Spiny-tailed Iguanas, Insular Evolution, and Seri Indians: How Long Does it Take to Make a New Species and Does it Matter Who Makes it?

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A general paradigm among many biologists and lay people alike is that "millions of years" are required for species to evolve. In many cases this is true, but numerous endemic species on young landbridge islands from throughout the world are only thousands of years old, indicating that the speed of evolution is not constant across or within taxonomic boundaries. Population genetics has shown us that evolutionary rates vary according to population size and the selection pressure on that population. Such phenomena are most efficiently studied and best exemplified in island populations such as those in the Gulf of California. This 1000-km-long inland sea lies between the Baja California Peninsula and continental mainland México and harbors a diverse array of islands that vary in geological origin, age, and size.

The herpetofauna of the Gulf of California has received considerable attention for nearly 50 years (e.g., Case 1975, 1983; Cliff 1954a,b; Dixon 1966; Grismer 1994a,b,c,d 1999a,b,c; Hews 1990a,b; Hollingsworth 1998; Murphy 1975, 1983a,b; Murphy and Ottley 1984; Petren and Case 1997; Radtkey et al. 1997; Robinson 1972, 1974; Savage 1960; Soulé 1964, 1966; Soulé and Sloan 1966; Upton and Murphy 1997; Wilcox 1978). Recently, Cryder (1999) presented a phylogeny of the four species of spiny-tailed iguanas of the *Ctenosaura hemilopha* group (*sensu* Grismer 1999a) based on mitochondrial DNA sequences of portions of the cytochrome b and cytochrome oxidase III genes (Fig. 1). These species are endemic to the circum-Gulf of California region of northwestern México and occur on a number of islands in the Gulf of California (Grismer 1999b; Fig. 2). Cryder's (1999) results supported previous hypotheses concerning the human-facilitated origin of *Ctenosaura* on Isla San Esteban (Grismer 1994b) and indicated that overwater dispersal by ctenosaurs to other islands is still a relatively recent (and perhaps

Ctenosaura conspicuosa.
Photograph: L. Lee Grismer

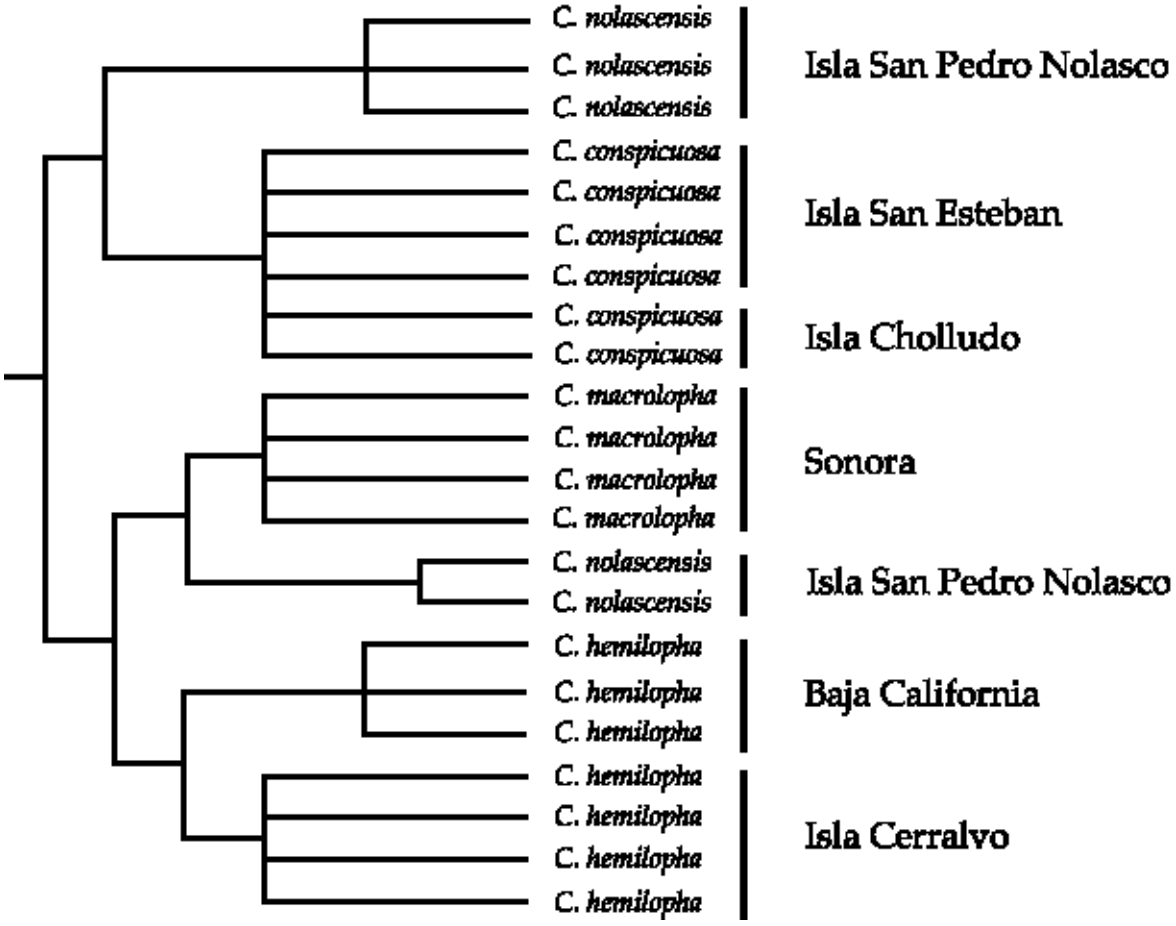


Figure 1. Relationships of the *Ctenosaura hemilopha* group based on cytochrome b and cytochrome oxidase III.

ongoing) phenomenon. Cryder's (1999) study used individual lizards from each of the four recognized species as the unit of analysis. Because his data were obtained from the maternally inherited mitochondrial genome, the resulting branching diagram produces a tree depicting the relationships between individual lizards. These relationships are then inferred to represent the relationships of the species to which those individuals belong.

The relationships between *Ctenosaura nolascensis* of Isla San Pedro Nolasco, *C. conspicuosa* of islas Cholludo and San Esteban, and *C. macrolopha* of mainland México (Fig. 1) provide the fodder for some intriguing and inextricably related issues concerning the consequences of insular isolation, human introduction, and species concepts. All individuals of *C. conspicuosa* analyzed grouped together (i.e., they were more closely related to each other than to any other individuals of other species). Grismer (1994b) hypothesized that the population of ctenosaurs on islas San Esteban and Cholludo were introduced by Seri Indians. This was based on a number of circumstantial lines of evidence. First, the coastal distribution of *C. macrolopha* (a presumable continental source) in mainland Sonora approaches Guaymas at its northern extent (Smith 1972), approximately 115 km south of the nearest coastal mainland locality adjacent to Isla San Esteban. The absence of *Ctenosaura* on the large, geographically intermediate island of Tiburón (Fig. 2) suggests that, if *Ctenosaura* had ever occupied more northerly areas of coastal Sonora, it would be present on Isla Tiburón, as is every other species of reptile that occurs on the adjacent Sonoran mainland (Grismer 1994c). If the presence of *C. conspicuosa* on Isla San Esteban is a natural occurrence, then a hypothesis is necessary to explain its absence from

Isla Tiburón and adjacent mainland México. Second, Isla San Esteban is the only island in the Gulf of California where the chuckwalla (genus *Sauromalus*) and *Ctenosaura* are sympatric. The potential sympatry of these large, herbivorous genera exists on at least 13 other major islands in the Gulf of California given the continental and peninsular distributions of these genera (Fig. 2). Two of these islands (San Pedro Nolasco and Cerralvo) have only *Ctenosaura*, whereas the other 11 islands (Espirítu Santo, Partida Sur, San Francisco, San José, San Diego, Santa Cruz, Santa Catalina, Monserrate, Carmen, Danzante, and Coronados) have only *Sauromalus* (Grismer 1999b). Third, the genetic data of Cryder (1999) were consistent with the Seri Indian introduction hypothesis in that *C. conspicuosa* was most closely related to another insular endemic, *C. nolascensis,* rather than a peninsular or continental population, which would have more likely been a source of origin had its continental distribution been farther north. We know that the Seri Indians collected and transported both *Sauromalus* and *Ctenosaura* as food sources (e.g., Case 1982, Felger and Moser 1985) and would release them on small islands where they could easily be recaptured (see Grismer 1994b for discussion). Fourth, and most compelling, is Gary Nabham's work on the ethnoherpetology of the Seri Indians (book manuscript in press). Nabham learned the Seri language and interviewed Seri elders about their use and views on the local herpetofauna. They informed Nabham that the Seri had always collected iguanas from Isla San Pedro Nolasco as a food source and brought them back to their families living on Isla San Esteban. This provides the best explanation to date for the presence of *Ctenosaura* on Isla San Esteban and the close relationship of *C. conspicuosa* and *C. nolascensis* (Fig. 1) on islands that are separated from one another by 146 km (Fig. 2) and share no common geological history.

Another paradigm often associated with insular biogeography is one in which island colonization is considered to be something that has happened rather than something that is happening. Wong et al. (1995) demonstrated recent colonization of zebra-tailed lizards (*Callisaurus draconoides*) on Isla Danzante in the Gulf of California. Cryder (1999) demonstrated that all individuals of *Ctenosaura macrolopha* from main-

Ctenosaura hemilopha. Photograph: L. Lee Grismer

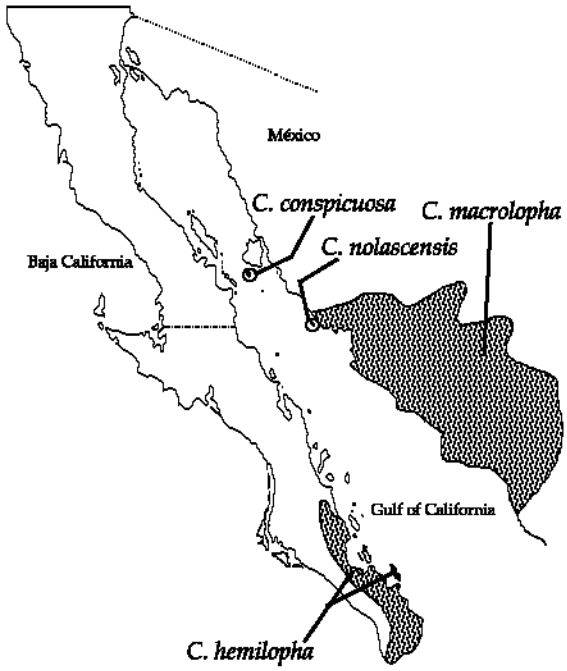
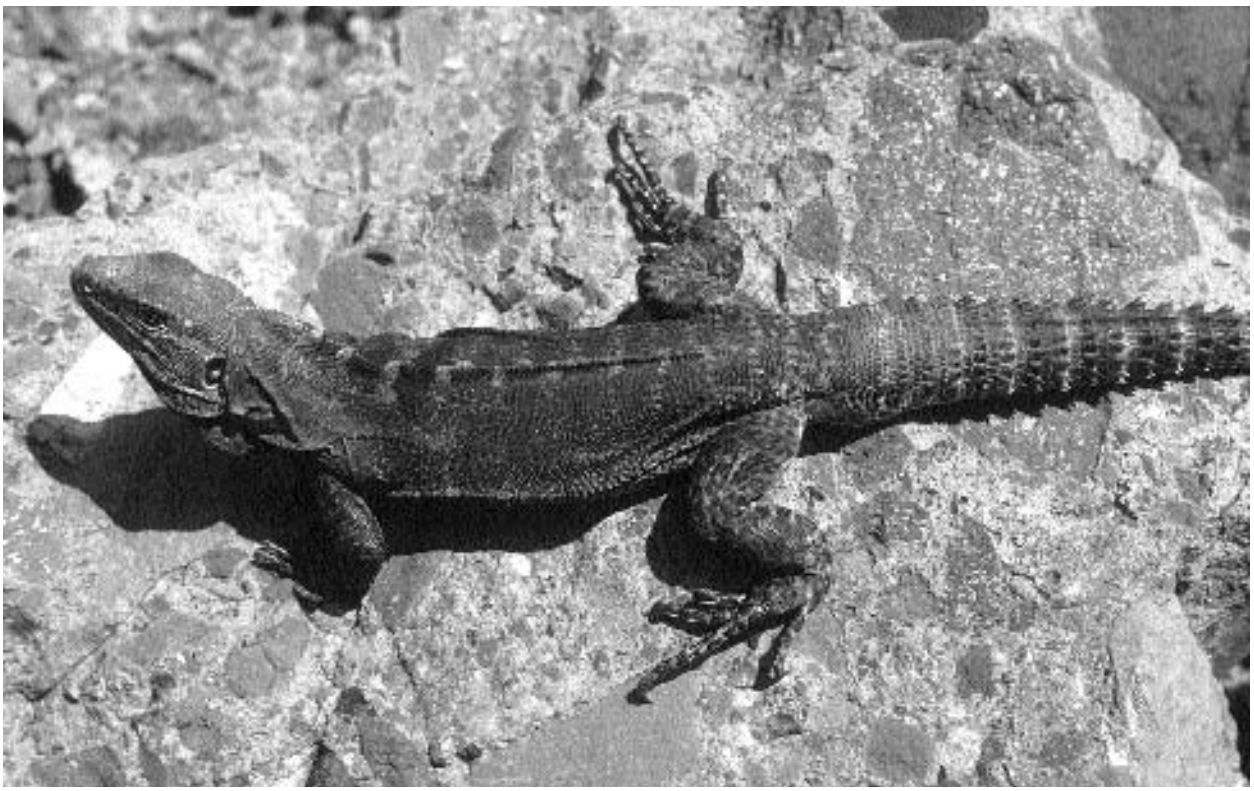


Figure 2. Distribution of the species of the *Ctenosaura hemilopha* group.

land México grouped together, but found that two individuals of *C. nolascensis* from Isla San Pedro Nolasco were more closely related to the individuals of *C. macrolopha* than to the other individuals of *C. nolascensis* (Fig. 1). The most parsimonious interpretation of these data is that these two individuals represent recent colonizers from the adjacent *C. macrolopha* gene pool on mainland Sonora to Isla San Pedro Nolasco. Isla San Pedro Nolasco lies 12 km off the coast of Sonora opposite significant drainages that purge large quantities of jetsam into the Gulf of California following heavy storms. A large arboreal lizard rafting on floating vegetation for short distances is not inconceivable.

The most debatable issue concerning ctenosaurs and man is how long does it take for a species to evolve? And, if such an event is the result of a human introduction, does it make it any less a natural event — especially if the human population was living as an aboriginal entity of nature. In part, this depends on one's concept of a species. In elevating the subspecies of *Ctenosaura hemilopha* to full species, Grismer (1999a) was using a lineage-based concept, emphasizing a population's inde-



Ctenosaura macrolopha. Photograph: L. Lee Grismer

pendent evolutionary history (as determined by its possession of unique characteristics) and its potential to continue to evolve separately from all other populations (as a result of its allopatry) as evidence for species status (see Grismer 1999a for discussion). Under this species concept, *C. conspicuosa* is recognizable as a valid species. Does it matter that the population may be the result of human introduction? My opinion is no. The genetic consequences of allopatric speciation are going to proceed as a mechanistic process of recombination operated on by selection unmindful of the cause of that selection process. Of course, one can take this to levels of absurdity and opine that fruit flies in a bottle could be considered valid species under this model. The uselessness of this extreme is obvious, but it does touch on more realistic issues such as those presented above. I do not know where the line should be drawn, but I do believe it lies somewhere between the two examples. Birds (a natural entity of nature) frequently contribute to seed dispersal on islands and I see no difference between this entity and aboriginal human populations.

The next issue is one of time. Some "experts" are of the opinion that thousands of years may be too short a time period for a species to evolve. Indeed, I have been criticized for describing as new some of the most distinctive and bizarre species from landbridge islands in the Gulf of California. The critique was not one of character analysis but one of time, in that landbridge islands are too young (8–10 thousand years) to have species (but they could have subspecies!). This implies that evolution happens at a constant rate for all taxa. However, evolution will proceed as fast as necessary within the genetic capabilities of the population in order to avoid the extinction of that population. The potential competition between two large herbivorous lizards on a small desert island could potentially be severe and serve to drive evolutionary change. Case (1982), however, noted little in the way of competition between *Sauromalus varius* and *Ctenosaura conspicuosa*. The change in *C. conspicuosa* may simply be genetic drift following a severe bottleneck.

The beauty of Cryder's (1999) work is that it provides us with an insight into the evolutionary history of this group of spiny-tailed iguanas that, using a morphological data set, was unobtainably imbedded in its phylogeny. Combining phylogeography with natural history, plate tectonics, and ethnoherpetology, we can begin to piece together a coherent scenario from a vast diversity of sources whose corroboration strengthens our interpretations of this group's history.

Ctenosaura nolascensis. Photograph: L. Lee Grismer

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