in southern Vietnam from the coastal lowlands of Minh Hai Province.

Natural History.—This species typically occurs in wet lowlands, including wet forests, swamps, marshes, and mangroves at elevations from sea-level to 1,300 m. Adults are strictly arboreal, sluggish, and are often encountered on the lower branches of trees or bushes where they feed on mammals, birds, lizards, and frogs. Juveniles prey on frogs and lizards, and occasionally feed on the ground.

This viviparous species usually gives birth to ca. 15 offspring, although in captivity as many as 41 offspring have been reported in a litter (Lim, 1990). We observed pregnant females with developing embryos from March to May.

DISCUSSION

A comparison of the biological patterns of snake species described here (Table 1) focuses on micro- and macrohabitats, reproduction, and prey. Among 20 taxa (*T. cornutus* is excluded due to lack of data) eight are terrestrial, seven are arboreal, and four are semiarboreal. We regard *Azemiops feae* as fossorial.

Morphological specialization of Asian arboreal pitvipers includes a slender body and green coloration in *Trimeresurus* and *Tropidolaemus* (Greene, 1992). *Protobothrops j. jerdonii*, *P. mucrosquamatus*, *T. karanshahi*, and *T. puniceus* occupy an intermediate position (semiarboreal) between the terrestrial (*Calloselasma*, *Deinagkistrodon*, *Gloydus*, *Ovophis*) and arboreal (*T. albolabris*, *T. erythrurus*, *T. macrops*, *T. popeorum*, and *T. wagleri*) pitvipers. There are no fully-aquatic forms among these species of pitvipers, but most taxa inhabit streams in valleys and feed on frogs (at least as juveniles). We note two unusual cases of pitvipers foraging in water for fish: *G. ussuriensis* and one population of *Gloydus h. halys* in eastern Mongolia (western piedmonts of Big Khingan).

The elevational distribution of pitvipers is associated with specific habitat preferences. The widest elevational range is for *G. h. halys* (200 to 3,500 m). The elevational distribution of “green” pitvipers has been affected by anthropogenic changes to habitats. *Trimeresurus stejnegeri* inhabits forested regions and prefers sites with closed canopies. This spatial preference can change with elevational distribution in disturbed areas, where *T. stejnegeri* shifts to more remote mountain regions. *Trimeresurus albolabris* appears to be better adapted to anthropogenic conditions, and occurs in or near villages in deforested areas. In general, *T. popeorum* and *T. stejnegeri* prefer more humid habitats than *T. albolabris*.

Among high-elevation species, *T. karanshahi* was not observed below 2,500 m. Both *T. tibetanus* from adjacent regions in Xizang (= Tibet), China, and *T. karanshahi* occupy the highest elevations among *Trimeresurus*, and thus are subjected to extreme cold conditions.

Viviparity, which has evolved independently multiple times in viperids (Greene, 1992), was noted among arboreal and semiarboreal *Trimeresurus*, arboreal *Tropidolaemus*, as well in the northernmost *Gloydus*. The terrestrial pitvipers (*Ovophis* and *Protobothrops*) and *Azemiops feae* are oviparous. In *D. acutus*, we confirm that eggs (before laying) contain well-developed embryos (see Pope, 1935; Fleck 1987), and that neonates measure 215–240 mm (TL).

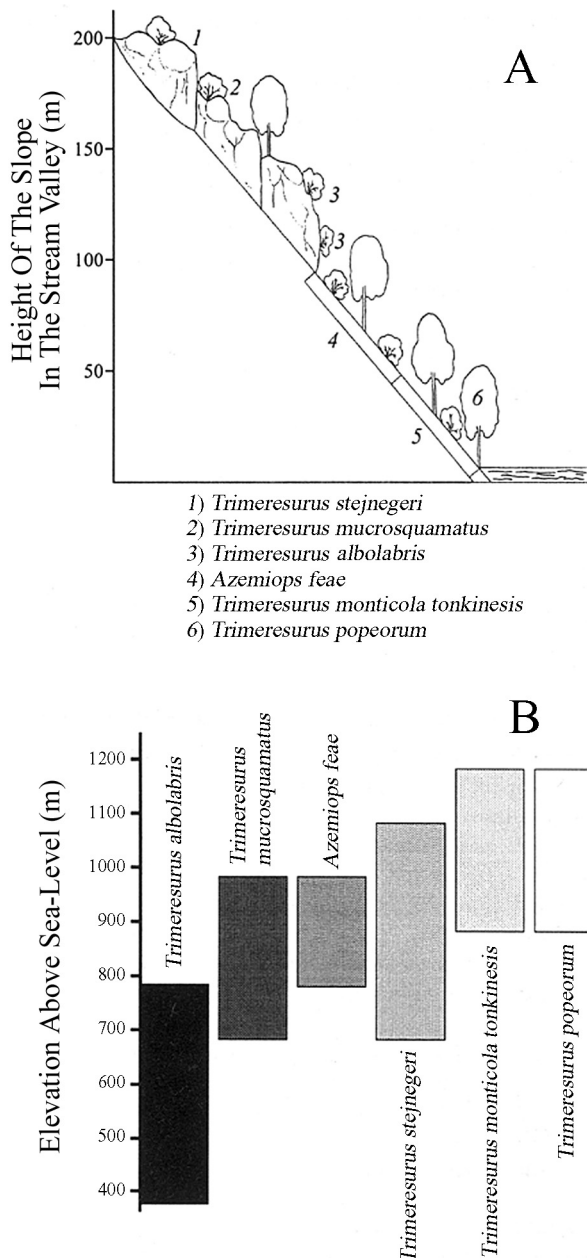


Fig. 2 (A) Spatial distribution of viperid snakes in Tam-Dao. (B) Elevational distribution of viperid snakes in Tam-Dao.

Among the pitvipers, a long gestation period was noted only for the high-elevation *T. karanshahi*.

Our data on clutch defense in females of *Callosellasma*, *Deinagkistrodon*, *Ovophis*, and *Protobothrops* confirm that these pitvipers remain with their clutches after oviposition (Greene, 1992; Greene et al., this volume) for extended periods (25–30 days in *D. acutus*; 35–40 days in *C. rhodostoma*). With respect to sexual behavior in nature, we found concentrations of males around single females in *T. albolabris*

and *T. stejnegeri*. In captivity females of each species copulated multiple times with different males.

Many Asian pitvipers use “sit-and-wait” (ambush) foraging strategies (Greene, 1992, 1997). They ambush on the ground (terrestrial forms) or at different heights in bushes and trees (Fig. 2). The species studied can be roughly partitioned into mammal and bird-feeders, frog-feeders, and mixed-prey feeders (Table 1). Ontogenetic dietary shifts were documented in *G. intermedius* and *G. ussuriensis*. Juveniles of both species consume mainly frogs, but adult *G. intermedius* will feed mostly on mammals, and adult *G. ussuriensis* prefer frogs but will consume mammals. Young *C. rhodostoma*, *O. monticola convictus*, and *O. tonkinensis* were observed to feed on frogs. The “green” pitvipers (*T. albolabris*, *T. popeorum*, and *T. stejnegeri*) are mostly frog-feeders, but adult snakes sometimes consume mammals and birds.

The maximum diversity and species richness of pitvipers is found in the mountains of Tonkin and Annam, and in the eastern Himalayas. Our long-term data on these mountain ranges show spatial (macro- and microhabitats) and elevational differences among sympatric species, and clear trophic and temporal overlapping (Orlov, 1997). Three sympatric “green” pitvipers occur in Tonkin and Annam, whereas five species occur in eastern Nepal-Sikkim (Shaw et al., 1939; Smith, 1943; our data). Such diversity is interesting, in the context of ecological niches of sympatric species with similar ecological requirements. A complicated mosaic of microhabitats in mountain tropical forests possibly supports this diversity.

Acknowledgments.—We are extremely indebted to Robert W. Murphy (Royal Ontario Museum, Toronto, Canada) for his efforts in organizing fieldwork in Vietnam, consultations and other favors, and to Notker Helfenberger (Zoological Museum, Zurich, Switzerland) for organizing expeditions to Nepal. We thank Cuc Thu Ho, Nguyen Van Sang (Vietnam), Karan Shah (Nepal), Munkhbayar and Terbish (Mongolia) for their assistance and onsite arrangements. We are also grateful to Claes Andren, Göran Nilson, Bob Macey, and Ted Papenfuss for fruitful discussions and accompanying us on several field trips to remote regions of Asia. We also thank Wolfgang Wüster, Gernot Vogel, and Frank Tillack for providing photographs. Partial support was received from RFFI-02-04-48720 and the National Geographic Society 7199-02.

LITERATURE CITED

- ANANJEVA, N. B., KH. MUNKHBAYAR, N. L. ORLOV, V. F. ORLOVA, D. V. SEMENOV, AND KH. TERBISH. 1997. Amphibians and Reptiles of Mongolia. Reptiles of Mongolia. In V.E. Sokolov (Ed.), Vertebrates of Mongolia. KMK Ltd., Moscow, (in Russian with English summary).
- ANANJEVA, N. B., L. BORKIN, I. S. DAREVSKY, AND N. L. ORLOV. 1998. Amphibians and Reptiles: Encyclopedia of the Nature in Russia. Moscow.
- AUFFENBERG, W. 1980. The herpetofauna of Komodo, with notes on adjacent areas. Bull. Florida State Mus. 25(2):39–156.
- BOURRET, R. L. 1936. Les Serpentes de l'Indochine. Tome 2. Henri Basuyau et Cie, Toulouse, France.
- CAMPDEN-MAIN, S. M. 1970. A Field Guide to the Snakes of South Vietnam, Smithsonian Institution, Washington.
- CHERNOV, S. A. 1934. On the systematics and distribution of *Agkistrodon* (Ophidia) in the Soviet Union. Proc. Acad. Sci. USSR, N. 6:350–356 (in Russian with English translation).
- COX, M. J. 1991. The Snakes of Thailand and Their Husbandry. Krieger Publishing, Malabar, Florida.
- DAS, I. 1994a. A check-list of the amphibians and reptiles of Andaman and Nikobar Islands. J. Andaman Sci. Assoc. 10(1-2):44–49.
- . 1994b. The reptiles of South Asia: checklist and distributional summary. Hamadryad 19:15–40.
- . 1997. Checklist of the reptiles of India with English common names. Hamadryad 22(1):32–45.
- DAVID, P., AND I. INEICH. 1999. Les serpents venimeux du monde: systématique et répartition. *Dumerilia*, Paris 3:3–499.
- , AND H. TONG. 1997. A translation of recent descriptions of Chinese pitvipers of the *Trimeresurus*-complex (Serpentes, Viperidae), with a key to the complex in China and adjacent areas. Smithsonian Herp. Inf. Service. 112:1–31.
- , AND G. VOGEL, 1996. The Snakes of Sumatra: An annotated checklist and key with natural history notes. Edition Chimaira, Frankfurt.
- DEUVE, J. 1970. Serpents du Laos. Mem. ORSTOM (Paris) 39:251.
- EMELIANOV, A. A. 1929. Snakes of the Far Eastern District. Vladivostok Sect. Russian Geogr. Soc., 3 (XX) (in Russian with English summary).
- FLECK, J. 1987. Bemerkungen zur Haltung von *Agkistrodon acutus* (Günther, 1888) (Serpentes: Crotalidae). Salamandra 23(4):193–203.
- GIANNASI, N., R. S. THORPE, AND A. MALHORTA. 2001. The use of amplified fragment length polymorphism in determining species trees at fine taxonomic levels: analysis of a medically important snake, *Trimeresurus albolabris*. Mol. Ecol. 10:419–426.
- GLOYD, H. K., AND R. CONANT. 1990. Snakes of the *Agkistrodon* Complex: A Monographic Review. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology 6. Oxford, Ohio.
- GOLAY, P., H. M. SMITH, D. G. BROADLEY, J. R. DIXON, C. MCCARTHY, J. C. RAGE, B. SCHATTI, AND M. TORIBA. 1993. Endoglyphs and other Major Venomous Snakes of the World. Azemiops. Herpetological Data Center, Geneva.
- GREENE, H. W. 1992. The ecological and behavioral context for pitviper evolution. Pp. 107–116 In J. A. Campbell and E.D. Brodie, Jr. (Eds.), Biology of the Pitvipers, Selva, Tyler, Texas.
- . 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, Berkeley and Los Angeles.
- GUMPRECHT, A. 1998. Die Bambusottern der Gattung *Trimeresurus* Lacepede. Teil II. Die Grosaugen-Bambusotter *Trimeresurus macrops* Kramer, 1977. Sauria 20(3):25–36.
- HOGUE, A. R. AND ROMANO-HOGE, S. A. R. W. D. L., 1981 [1978/79]. Poisonous snakes of the world. Part 1: Check list of the pit vipers Viperioidea, Viperidae, Crotalinae. Mem. Inst. Butantan, 42/43:179–283.
- HU, S. Q., E. M. ZHAO, Y. M. JIANG, L. FEI, C. Y. YE, Q. X. HU Q. Y. HUANG, Y. Z. HUANG, AND W. S. TIAN. 1987. Amphibia-Reptilia of Xizang (The Comprehensive Scientific Expedition to the Quinghai-Xizang Plateau, Academia Sinica). Science Press, Beijing.
- KLEMMER, K., 1963. Liste der rezenten Giftschlangen, Elapidae, Hydrophidae, Viperidae und Crotalidae. Pp. 255–464 In Die Giftschlangen der Erde, Behringwerk-Mitteilungen, Marburg, Germany.
- KOROTKOV, YU. M. 1978. Ecological notes on the population of snakes of Primorsky Territory. Vladivostok (in Russian).
- KRAMER, E. 1977. Zur Schlangenfauna Nepals. Revue suisse Zool. 84:721–761.
- LIM, B. L. 1990. Venomous land snakes of Malaysia. Pp. 387–417 In Gopalakrishnakone, P. and L. M. Chou (Eds.), Snakes of Medical Importance (Asia-Pacific region). National University of Singapore.

- MARX, H., AND T. S. OLECHOWSKI. 1970. Feae's [*sic*] viper and the common gray shrew: a distribution note on predator and prey. *J. Mammal.* 51:205.
- MCDIARMID, R. W., J. A., CAMPBELL, AND T. A. TOURÉ. 1999. Snake species of the world. A taxonomic and geographic reference, Vol. 1. The Herpetologists' League, Washington, D.C.
- MERTENS, R. F. W. 1930. Die Amphibien und Reptilien der Inseln Bali, Lombok, Sumba und Flores. *Abh. Senckenb. Naturf. Ges.* 42(3):115–344.
- NGUYEN, V. S., AND T. C. HO. 1996. Danh lục bò sát và ech nhai Việt Nam. Nha Xuất Ban Khoa Học Và Kỹ Thuật. Science and Technology Publishers, Hanoi (in Vietnamese).
- ORLOV, N. L. 1995. Rare snakes of the mountainous forests of Northern Indochina. *Russian J. Herpetol.* 2:179–183.
- . 1997. Viperid snakes (Viperidae Bonaparte, 1840) of Tam-Dao mountain ridge (Vinh-Phu and Bac-Thai Provinces, Vietnam). *Russian J. of Herpetol.* 4:64–74.
- . 1998. Die Giftschlangen der vietnamesischen Bergwälder. Teil 2. Familie Viperidae. *Herpetofauna* 20 (116):5–14.
- , AND A. V. BARABANOV. 1999. Analysis of nomenclature, classification and distribution of the *Agkistrodon halys*-*Agkistrodon intermedius* complexes: a critical review. *Russian J. Herpetol.* 3:167–192.
- , S. A. RYABOV, K. A. SHIRYAEV, AND V. S. NGUYEN. 2001. On the biology of pitvipers of the genus *Protobothrops* (Serpentes: Colubroidae: Viperidae: Crotalinae). *Russian J. Herpetol.* 8:159–164.
- POPE, C. H., 1935. The Reptiles of China. *Amer. Mus. Nat. Hist.*, New York.
- REGENASS, U., AND E. KRAMER. 1981. Zur Systematik der grünen Grubenottern der Gattung *Trimeresurus* (Serpentes, Crotalidae). *Revue suisse Zool.* 88:163–205.
- SAINT GIRONS, H. 1972. Les Serpents du Cambodge. *Mem. du Mus. Nat. D'Histoire Natur., Serie A., Zoologie.* Tome LXXI, Paris.
- SHAH, K. 1995. Enumeration of Amphibians and Reptiles of Nepal. *Techn. Publ. No. 2, Est. Biodiversity Profile of Nepal.*
- SHAW, G. E., E. O. SHEBBEARE, AND P. E. BARKER. 1939. *Journ. Darjiling Nat. Hist. Soc.* 14(2):1–97.
- SMITH, M. A. 1943. The Fauna of British India, Ceylon and Burma, Including the Whole of the Indo-Chinese Sub-region. Reptilia and Amphibia, Vol. 3, Serpentes. Taylor and Francis, London.
- SZYNDLAR, Z., AND V. S. NGUYEN. 1996. Terrestrial snake fauna of Vietnam: distributional records. *The Snake* 27(2):27–28.
- TAYLOR, E. H. 1965. The serpents of Thailand and adjacent waters. *Univ. Kansas Sci. Bull.* 45:609–1096.
- TERENTJEV, P. V., AND S. A. CHERNOV. 1949. Guide to Amphibians and Reptiles of the USSR. 3rd ed. Moscow, Sovetskaya Nauka (in Russian).
- TORIBA, M., 1986. The classification of genus *Agkistrodon* with 21 scale rows in eastern Asia. *Acta Herpetologica Sinica* 5:61–62.
- WELCH, K. R. G. 1988. Snakes of the Orient: A Checklist. Krieger Publishing, Malabar, Florida.
- ZHAO, E., AND K. ADLER. 1993. Herpetology of China. Society for the Study of Amphibians and Reptiles, Contribution to Herpetology 10, Oxford, Ohio.
- , HUANG M., Y. ZONG, J. ZHENG, J. HUANG, D. YANG, AND D. J. LI. 1998. Serpentes. *In Fauna Sinica, Reptilia, Vol. 3, Squamata. Serpentes.* Science Press, Beijing.
- , AND D. T. YANG. 1997. Amphibians and Reptiles of the Hengduan Mountains Region, Beijing, Science Press (in Chinese).

