

methods that have been widely used in the past. We have not, however, tried this technique on *S. miliarius* less than one year old. PIT-tagging in small animals needs to be studied further in the field to determine its effects.

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Visually-oriented Foraging in a Natural Population of Herbivorous Lizards (*Ctenosaura similis*)

FREDRIC J. JANZEN^{1,3} AND EDMUND D. BRODIE III,^{2,4}
¹Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637, USA, ²Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, USA.

Most species of lizards are primarily carnivorous (Adler and Halliday, 1986; Pianka, 1986): only about 2% are herbivorous, frugivorous, or folivorous. Foraging behavior in carnivorous lizards can generally be classified into two broad categories: living prey are either ambushed by sit-and-wait predators or are actively sought (Pianka, 1966; Schoener, 1971). Although chemoreception may play a role (e.g., Phillips and Alberts, 1992), accurate visual systems for assessing an object as a likely or unlikely prey item are critical in these species. In fact, lizards in general are suspected of possessing color vision (Tiemann, 1972; Cooper and Greenberg, 1992).

Although herbivorous lizards frequently exhibit specific food preferences (e.g., Dearing and Schall, 1992), very little is known about what cues these animals use in making foraging decisions. For instance, herbivorous lizards may not require as much visual orientation as carnivorous lizards to obtain food, because foliage could potentially be detected by olfactory cues. The vomeronasal and olfactory systems of lizards are indeed well-developed (reviewed in Simon, 1983); hence blooming flowers and ripening fruit that emit obvious odors (that attract pollinators and seed dispersers) may be readily located by herbivorous lizards using chemoreception. Visual cues, particularly color, contrast, and pattern, nonetheless may play a significant role in detection of food items.

³ Present Address: Department of Zoology and Genetics, Iowa State University, Ames, Iowa 50011, USA.

⁴ Present Address: T. H. Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506-0225, USA.



FIG. 1. Tricolor (top), unmarked brown (middle), and bicolor (bottom) plasticine replicas placed on a semi-natural background for illustrative purposes. Yellow bands appear white, red bands appear dark gray, and both black bands and the brown replica appear black in the photograph.

The black iguana or ctenosaur (*Ctenosaura similis*: Iguanidae) is among the minority of lizard species that are primarily herbivorous (Hotton, 1955; Fitch and Hackforth-Jones, 1983). These large, diurnal lizards associate mainly with dry forest and scrub habitats from southern Mexico to Panama (Fitch and Hackforth-Jones, 1983). Ctenosaurs eat most available succulent vegetation when food is abundant, but become selective in the dry season when resources are scarce. For example, during the dry season in Costa Rica, ctenosaurs reportedly travel unusually great distances (>100 m) to consume the yellow flowers of *Tabebuia* spp. (Bignoniaceae) (Fitch and Henderson, 1978; Fitch and Hackforth-Jones, 1983). Although these flowers may produce a detectable odor, few trees contain leaves at this time of year in the dry forest of Costa Rica; hence the ability to visually detect flowering trees may be considerable. Nonetheless, the sensory mechanism (olfactory or visual) used by ctenosaurs to locate these patchily-distributed resources is unknown.

In the course of a field study on coral snake mimicry in Costa Rica (Brodie and Janzen, *in press*), we inadvertently exposed different types of colored snake replicas to attack by *C. similis*. The soft plasticine replicas permitted us to assess the incidence of sampling

by ctenosaurs, because attacks by the lizards were observable as bite marks in the replicas. The experimental design allowed us to determine whether visual cues are used by ctenosaurs to evaluate potential food items.

This experiment was conducted from 14–16 February 1992 at Palo Verde Biological Station in the dry tropical forest of Guanacaste in northwest Costa Rica. We created 120 plasticine (Sculpey-III) snake replicas in each of three categories: red-yellow-black-yellow-red banded (tricolor), red-black banded (bicolor), and solid brown (Fig. 1). The tricolor replicas were representative of a local venomous coral snake (*Micrurus nigrocinctus*), the bicolor replicas resembled another venomous, but allopatric, coral snake (*Micrurus multifasciatus*), and the solid brown replicas represented various unmarked, nonvenomous snakes at the site (e.g., *Coluber mentovarius*) (Scott and Limerick, 1983; E. D. Brodie III and F. J. Janzen, pers. obs.). Details of the construction of these replicas are provided in Brodie (1993) and more specifically in Brodie and Janzen (*in press*).

We placed replicas at 10 m intervals along two widely-separated (1–3 km apart) transects through the dry forest south and east of the field station. Replicas were anchored to the ground in random order about

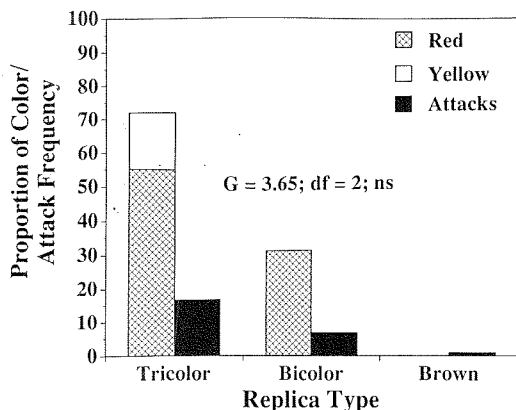


FIG. 2. The proportion that is brightly colored (yellow and/or red) and the frequency of attacks by *C. similis* for each replica type. The distribution of attacks among replica types is not significantly different from that expected if ctenosaurs attack models proportional to the amount of total color on the replica. Ratios of attack frequency/proportion of total color are 0.23 for tricolor, 0.22 for bicolor, and undefined for brown.

0.5 m off the trails that formed each transect. We collected the replicas 48 h later and recorded all marks. Lizard attacks were readily differentiable from avian or other disturbances, judging from the regular array of similar, conical-cusped teeth (Fitch and Hackforth-Jones, 1983) in bite marks on the replicas. Frequency of attack by ctenosaurs on the different replica types was analyzed using a G-test (Sokal and Rohlf, 1981). Disturbances by birds and other animals are discussed elsewhere (Brodie and Janzen, *in press*).

Overall 29 of 360 plasticine replicas were attacked by lizards. Sampled replicas were found with numerous bite marks and frequently were in pieces. In some cases, the plasticine was almost completely stripped from the wire frame in the center of the replica and apparently was ingested by the attacking lizards. The distances among attacked replicas, determined both by the length of each individual transect (nearly 1.8 km) and by the distance between the two transects (approximately 2 km), suggest that more than a few individual lizards were involved in the attacks.

Although we did not observe *C. similis* interacting with the replicas, we can infer with confidence that these animals are the lizards that attacked the plasticine replicas. Reptilian teeth and lizard tooth arrangements are distinctive from bird beaks and mammalian dentition (Romer and Parsons, 1977). The dentition of ctenosaurs consists of similar, conical-cusped teeth (Hotton, 1955; Fitch and Hackforth-Jones, 1983), which is reminiscent of the large bite marks we observed on the attacked replicas. The only other large-bodied species of lizard at Palo Verde is the closely-related, herbivorous, green iguana (*Iguana iguana*). However, ctenosaurs are considerably more common in the dry forest where the plasticine replicas were placed than are green iguanas, which are

typically found only near the distantly-located Rio Tempisque.

Tricolor replicas (N = 20) were attacked more frequently by ctenosaurs than bicolor replicas (N = 8), which in turn were attacked more often than brown replicas (N = 1) ($G = 23.20$, $df = 2$, $P < 0.001$). Frequencies of attacks on the three categories of replicas were proportional to the total percentage of yellow and red on the replicas (Fig. 2; $G = 3.65$, $df = 2$, $P > 0.05$). In other words, 16.67% of tricolor replicas (71.88% colored), 6.67% of bicolor replicas (31.25% colored), and 0.83% of brown replicas (0% colored) were attacked by ctenosaurs (Fig. 2).

Our results indicate that herbivorous lizards (i.e., *Ctenosaura similis*) have a clear visual preference for attacking brightly-colored objects. This result is consistent with the finding that most, if not all, lizards examined have color vision (Tiemann, 1972; Cooper and Greenberg, 1992), including iguanids (Rensch and Adrian-Hinsberg, 1963). The lizards were probably attracted by the bright colors, because frequencies of attack on the three types of plasticine replicas were proportional to the amount of red and yellow comprising the replicas. It is also possible that yellow and red function differently as stimulatory visual cues for foraging; hence the high frequency of lizard attacks on tricolor replicas may be a result of a foraging preference for yellow over red. Preference for attacking brightly-colored replicas could also indicate an affinity for the contrasting light and dark bands on the replicas (e.g., Rensch and Adrian-Hinsberg, 1963). The experimental design employed in this study unfortunately did not permit us to determine which visual stimulus components were used in food recognition by free-ranging ctenosaurs.

The most likely explanation of our results is that the ctenosaurs perceived the snake replicas as colored fruits or flowers. Adult ctenosaurs mainly eat fruits and flowers, although they may occasionally ingest animal material, such as insects, lizards, and rodents (Fitch and Hackforth-Jones, 1983). Snakes have never been recorded as a food item for *Ctenosaura similis* despite considerable research (Hotton, 1955; Tamsitt and Valdivieso, 1963; Fitch et al., 1971; Henderson, 1973; Fitch and Henderson, 1978; Fitch and Hackforth-Jones, 1983). The yellow flowers of *Tabebuia* spp. (Bignoniaceae) are frequently consumed by *C. similis* during the dry season in Costa Rica (Fitch and Hackforth-Jones, 1983). Similarly, ctenosaurs reportedly eat yellow, red, and pink flowers in Belize (Henderson, 1973) and mainly yellow and pink flowers in Nicaragua (Fitch and Henderson, 1978). During our experiment, we noted that several *Tabebuia ochracea* trees were flowering and that ctenosaurs avidly consumed their yellow flowers. We also observed at this time that *Jacquinia pungens* (Theophrastaceae) was producing its orange-red flowers and that *Gliricidia sepium* (Fabaceae), which produces pink flowers, was flowering and dropping numerous petals on the ground. The availability of these colored flowers as a food source for ctenosaurs during this study is consistent with the high frequency of attack by these lizards on the brightly-banded replicas, particularly on the tricolor replicas that contained both yellow and red bands.

It is implausible that ctenosaurs perceived the replicas as snakes, because they would be subject to strong

selection against attacking live, brightly-banded snakes at Palo Verde. One banded snake at Palo Verde is ostensibly harmless to ctenosaurs, because it is small and nonvenomous (*Enulius flavitorques*). However, others are large (*Lampropeltis triangulum*) or venomous (*Erythrolamprus bizona*, *Micrurus nigrocinctus*, and *Scolopophis atrocinctus*), and physical encounters with these species could result in significant injury or death (Savage and Vial, 1974; Greene and McDiarmid, 1981; Pough, 1988; Brugger, 1989). All these species of snakes exhibit reddish, black, and light-colored banding (Savage and Vial, 1974; Campbell and Lamar, 1989), which functions aposematically to avian predators (Brodie, 1993). Evidence suggests that some lizard species may possess an innate avoidance of red color (e.g., Benes, 1969), although this was not the case in our experiment. Additional research has also shown that naive, ophiophagous lizards avoid venomous snakes (Phillips and Alberts, 1992). Despite the potential danger to ctenosaurs posed by brightly-banded snakes at Palo Verde, these lizards nonetheless preferentially attacked the brightly-banded plasticine replicas in this experiment, indicating that they clearly did not perceive the replicas as snakes.

Employing colored plasticine, we demonstrated that ctenosaurs (*Ctenosaura similis*) utilize visual cues during foraging bouts. Unusually long foraging trips to flowering trees in the dry season by ctenosaurs (Fitch and Henderson, 1978; Fitch and Hackforth-Jones, 1983) consequently may be directly primarily by use of the visual sensory system. The application of colored plasticine permitted identification of the predators on the replicas and allowed quantification of prey preference. Modification of the plasticine paradigm could provide a useful technique to determine which visual cues (color, contrast, pattern) are important for ctenosaurs when foraging. Experiments using replicas shaped like naturally occurring fruits and flowers would be illuminating, and these replicas could include solid colored items (e.g., red or yellow), contrasting banded items using other colors, and even other pattern types. It would be especially interesting to place models in plants to determine if spatial context plays a role in prey recognition by *Ctenosaura similis*. This novel methodology could also prove instructive in other experimental field studies of predator-prey systems.

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An Invalid Neotype Designation for *Caiman latirostris* (Daudin, 1802) (Crocodylia, Alligatoridae)

ULISSES CARAMASCHI AND MARCELO A. SOARES, *Departamento de Vertebrados, Museu Nacional do Rio de Janeiro, Quinta da Boa Vista 20.940-040, Rio de Janeiro, RJ, Brasil.*

The designation of neotypes is explicitly regulated in Article 75 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1985). The neotype is to be designated only in connection with revisory work, and only in exceptional circumstances when a name-bearing type is necessary in the interest of stability of nomenclature. A neotype is validly designated when it is published including; (1) a differentiating diagnosis, (2) data and description assuring recognition of the specimen designated, (3) the author's reasons for believing the former name-bearers to be lost or destroyed, and the steps that had been taken to trace them, (4) evidence that the neotype is consistent with what is known of the former name-bearing type, (5) evidence that the neotype came as nearly as practical from the original type locality, and (6) that the neotype is the property of a recognized scientific institution.

A neotype for *Caiman latirostris* (Daudin, 1802) was designated by Freiberg and Carvalho (1965), based on a specimen in the collection of the Museu Nacional do Rio de Janeiro (MNRJ 1258), collected at Joinville, State of Santa Catarina, Brasil, on 5 May 1942, by Hans Dalibor. Additionally, a "neoparatype" was also designated, based on a specimen in the collection of the Museo Argentino de Ciencias Naturales, Buenos Aires (MACN 01544), collected at Rio Guaíba, Porto Alegre, State of Rio Grande do Sul, Brasil, in 1961, by Dr. Leech. And, by considering that Daudin (1802) did not cite the type locality, they restricted it to Joinville, State of Santa Catarina, Brasil. Medem (1983) surprisingly accepted the holotype (MNHN 7769), the neotype (MNRJ 1258, treated as "neo-holotipo"), and the "neoparatype" ("Museu Nacional no. 01544" = MACN 01544, treated as "neo-paratipo"), and cited two distinct type-localities ("localidad típica"), for the species.

All requirements for designation of a neotype were attained except, and probably most importantly, that

the name-bearer type was lost or destroyed. In fact, Freiberg and Carvalho (1965) recognized that a type was housed at the Muséum Nationale d'Histoire Naturelle de Paris (MNHN 7769), following Vaillant (1898). This author presented good reasons for considering that specimen as the type for the species, and analysed the original description, compared the measurements presented by Daudin (1802) with his data, and provided a good illustration of the specimen. The type, currently the holotype for *Caiman latirostris*, is a young, dry specimen, 850 mm in total length, without locality; its possible collector or donor, Jussieu, was treated with reserve. Freiberg and Carvalho (1965) considered this specimen inadequate as a name-bearing type because it is a young specimen, from which it is impossible to observe cranial details. Accordingly, the neotype and the "neoparatype" are the skulls of adult specimens.

The designation of a neotype for *Caiman latirostris* by Freiberg and Carvalho (1965) is invalid because a name-bearing type is currently deposited in the MNHN collection. However, the restriction of the type locality for the species to Joinville (26°15'S, 48°55'W), State of Santa Catarina, Brasil, is perfectly valid according to Article 72, Section F, and Recommendation 72H of the International Code of Zoological Nomenclature (I.C.Z.N., 1985).

Although the original description by Daudin (1802) of *Caiman latirostris* proved to be inaccurate, good synonymy, characterizations, illustrations, and geographical distribution for the species are provided by Mook (1921), Schmidt (1928), Werner (1933), Mook and Mook (1940), Mertens (1943), Carvalho (1951), Wermuth (1953), Mertens and Wermuth (1955), Freiberg and Carvalho (1965), and Brazaitis (1974). The subspecies of *Caiman latirostris* recognized by Freiberg and Carvalho (1965), *Caiman l. latirostris* and *Caiman l. chacoensis*, were synonymized and the taxon reduced to the nominal species by Crea et al. (1989). A very complete bibliography on the species was compiled by Vanzolini (1993).

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