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Observations on the Behavioral Ecology of Three Species of
Imantodes (Reptilia, Serpentes, Colubridae)

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ABSTRACT—Aspects of the behavioral ecology of *Imantodes cenchoa*, *I. gemmistratus* and *I. lentiferus* were studied in large glass enclosures and in a greenhouse. *Imantodes* is crepuscular and nocturnal and 90% of all daylight hours were spent coiled in bromeliads. Emergence from bromeliads can be divided into three stages. Shifting and rearranging of coils and head emergence occurred between 4-0 foot candles (ft-c) in *I. cenchoa* and between 19-1 ft-c in *I. gemmistratus*. Emergence of the head and neck outside of the bromeliad occurred between 4-1 ft-c and 14-1 ft-c in *I. cenchoa* and *I. gemmistratus*, respectively. Complete emergence occurred between 1-0 ft-c in *I. cenchoa* and between 3-0 ft-c in *I. gemmistratus*. Individuals of *Imantodes* are morphologically adapted to arboreal living and have SVL-weight relationships that allow movement on the distal ends of branches and the bridging of wide gaps between arboreal perches. At night *I. cenchoa* and *I. gemmistratus* foraged for food and *I. cenchoa* fed on sleeping anoles. All species drank water beaded on their own bodies and *I. gemmistratus* frequently entered pools of water.

* * *

There is a paucity of information on the behavior and ecology of Neotropical snakes. Scattered accounts deal chiefly with macrohabitat, food, and aspects of reproduction and behavior that were observed fortuitously. The main reasons for the lack of information are that snakes in Neotropical lowland habitats are secretive and/or exist at low population densities; a researcher might search for months without finding two individuals of the same species. We alleviated these problems by bringing three species of the Neotropical colubrid genus *Imantodes* into the laboratory to study aspects of their behavior under semi-natural conditions.

MATERIALS AND METHODS

Ten specimens of *Imantodes cenchoa* from Honduras and Costa Rica, six *I. gemmistratus* from Mexico and



FIGURE 1. A portion of the greenhouse where *Imantodes* was studied.

Honduras and one *I. lentiferus* from Ecuador were used in the study. All except the *I. lentiferus* were purchased from commercial animal dealers. The snakes were housed in glass enclosures 61 X 32 X 42 cm and 100 X 36 X 41 cm containing a bark litter substrate, one or two potted bromeliads (*Aechmea* sp.) and one potted "non-bromeliad." Observations were made while the snakes were in the enclosures and also while "free" in a greenhouse on the roof of the Milwaukee Public Museum. The greenhouse, 5 m X 7 m X 5 m high, had a glass roof and three glass walls. It contained four oleander bushes (*Nerium* sp.), one *Ficus*, and one *Monstera*. The maximum height of the vegetation was 2.6 m. On the floor around the bushes and trees were four plastic swimming pools 130 cm in diameter and filled with water, aquatic vegetation, and a variety of turtles. The rest of the floor was covered with bark litter (Fig. 1).

Observations were made during daylight hours and at night with the aid of dim red incandescent lights (pure red in the 6000-7000 nm range) 4 m above the floor. Additional observations were made with a closed-circuit television camera (Panasonic model WV220P) that used an infra-red light source that allowed observations to be made in the dark on a monitor (Panasonic model AU2200S). Light levels were determined with a Weston portable photoelectric photometer (Model 756). Most of the observations were made in November and December 1973 and January 1974. The temperature in the greenhouse ranged from 18-35°C.



FIGURE 2. *Imantodes gemmistratus* coiled in a bromeliad. Milwaukee Public Museum photo by Janice Mahlberg.

RESULTS AND DISCUSSION

Diurnal behavior.—*Imantodes* is usually crepuscular and nocturnal. Unfortunately most published field observations of *Imantodes* do not indicate at what time of day the observations were made. If the snake's activity was noted, however, it was possible for us to deduce whether it was day or night. By day *Imantodes cenchoa* has been taken from bromeliads (Dunn, 1937:164), from "hidden between two...broad overlapping, horizontal leaves" (Test, Sexton and Heatwole, 1966:39); from "low vegetation" (Duellman, 1963:240); from leaf litter (Landy, et al., 1966:96); and from under a rotting log (Stuart, 1958:27). Diurnally *I. gemmistratus* has been observed in bromeliads (Smith, 1943:435), under loose bark (Alvarez del Toro, 1960:160), and on the ground beneath palm leaves (Hardy and McDiarmid, 1969:172). *Imantodes cenchoa* and *I. gemmistratus* spent approximately 90% of all daylight hours coiled in bromeliads (Fig. 2). These two species also spent days coiled on branches protected by leaves, between horizontal layers of leaves, coiled at the bases of plants, buried in bark litter (either partially or completely) and

under pieces of bark. Although all of our specimens had continual access to bromeliads, our one individual of *I. lentiferus* never entered a bromeliad, but often rested at the base of one; it slept concealed in vegetation either close to, or on, the cage floor. Occasionally two *I. cenchoa* would

occupy different parts of the same bromeliad. *Imantodes cenchoa* also shared a bromeliad with a small *Hyla*.

Imantodes cenchoa would not hesitate to enter a bromeliad filled with water, nor would it leave its coiled position in a bromeliad as water was poured in. Allee (1926:457) found an *I. cenchoa* "in the moist center of a wild pineapple plant" during the dry season and he suggested that the entire dry season would be spent there. Smith (1943:435) found 12 *I. splendidus* (= *I. gemmistratus*) in "dead, dry bromelias, during the dry season" in southern Mexico and he (Smith, 1941:39) suggested that snakes vacate bromeliads that become moist. One of our *I. cenchoa* spent eight days in a moist bromeliad without leaving it.

Rarely would *Imantodes* be in an exposed location by day. In a simple experiment, we placed four *I. gemmistratus* in a 61 X 32 X 42 cm glass enclosure containing only one small sprig of artificial leaves. Within one hour three of the four snakes were coiled among the leaves. On other occasions, snakes that were placed on leafless branches immediately crawled to those protected by foliage.

Emergence from Bromeliads.—The proclivity of *Imantodes* to hide in bromeliads, at least in parts of its range, is well documented (Allee, 1926:457; Alvarez del Toro, 1960:160; Beebe, 1946:29; Dunn, 1937:164; Mole, 1924:251; Smith, 1941:39 and 1943:435; Stuart, 1948:80, thus indicating that bromeliads are important in the ecology of the genus. Therefore we spent about 40 h observing the behavior of the snakes emerging from, entering, and inside bromeliads. Behavior associated with emergence from bromeliads can be divided into three stages: arousal, pre-emergence, and emergence.

1. Arousal: As daytime light levels began to decrease, the snake began to shift or rearrange its coils in the cup of the bromeliad. The head, which was hidden among coils while the snake was sleeping, emerged. On several occasions both *I. cenchoa* and *I. gemmistratus* raised their heads, looked around, and then buried their heads in a coil again. It appeared that the light level might not have been low enough for emergence. That behavior was sometimes repeated several times before the head remained exposed. Head emergence was often accompanied by tongue flicking in *I. gemmistratus* and by "yawning" in both species. *Imantodes cenchoa* performed arousal activities between 4-0 (ft-c) of light (\bar{x} = 1.5 ft-c); *I. gemmistratus* performed these activities between 19-1 ft-c (\bar{x} = 6.4).

2. Pre-emergence: The snake's head and neck remained emerged from its coils, then it moved to the edge of the bromeliad's cup, hesitated, and then moved over the edge of the cup. This was followed by prolonged hesitation. Pre-emergence was sometimes accompanied by tongue flicking in *I. gemmistratus* and "yawning" in both species. Stage 2 activity occurred between 4-1 ft-c (\bar{x} = 1.3 ft-c) in *I. cenchoa* and between 14-1 (ft-c (\bar{x} = 3.4 ft-c) in *I. gemmistratus*.

3. Emergence: After the prolonged hesitation the snakes uncoiled and emerged from the bromeliad. Once it started, emergence was usually rapid. Emergence occurred between 1-0 ft-c (\bar{x} = 0.4 ft-c) in *I. cenchoa* and 3-0 ft-c (\bar{x} = 1.0 ft-c) in *I. gemmistratus*.

The total amount of time that elapsed between initial shifting and rearrangement of coils inside of a bromeliad and complete emergence ranged from 19-37 min (\bar{x} = 22.8 min) for *I. cenchoa* and 21-75 min (\bar{x} = 37.3 min) for *I. gemmistratus*.

Movements and Locomotion.—Unlike snakes of the arboreal colubrid genera *Leptophis* and *Oxybelis*, which were also studied in the greenhouse and which could be allowed to move freely in the greenhouse for days or weeks at a time with little prospect of "losing" them, *Imantodes* could be lost in minutes if not watched continuously. For this reason we can make no statements on the movements of *Imantodes* except that it appears to be much more vagile at night than are the diurnal *Leptophis* and *Oxybelis* by day. After becoming active, *Imantodes* would frequently travel 5-10 m in 5 min; it was not unusual for *Oxybelis aeneus* or *O. fulgidus* to remain in one bush for days or weeks at a time, moving less than 1 m.

Although primarily arboreal, it is not unusual for *Imantodes* to be found on the ground. Hardy and McDiarmid (1969:172) collected 30 *I. gemmistratus* on roads in Sinaloa, Mexico; Smith (1943:434) took *I. gemmistratus* on the ground in Chiapas; Duellman (1965:608) found

I. tenuissimus on a road in Yucatan; and Test, et al. (1966:39) took 5 *I. cenchoa* from roads in Venezuelan cloud forest. Our *I. cenchoa* and *I. gemmistratus* descended to the ground and remained there either foraging, moving to another arboreal site, or making longer movements (10-15 m) into adjacent greenhouses.

Morphologically, few snakes seem better adapted to arboreal living than *Imantodes*. Adaptations for arboreal habits include elongation of the body and tail, ability to direct the eyes downward, lateral compression of the body, widening of the vertebral scale row (see Peters, 1960:18, for a discussion of these four adaptations), and a laterally projecting shelf running between the vertebral zygapophyses. The vertebral shelf is common in arboreal snakes, but reaches its extreme in *Imantodes* (see Johnson, 1955:383, for a thorough discussion). All of

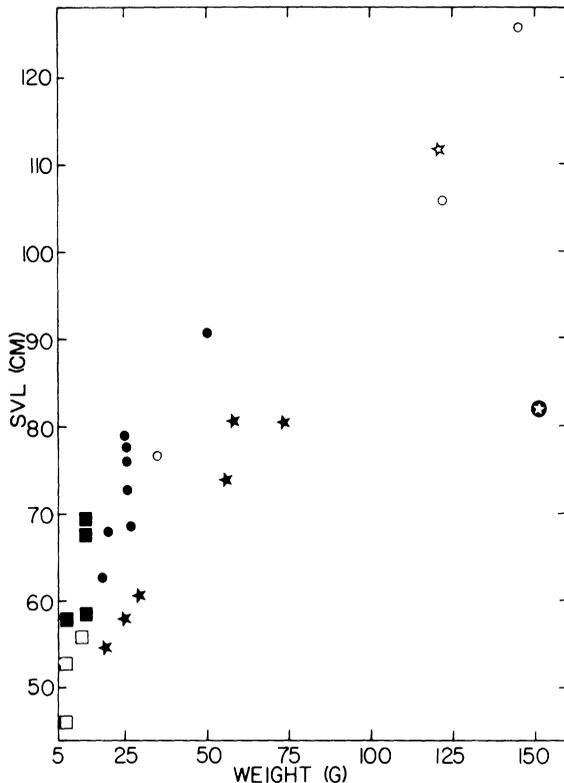


FIGURE 3. The snout-vent length (SVL)—weight relationship in several species of arboreal snakes. Closed circle with a star = *Corallus enydris*; closed squares = *Imantodes cenchoa*; open squares = *I. gemmistratus*; closed stars = *Leptophis mexicanus*; open stars = *L. ahaetulla*; closed circles = *Oxybelis aeneus*; and open circles = *O. fulgidus*. There are no data available for *I. lentiferus*.

only in its jaws. Food items recorded for *I. cenchoa* include a variety of frogs and lizards (particularly *Anolis*) and reptile eggs ("probably *Anolis*"; Landy, et al., 1966:96). Prey items recorded for *I. gemmistratus* are *Anolis* and, in captivity, frogs and *Tenebrio* larvae (Taylor, 1964:46); *I. lentiferus* is known to feed on frogs (W. E. Duellman, *in litt.*).

All *I. cenchoa* and *I. gemmistratus* fed only at night and only on *Anolis*. Several species of small frogs were continuously rejected. Limited data suggests that *I. lentiferus* ambushes prey rather than actively searches for it. *Imantodes cenchoa* and *I. gemmistratus* foraged at night. If both species do feed primarily on the diurnal *Anolis*, it would necessitate active searching at

the adaptations for arboreal dwelling found in *Imantodes*, except the ability to see downward, aid the snakes in bridging gaps between arboreal perches. When *Imantodes* is ready to bridge a long gap, it usually gathers its body into a small area on the site it is leaving and then begins moving to the new site. *Imantodes* is capable of bridging a gap equal to approximately one-half of its length. The posterior part of the body is anchored to the original site as the anterior part moves to the new site. Because of the snout-vent length (SVL)-weight relationship in *Imantodes* (Fig. 3), it is able to move on the distal portions of slender branches without weighing them down and making gap-bridging more difficult. The heavier bodied tree snakes *Oxybelis* and *Leptophis* often weigh down branches they are moving from and to, thus making the bridge more difficult, more time and energy consuming, or even impossible. The increase in length without a corresponding increase in body weight allows *Imantodes* to inhabit parts of bushes and trees that heavier-bodied tree snakes must avoid. This might be an effective aspect of habitat and food partitioning in arboreal snakes.

Feeding.—Little is known about the feeding behavior of *Imantodes*. Alvarez del Toro (1960:160) stated that *I. splendidus* (= *I. gemmistratus*) sometimes held prey with its coils and at other times

night while the anoles sleep on vegetation. This also suggests that prey movement is not necessary for *Imantodes* to locate prey. Indeed, this was the case. *Imantodes cenchoa* was observed preying on anoles that had been motionless for up to 94 min. However, both species also fed on moving anoles (one struck at Henderson's wriggling finger). Unlike the diurnal *Oxybelis* that stops moving toward a prey item when the prey stops moving and that grabs prey with a fast, rushing motion (pers. obs.), *Imantodes* is not exclusively movement oriented and grabs prey with a quick striking movement from an S-shaped coil. Once prey is grabbed, it is moved to the back of the jaws where the small rear fangs can administer the venom. After becoming immobilized, lizards were invariably swallowed head first. One snake ingested three anoles in a two hour period.

Activity.—Two *I. gemmistratus* returned to their daytime resting sites within 45 min after feeding; one of them became active again shortly thereafter. One *I. cenchoa* was inactive for 15 days after feeding on an anole.

One *I. gemmistratus* was observed for an entire night. It emerged from a bromeliad at 1629 (<1 ft-c of light) and remained active on the ground and on plants until it coiled on top of a bromeliad at 2030. At 2345 it was coiled inside of the same bromeliad from which it had emerged. It remained in the bromeliad with its head exposed and alert. By 0430, still in darkness, it had buried its head in its coils. The sky began to brighten at 0620.

Active *Imantodes* stopped moving or returned to bromeliads when white incandescent lights were turned on or when any light level reached 5 ft-c. An *I. gemmistratus* returned to a bromeliad 15 min after it had emerged when red light level was increased. It emerged from the bromeliad again within 2 min after the light had been removed. *Imantodes cenchoa* and *I. gemmistratus* entered bromeliads by crawling down one inner side of a bromeliad cup and up the opposite side, then down the first side again, up the opposite again, etc. This was repeated until the entire snake was inside of the bromeliad in a more or less vertical coil.

Water-getting.—*Imantodes* was observed drinking water from bromeliads, from beads of water on leaf surfaces, from beads of water on its own body (similar behavior has also been observed in arboreal *Leptodeira* and *Trimeresurus*), and from a large pool of water while hanging from a nearby bush.

Imantodes gemmistratus frequently entered pools of water. They would usually hang over the surface touching it with the snout before entering. They would swim close to the surface of the water. We never witnessed any foraging behavior while they were in the water.

Defense.—*Imantodes* was extremely passive and could not be induced to bite in defense. When disturbed in a bush or tree, *Imantodes gemmistratus* would drop from its perch to lower vegetation. One individual dropped nearly 2.0 m when molested. Its light weight allowed it to land successfully on any branch with little bending and no breaking of the branch.

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