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lateral convexity of the skull removed over either the right or left hemisphere. After the dura mater was cut and laid aside, the neocortex was removed with gentle suction through a glass pipette. The intended area of ablation included virtually all of the neocortex extending anteriorly to the frontal pole, medially to the saggital sinus, laterally to the rhinal fissure, and posteriorly to the caudal border of the hemisphere.

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## Parthenogenetic Lizards

Cuellar's article (1) on animal parthenogenesis cites some data that I published (2) on *Cnemidophorus lemniscatus*. The quotation is not entirely faithful, and the implications seem to me relevant. The issue is the distribution of bisexual and all-female populations of the lizard along the main course of the Amazonas.

Cuellar says that according to me "only unisexual populations occur along the river. . . ." In reality, I stated (3) clearly that bisexual populations existed at Santarém and Alter do Chão, respectively, at the mouth of the Tapajós and 50 km upstream; I further cited male specimens from Parintins (56°44'W) in an old collection. In 1974, Peccinini-Seale and Frota-Pessoa (4), not cited by Cuellar, listed five localities on the main course where bisexual populations occurred, the three previously noted in my 1970 paper, plus Terra Santa and Urucurituba, located by myself during a survey. The picture at present is: (i) *C. lemniscatus* occurs along the main course of the Amazonas from the coast to Urucurituba (57°40'W), no farther west; (ii) all-female populations predominate, but disjunct bisexual ones are found in the Tapajós and at the westernmost localities, Parintins and Urucurituba; and (iii) there are at least five chromosomal arrangements (4), and their geographical distribution is complex. This mosaic distribution seems to me to be the dominant feature of the problem, indicating, as it does, repeated shift to parthenogenesis in situ. This is

made more probable by the shift actually observed in the Obidos population (2). A probable mosaic has also been found in the microteiid *Gymnophthalmus underwoodi* (3).

In addition, I called attention to the striking preference of *C. lemniscatus* for sizable villages and towns. Cuellar says that "While its distribution along the main course of the Amazonas has not been well studied . . . adequate sampling will probably reveal a uniform riparian distribution from which adjacent towns draw their unisexual populations."

"Adequate sampling" as meant by Cuellar is probably defined by its results, but I shall briefly describe what we ("Expedição Permanente da Amazônia") did about the problem. We traveled several times between Belém and Manaus in our boats *Lindolpho R. Guimarães* and *Garbe*, stopping at all villages and at numerous settlements and estates, working inland and along the rivers, doing general collecting but stressing the collection of *C. lemniscatus*. Of the latter we obtained 7332 specimens at 30 localities among several hundred visited. No specimens were seen in natural habitats; in that many other lizards were obtained at such places, I take it that the sampling was not entirely inadequate. Of the 30 localities, 24 were villages (with definite streets) or towns, and accounted for 7226 (98.6 percent) specimens. Of all towns visited between Belém and Urucurituba only one (Juruti) failed to pro-

duce *Cnemidophorus*. The remaining six localities were sizable estates; they afforded 106 specimens. This disparity in numbers is actually an underestimate because, in places where the lizard was rare, special pains were taken to obtain it; but in towns we usually stopped buying it from the children on the second day, as many as 300 specimens a day being sometimes collected.

I think that it is inescapable that this lizard is traveling with man and settling at places of maximum disturbance. That these places are riparian is probably due to the fact that all Amazonian settlements are riparian. I have enough experience in the field not to be too dogmatic about the absence of "a uniform riparian distribution," but I think the probability of its existence is at best remote.

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In his effort to develop a new evolutionary-ecological model for parthenogenesis in animals, Cuellar (1, p. 837) stated, "Here, I attempt to elucidate the evolutionary ecology of parthenogenesis in light of what is known in all parthenogenetic animals." A model based on such an analysis would indeed be new and welcome, but Cuellar failed to accomplish his stated intention. His model suffers most critically from the lack of consideration of the evolutionary implications of readily available information on the genotypes of parthenogenetic animals. This omission is most pronounced in the case of the vertebrates emphasized in his discussions. Cuellar placed the greatest emphasis on two parthenogenetic species of the genus *Cnemidophorus*—*C. neomexicanus* and *C. tessellatus*—for which he related ecological observations and presented maps of the respective geographical distributions. In terms of genetic data, these are the two species of the genus about which the most has been published. For example, in their analysis of the chromosomes of *C. neomexicanus*, Lowe and Wright (2) found that the karyotype consisted of two quite distinct haploid complements, between which there was little, if any, morphological homology. They concluded that *C. neomexicanus* was an allodiploid that resulted from hybridization between the

bisexual species *C. tigris* and *C. inornatus*. Later they (3) reported the results of karyological analysis of the various pattern classes (4) of *C. tessellatus*. They found that the species consisted of both diploid and triploid populations. Pattern classes C through F were found to be diploid with two distinct haploid complements. One of the complements could have come only from *C. tigris* and the other from some member of the *sexlineatus* species group (they hypothesized the involvement of *C. septemvittatus*); thus these *C. tessellatus* were allodiploid. The triploids (pattern classes A and B) contained the same two haploid complements and an additional one also characteristic of members of the *sexlineatus* species group. They hypothesized that the presence of the third genome resulted from the hybridization of an allotriploid and the bisexual *C. sexlineatus*, itself. Thus, the allotriploid *C. tessellatus* contained a haploid genome from each of three species. These studies were extended to other species and incorporated into a report of the chromosomal evolution in both bisexual and parthenogenetic species of *Cnemidophorus* (5).

An independent estimate of the genotypes of several parthenogenetic species of *Cnemidophorus*, emphasizing *C. neomexicanus* and *C. tessellatus*, was provided by electrophoretic analyses of proteins (6, 7). Neaves has summarized the data from these sources [table 1 in (6)] and used them to test the hybridization hypotheses based on karyology and morphology as proposed for *C. neomexicanus* and *C. tessellatus*. Electrophoretic data were obtained for five widespread, bisexual species (*C. tigris*, *C. sexlineatus*, *C. inornatus*, *C. gularis*, and *C. septemvittatus*) in addition to parthenogenetic species. Each of the five bisexual species was found to have homozygously fixed alleles for each of three enzymes—lactate dehydrogenase (LDH), adenosine deaminase (ADA), and phosphogluconate dehydrogenase (PGDH). Two LKH alleles were identified, one (b') found only in *C. tigris*. The other four species were fixed for the other allele (b). The parthenogenetic species, for which the hybridization hypotheses predicted the involvement of *C. tigris*, were heterozygous for the two alleles in the following combinations: *C. neomexicanus*—bb'; diploid *C. tessellatus*—bb'; and triploid *C. tessellatus*—bbb'. Four alleles were found at the ADA locus. Both *C. tigris* and *C. sexlineatus* shared the same allele (ADA<sup>3</sup>), whereas *C. inornatus* and *C. septemvittatus* had other fixed alleles (ADA<sup>4</sup> and

ADA<sup>1</sup>, respectively). Again each of the three parthenogenetic populations were found to have the ADA<sup>3</sup> allele as predicted, with the triploid having two such alleles, one each presumably from *C. tigris* and *C. sexlineatus*. In addition, the ADA<sup>4</sup> allele (from *C. inornatus*) was present only in *C. neomexicanus*, and the ADA<sup>1</sup> allele (from *C. septemvittatus*) was present in both the diploid and triploid *C. tessellatus* as hypothesized. Only two alleles were found at the PGDH locus: PGDH<sup>2</sup> occurred only in *C. sexlineatus*, and the other four species shared the PGDH<sup>1</sup> as a fixed allele. Among the three parthenogenetic populations, the PGDH<sup>2</sup> allele was found only in the triploid *C. tessellatus*, as predicted. Thus, in each case the electrophoretic data were entirely consistent with hybridization sequences as hypothesized.

Parker and Selander (8), using more proteins and larger sample sizes, have conducted a more extensive electrophoretic analysis of *C. tessellatus* populations and their hypothetical bisexual ancestors. For the purposes of this discussion, the first two sentences of their abstract are worthy of direct quotation: "The parthenogenetic lizard species *Cnemidophorus tessellatus* is composed of diploid populations formed by hybridization of the bisexual species *C. tigris* and *C. septemvittatus*, and of triploid populations derived from a cross between diploid *tessellatus* and a third bisexual species, *C. sexlineatus*. An analysis of allozymic variation in proteins encoded at 21 loci revealed that, primarily because of hybrid origin, individual heterozygosity in *tessellatus* is much higher (0.560 in diploids and 0.714 in triploids) than the parental bisexual species (mean, 0.059)."

The above summary was restricted to data for *C. neomexicanus* and *C. tessellatus* in order to emphasize the extent of genetic information which Cuellar omitted. There is also a considerable amount of information on the genotypes of other parthenogenetic species of *Cnemidophorus*, as well as parthenogenetic species of the lizard genus *Lacerta* (9), none of which Cuellar discussed. All available genotypic data for these species of these genera underscore their allopolyploid nature (5, 6, 9–11). This is now also true for the parthenogenetic populations currently assigned to the otherwise bisexual *C. lemniscatus* (12).

In spite of the large quantity of genotypic data on parthenogenetic lizards, Cuellar can still ignore the implications of hybridization and propose the following scenario (1, p. 843) for the spontaneous origin of parthenogenetic species:

"Recent evidence from histocompatibility studies . . . reveals a remarkable degree of genetic homogeneity in some parthenogenetic lizards, so that entire species may have evolved from single individuals. If this is true, the evolution of present parthenogenetic species probably involved the production of numerous but successive clones, each new advantageous mutation evolving a superior clone that replaced older, less well adapted ones." This of course would be occurring in areas without bisexual species as (1, p. 843): "Parthenogenesis can only evolve in areas devoid of the generating bisexual species, because such species would prevent newly formed unisexuals from establishing clones due either to hybridization or competition." Apparently Cuellar would have us believe that an animal such as *C. neomexicanus* (one of the species he used in histocompatibility studies) originated spontaneously from some bisexual populations and then slowly evolved so as to end up with the morphology, karyology, and allozymes of an F<sub>1</sub> hybrid between *C. tigris* and *C. inornatus*. Moreover, this same mimicking of an F<sub>1</sub> hybrid would have occurred in *C. tessellatus* (twice), *C. cozumela* (10), *C. laredoensis* (11), and so forth. If this were true, such a remarkable set of convergences would be the most startling revelation to hit evolutionary biology in the past century.

Needless to say, the issue is still open as to whether hybridization can give rise *directly* to parthenogenesis, but if the parthenogenetic species, as they live and breathe in nature, have the morphology of a hybrid, the karyotype of a hybrid, and/or the allozymes of a hybrid, there would be reason to suspect that they also might have hybrid-influenced ecologies. To use ecological observations for these hybrid-appearing organisms to support a model of their origin that excludes the possibility of hybrid involvement is absurd at best.

Cuellar stated that this article represents an extension of an earlier paper where he proposed that parthenogenesis may evolve spontaneously (13) rather than involving hybridization. Despite the fact that this earlier paper contained a number of unsupportable, provocative statements, few could disagree with his concluding remark concerning the origin of parthenogenesis (13, p. 644): "Clearly both possible methods of origin, as well as their supportive evidence, must be kept in mind in future studies in order to elucidate best this complex and enigmatic problem." In the *Science* article (1) apparently he chose not to keep both possible methods in mind, he chose to ig-

nore supportive evidence, and he tried to convince a broad audience that no relation between parthenogenesis and hybridization exists.

After reading and analyzing Cuellar's model, I was struck with the appropriateness of the title he chose: "Animal parthenogenesis. A new evolutionary-ecological model is needed." This title as a statement is the best conclusion that could be drawn from his article.

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Cuellar's article (1) on parthenogenesis contains gross distortions of the literature, including: discussion of "controversy" that stems from misunderstanding or misrepresentation of what others reported; failure to cite some papers containing data and thoughtful discussions that contradict some of his statements; and presentation of some observations and viable hypotheses as if they were original, without citation of their appearance in earlier papers.

Cuellar (1) cited Wright and Lowe (2) as the "... one work ... devoted exclusively to" "ecological factors" relating to parthenogenesis (1, p. 837). However, there exist several reports [(3-6), for example] having information on two or three of the following, in addition to ecology: external morphology, karyotypes, and biochemistry. Although additional ecological research is needed, considerably more has been published than Cuellar indicated.

Cuellar's (1) rendition of the paper by Wright and Lowe (2) is largely misleading and his criticisms are not justified. In fact, much of his discussion of habitats is very similar to what Wright and Lowe published in 1968. For example, Cuellar described "perpetually disturbed floodplains" (1, p. 839) as typical habitat for some species, including *Cnemidophorus neomexicanus*, concerning which Wright and Lowe wrote: "The majority of the range of this species is within the valley of the Rio Grande where ... periodic flooding provides a perpetually disturbed, sandy habitat" (2, p. 135). And portions of Cuellar's section on "Beach dwelling and parthenogenesis" (1, pp. 841-842) are also similar to Wright and Lowe's section "Beach strand-thornscrub ecotone" (2, p. 136), which was not cited. In the introduction to the part of his article dealing with habitats, Cuellar writes, "By examining ecological characteristics of parthenogenetic animals, I discovered several patterns that apparently support the importance of ecological isolation from hybridization and competition with congeneric bisexuals" (1, p. 839). In discussing "disclimax" and "disturbed" habitats, Wright and Lowe said: "... the availability of such habitats to the newly generated allopolyploid parthenoform is obviously a matter of critical importance. It is undoubtedly this that largely determines the ecological-evolutionary success or failure of the newly constituted genetic combinations that have been produced originally by hybridization in *Cnemidophorus*" (2, p. 137).

Cuellar even suggested that Wright and Lowe attributed "weedy tendencies" to some ecological formations "in order to correlate the existence of parthenogenesis there with the well-known rule of geographical parthenogenesis" (1, p. 837). This misrepresents their discussion, however, which was in the context of evolutionary history, including ecological disturbances due to "Pleistocene to Recent climatic changes" followed by a "trend toward stability" (2, pp. 130-131).

Examples of parthenogenetic lizards that do not occur in "regional ecotones" do not contradict the ecological theory of Wright and Lowe, as Cuellar suggested. Consider one of Cuellar's examples, *Cnemidophorus lemniscatus*; in citing Vanzolini's report (7) of parthenogenetic populations of this species he did not take into account this comment: "We have collected in the last 3 years some 2500 specimens in Amazonia, and never found one in undisturbed situations ... it is really a 'weed' in the sense of Wright and Lowe (1968)" (7, p. 63).

Uzzell and Darevsky (6) also were criticized unjustly by Cuellar: "These investigators proposed ... that parthenogenesis evolved in 'ancient' times when conditions were more arid, but they did not explain how!" (1, p. 840). In fact, Uzzell and Darevsky, using data on electrophoretic mobilities of proteins, chromosomes, geographic and ecological distributions, and Pleistocene and post-Pleistocene history, presented a discussion (6, pp. 210-219) of how parthenogenesis may have evolved in *Lacerta*. They concluded that the parthenogenetic species evolved following hybridization between bisexual species, which occurred as a result of shifts in geographical distributions, accompanying climatic changes. Of course, numerous questions remain concerning the evolution of parthenogenesis, and some hypotheses need further testing.

Cuellar proposed (1, p. 837) that Lewis' "catastrophic selection" may be involved in the evolution of parthenogenetic species, but although he cited him on other points, he did not cite Zweifel for suggesting this 12 years earlier: "Catastrophic selection such as H. Lewis (1962, p. 270) described could be an important factor in the survival and variation of such marginal populations ..." (8, p. 30).

Many who investigate parthenogenetic lizards agree that the data on external morphology, ecological and geographical distribution, karyotypes, and biochemistry indicate that evolution of parthenogenesis in many instances involved hybridization between bisexual species (5, 6, 9, 10). Cuellar, however, proposed "... that parthenogenesis may evolve spontaneously rather than directly by hybridization. ... Since publication of this idea in 1974, the controversy between the hybridization and spontaneous modes of origin has not been further clarified ..." (1, p. 843). In dismissing the hybrid theory, Cuellar brushed aside or ignored considerable evidence, compiled by independent investigators, indicating that hybridization was involved in the evolution of parthenogenesis in many species of lizards. Indeed, some of the evidence was published after 1974 [(6, 10), for example] and Cuellar provided no data that are inconsistent with the hybrid theory, as it is generally presented.

Furthermore, Cuellar's report of a "controversy" is inaccurate. Proponents of the hybrid theory for some populations often support the nonhybrid theory for others. In 1970, Vanzolini (7) first proposed a nonhybrid origin of parthenogenesis in *C. lemniscatus*. And in 1972, Bezy (3) also formulated a nonhybrid theory of evolution of parthenogenesis in

*Lepidophyma*; he supports the hybrid theory for many species of *Cnemidophorus* (3, 4). These references and many others are included in my review (11) that supports both the hybrid and nonhybrid modes of evolution of parthenogenesis in reptiles. Although Cuellar received the reprint of this review that I sent to him in 1975 (12), his recent article (1) did not acknowledge the dual philosophy of the other workers.

Readers who need accurate information should refer directly to the primary literature, following Cuellar's suggestion: "For the sake of clarifying what is inherently a highly complicated biological problem, future workers theorizing on this subject should strive to be meticulous in search of the facts" (1, p. 841).

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Concerning my statement that bisexual *Cnemidophorus lemniscatus* are not found in the Amazonas River, it was, unfortunately, my impression, at the time, that the bisexual populations Vanzolini (1) alluded to were either rare or had been replaced by the unisexuals. Regarding his comments (2) on distribution I have no doubt, as he states (1) that *C. lemniscatus* occurs predominantly in urban and periurban environments. My concern is how it is colonizing such environments where, according to Vanzolini "cities are separated by forests in a series of nuclei of very dense populations separated by broad areas where density is zero or negligible . . ." I merely added to his guess that *C. lemniscatus* appeared to be expanding its range along the main course of the Amazonas and was proceeding westward (1). By uniform distribution I did not imply high density but simply presence in the natu-

ral communities. This view does not really differ from his own. For instance, he stated that more research was needed to show whether the present geographical distribution of unisexual populations resulted from the spread of a single original strain with superior powers of migration and selective advantages as compared to local bisexual populations, or whether unisexuality was evolving locally. He suggested that gradual expansion along the deforested banks was a more probable mechanism than was rafting and roads, which he excluded. He also added that they had not yet found the species in farms and pastures. In reference to such comments I stated (3), "adequate sampling will probably reveal a uniform riparian distribution from which adjacent towns draw their unisexual populations." Recent tissue grafting studies (4, 5) in some North American *Cnemidophorus* indicate that large populations or entire species may be isogenic, suggesting their evolution from single individuals rather than from multiple origins. Similar studies, if conducted on *C. lemniscatus*, may reveal much on the evolution of this most interesting unisexual species.

In answer to Cole's remarks (6) that I did not cite certain papers because they would contradict my own divergent philosophy regarding the hybridization theory, I should say that whenever I deliberately omitted a paper I did so only because I did not consider it sufficiently original or relevant to a general and theoretical review of the ecology of animal parthenogenesis. My article (3) was not intended to be an exclusive review of lizard parthenogenesis nor of the hybridization theory. As far as that goes, I suspect that I omitted at least 50 papers dealing in one way or another with parthenogenesis among insects and other invertebrates. I find it paradoxical that Cole should raise the issue of omission since his own review (7) omitted the one critical paper questioning the fundamental basis of the hybrid theory (8). Although White (9, 10), who previously upheld the spontaneous theory, has now convincingly established a hybrid origin for the parthenogenetic grasshopper *Warramaba virgo*, he does not ignore, as did Cole, the cytogenetic difficulties inherent in this mode of origin.

Wright's (11) comments largely deal with cytogenetic and biochemical questions rather than ecological ones. Therefore, his comment would be more appropriately discussed in light of my article (8) dealing with the cytogenetic factors on the origin of parthenogenesis, and I suggest that this article provides clarification of Wright's comments. I should

clarify a misconception in both Wright's and Cole's remarks concerning my views on the role of hybridization in parthenogenesis. In no instance have I denied the hybrid nature of parthenogenetic organisms. I have indeed questioned the cytogenetic relationship between hybridization and parthenogenesis (6), but not, as is claimed, the existence of parthenogenetic hybrids. The correlation between parthenogenesis polyploidy and hybridization has long been recognized in both plants and animals (12) and I have emphasized this point previously (3, 8). The essential question is not whether parthenogenetic organisms are hybrids, but whether hybridization results directly in parthenogenesis (8). According to White *et al.* (9, 10) it is extremely difficult to conceive that hybridization would automatically cause major modifications of the maturation divisions or that an act of hybridization and a cytological macromutation would happen simultaneously. Thus "the cellular causes for this remain mysterious" (9).

The fact that technical comments were prompted by this issue is good evidence of a controversy, and controversy is a healthy practice in science, particularly when the questions are mysterious, as they are in the evolution of parthenogenesis. Wright has played a major role in exploring this difficult problem and his contributions have undoubtedly influenced my own ideas. As I now see it, it was precisely this clashing of viewpoints that has set the stage for future workers to focus on precise issues that will ultimately unveil the enigma of parthenogenesis. Evidence that this may now be in progress is provided by the discovery of White *et al.* (9) that "a very few species-hybrid combinations spontaneously manifest premeiotic doubling and it is precisely these which have given rise to the parthenogenetic species."

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