Animal Parthenogenesis

A new evolutionary-ecological model is needed.

O. Cuellar

From what little is understood at present, two requirements seem absolutely necessary for the establishment of parthenogenesis in nature. One is the ability of an organism to become parthenogenetic, that is, the ability to reproduce successfully without fertilization. The second requirement is ecological. Given that an individual has acquired the ability to reproduce by parthenogenesis, it must then generate and maintain a population in the midst of or adjacent to its parental source or sources without being eliminated by competition or hybridization. Both are equally essential for the evolution of parthenogenesis. For instance, potential habitats for colonization by parthenogenetic species may be available regularly, but in the absence of essential gametogenic mechanisms for parthenogenesis the species will not be colonized. Conversely, parthenogenetic individuals may arise frequently but, without a suitable habitat affording them protection from their bisexual progenitors, they may not be able to establish clones. At present, both cytogenetic and ecological factors in the origin of parthenogenesis are poorly understood. A recent review of the present status of the cytogenetic factors revealed that this aspect is more complex than previously considered (*1*).

By comparison, relatively little has been published concerning the ecological factors. Up to now, only one work has been devoted exclusively to this subject. Wright and Lowe (*2*) proposed that parthenogenetic lizards of the genus *Cnemidophorus* occupy a broad ecologically unstable (ecotonal) area of the southwestern United States and hence behave as weeds. They further proposed that within this ecotonal area each species occupies a distinct habitat. That parthenogenesis (in both plants and animals) predominates throughout the world in disclimax situations is a well-known phenomenon (*3–9*), and formed the basis for the rule of "geographical parthenogenesis" in animals (*3*). In this connection the weed hypothesis for *Cnemidophorus* is undoubtedly correct. However, the second premise claiming distinct habitats for each species seems to contradict the first, since such habitats are actually considered local climax formations in that region (*10, 11*) and are not at present regarded as weedy. Apparently, weedy tendencies were attributed to these formations in order to correlate the existence of parthenogenesis there with the well-known rule of geographical parthenogenesis.

Analysis of other species suggest that not all known parthenogenetic lizards inhabit regional ecotones. Three species of geckos, for instance, inhabit tropical islands (*12–14*) as does the teiid *Gymnothalmus underwoodi* (*15*), *Cnemidophorus cozumela* and *C. rodecki* occur on the Mexican peninsula of Yucatan and its offshore islands (*16*), and *C. lemniscatus* is parthenogenetic only along the Amazonas River in Brazil (*17*). In fact, even those species of North American *Cnemidophorus* for which specific habitats have been proposed exhibit distinct riparian dwelling affinities. While the ecotonal concept provided significant pioneering insights into the ecology of lizard parthenogenesis, emerging new data, reanalysis of existing facts, and knowledge from other parthenogenetic groups indicate that present interpretations do not adequately explain the complex nature of this problem. Here, I attempt to elucidate the evolutionary ecology of parthenogenesis in light of what is known in all parthenogenetic animals.

I should mention, however, that none of the ecological relationships to be discussed are applicable to a gynogenetic mode of reproduction (unisexuality requiring pseudofertilization), which may perhaps be better understood in the context of parasitism. Contrary to obligatory thelytoky, which requires special isolation from bisexuality, the geography of gynogenesis is of necessity exactly that of its bisexual parents on whom they depend for their existence.

Theoretical Considerations of Origin

Although no uniform theory has yet been advanced concerning the evolutionary ecology of animal parthenogenesis, two unique features have been singled out by many workers: (i) the presence of parthenogenetic populations in newly created habitats, and (ii) their higher potential rate of increase compared to bisexual species. According to Suomalainen (*6*), parthenogenetic animals are usually found in more unfavorable conditions than the corresponding diploid forms. This is because "even a single individual may give rise to a new strain." In reference to cyclical parthenogenesis, Mayr (*18*) similarly concluded that in insects a single colony can establish a new population in an area not previously occupied by the species because all zygotes are egg-producing females that do not waste half of their eggs on males. According to White (*19*), "the prolificity of parthenogenetic organisms is thus nearly always higher than that of related bisexual forms; even if the average number of offspring per female is the same. The potential increase in numbers per generation is double that of a bisexual species since every individual is a female." These same attributes are also characteristic of apomictic plants. Stebbins (*5*) states that apomixis allows "the building up of large populations of genetically similar individuals for the rapid colonization of newly available habitats." Almost identical conclusions as those provided above have been formulated by many other workers on parthenogenesis (*3, 8, 19, 20*).

There are three compelling reasons for believing that parthenogenetic species can only evolve in isolation from the generating bisexuals: hybridization by males of congeneric species would impede clone establishment, competition would impede clone expansion, and present distributions show largely distinct habitats between congeneric unisexual and bisexual species. Hence, it is reasonable to assume that parthenogenesis evolves either at the periphery of the range, or if within the range, in areas periodically devoid of the generating species.

While the majority of habitats in nature remain more or less permanently occupied, occasional natural disturbances may create temporary ecological vacuums serving as refuges for the origin of parthenogenesis. Lewis (*21*) was the first worker to consider catastrophic selec-

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tion seriously as an important factor in speciation. His conclusions were derived from studies with the plant genus *Clarkia*. He states, "if environments which eliminate whole populations are common, vast numbers of individuals are in turn screened for exceptional adaptation." Many other groups of plants besides *Clarkia* also provide evidence for catastrophic selection (*21*); however, only drought has been considered, and even this, as pointed out by Lewis, has received little attention among botanists. Existing geographical distributions of many parthenogenetic animals suggest that similar natural disturbances may have played a role in the evolution of animal parthenogenesis. These disturbances are principally flooding, glaciation, and fire, each of which, like drought, may temporarily denude a site of its biotic occupants, although other factors such as islands and edaphic conditions may also be important.

The dramatic difference in intrinsic rate of increase between bisexual and unisexual modes of reproduction can be shown simply on a logarithmic scale (Fig. 1). Such a rate of increase is, of course, a superficial means of denoting intrinsic rate of increase since this capacity in nature is subject to numerous changes and can only be defined for a particular environment (*22*). With few exceptions, most species have long passed through the exponential phase early in their evolution. If their populations fluctuate now, it is mainly in response to seasonal effects determining *K* (carrying capacity) (Fig. 2). Hence, most species remain numerically stable from year to year. However, precisely the opposite conditions may be necessary for the origin of parthenogenesis, for, only if a certain degree of instability exists in nature, can new habitats develop in which the high intrinsic rate of increase latent in parthenogenesis be expressed in isolation from bisexuality.

Smith (*23*) correctly points out that the selective advantage of parthenogenesis is the potential to double population size in each generation. However, since parthenogenesis is a relatively rare mode of reproduction among animals, he proposed "that this long term selection acts not by eliminating parthenogenetic varieties when they arise, but by favoring genetic and developmental mechanisms which cannot readily mutate to give a parthenogenetic variety." Unfortunately, this view is not supported by the vast body of knowledge of the commonness of tychoparthenogenesis among animals, which is considered by most authorities in this field to be the principal means by which parthenogenesis arises [see Cuellar (*1*) for a review].

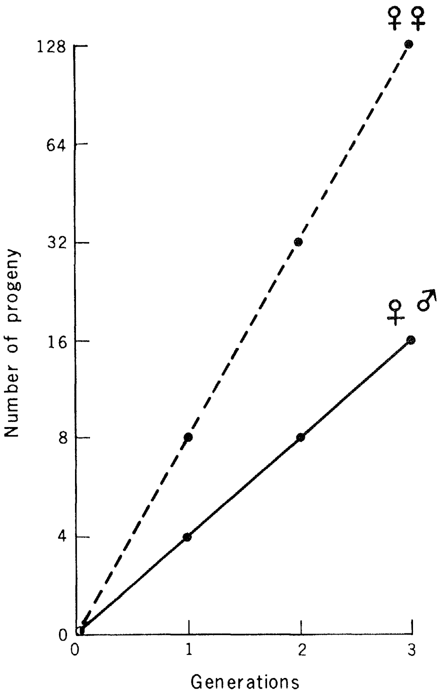


Fig. 1. Comparison of the theoretical intrinsic rates of increase between a bisexual (♂♀) and unisexual (♀♀) species where clutch size is four and longevity 1 year. The first generation consists of two individuals, one male and one female for the bisexuals, and two females for the unisexuals.

A fundamental premise of this article is that parthenogenesis is rare, not because it cannot arise frequently by mutation, but because it can only evolve successfully in special and limited habitats devoid of bisexual species. Therefore, the limiting factor is habitat availability rather than meiotic inability to produce unreduced eggs. This viewpoint contradicts that proposed by Williams (*24*). He states, "Ultimately there will be two species. The sexual one will survive in limited numbers in rare refuges where it is free from competition from its asexual relatives. . . . If novel habitats persist long enough it may be that the success of the uniparentals will prove temporary. Better adapted outcrossed forms may evolve and crowd them out." As will become apparent, it is the parthenogenetic species that rely on novel habitats rather than the sexuals.

Williams (*24*) has further suggested that sexual reproduction may not always be a positive factor in the evolutionary survival of populations. He states, "The fact that parthenogenesis or its equivalent, if found in a vertebrate population, has always replaced sexual reproduction entirely, is decisive evidence of the maladaptive nature of sexuality in these organisms." His rationale was based on the casual observation that some parthenogenetic animals and apomictic plants are often more widespread than their sexual progenitors, and therefore seem more versatile.

It is true that in many of the apomictic complexes such as *Hieracium* (hawkweeds), *Crepis* (hawk's-beard), and *Rubus* (blackberries) the unisexuals tend to be more widely distributed than the sexuals, but there are also sexual species with extensive distributions, which are by no means relictual. In *Taraxacum* many of the diploid sexuals are widely distributed throughout central and eastern Eurasia, and it is the apomictic species that range into the Arctic region and show weedy tendencies (*25*). The same is true of other complexes such as *Bouteloua*, in which the sexuals are more widely distributed than the apomicts. In fact, the apomicts are essentially confined to the Sonoran and Chihuahuan deserts, whereas the sexuals range from southwestern Mexico to Minnesota (*26*). This is complicated even more by the fact that many of the sexuals are polyploids, and the apomicts may be either facultative or obligate (*9*). Also, the taxonomy of these complexes is highly complicated. "The almost inexhaustible variation of the blackberries" has led to the publication of thousands of Latin names (*27*) and additional sexual species are being discovered (*9*).

All of these groups in which the apomicts have extensive distributions consist predominantly of perennial herbs (*Hieracium, Rubus, Taraxacum, Crepis*) and grasses (*Poa, Bouteloua*) that propagate vegetatively. This perennial growth habit, vegetative reproduction, polyploidy, and apomixis are all considered adaptive specializations for rapid propagation and the occupancy of extreme habitats (*5, 9, 28, 29*). Apomixis (viable seed production without fertilization) permits rapid colonization of new habitats, and vegetative growth permits rapid recovery from climatic extremes. There is much evidence showing that perennial herbs with vegetative reproduction are abundant in arctic and subarctic alpine zones. According to Stebbins (*5*), new open habitats have been created by the retreat of ice sheets in the far north and high mountains and have been colonized largely by herbacious perennial species. Cold is by no means the only extreme environmental factor favoring vegetative reproduction. The aspen *Populous tremuloides* propagates by both viable seeds and vigorous suckers, but in certain areas it reproduces entirely by vegetative means as a result of the climatic regime of summer drought (*30*). In North

America, aspen is a fairly reliable fire indicator (*31*). It is also common knowledge that vegetative propagation is characteristic of floras—such as chaparral, grasslands, and mallee—that are subject to frequent natural burning (*31–34*). The conclusion by Williams (*24*) that sexuality is therefore maladaptive represents a gross oversimplification of the facts. It overlooks a vast body of botanical evidence showing that such agamic complexes are largely confined to areas with unfavorable or extreme climates, and that the majority of sexual plants occupy the favorable ones. In the broad picture it is the agamic species rather than the sexuals that are relictual.

According to Babcock and Stebbins (*35*), in the *Crepis occidentalis* complex which contains both obligate and facultative apomicts and sexual diploids, the variability is greater in areas occupied by the sexuals but is limited to a few types occupied exclusively by the apomicts. They state:

> The ultimate fate of an agamic complex of which the sexual ancestors have become restricted or extinct can be predicted; it will flourish as long as the conditions that existed during its formation prevail, but it will be unable to meet any new changes of environment, and will therefore in time become more and more restricted, and will finally die out.

Similarly, Stebbins (*5*) concludes:

> There is no evidence that apomicts have ever been able to evolve a new genus or even a subgenus. In this sense, all agamic complexes are closed systems and evolutionary "blind alleys." . . . While sexual species may, during the course of their existence, give rise to entirely new types by means of progressive mutation and gene recombination, agamic complexes are destined to produce only new variations on an old theme.

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. The habitats of many parthenoforms can be grouped into several seral transitions which furnish situations where occupation by bisexuals is less likely than that by parthenoforms. The remaining part of this article is devoted to analyzing these relationships.

River Dwelling Affinities in Parthenogenetic Lizards

The dominant parthenogenetic species of whiptail lizards in North America are *Cnemidophorus velox*, *C. exsanguis*, *C. tesselatus*, *C. uniparens*, and *C. neomexicanus*. With minor exceptions, these are situated principally in New Mexico, west Texas, and northern Chihuahua, Mexico. The remaining three species—*C. opatae*, *C. sonorae*, and *C. flagellicaudus*—have rather limited distributions (particularly *C. opatae*) in southeastern Arizona, northern Sonora, and Chihuahua (*2*). With the exception of these latter three, the majority are found predominantly in New Mexico. Toward the north *C. velox*, *C. neomexicanus*, *C. exsanguis*, and *C. tesselatus* (*36–38*) are all found together in the floodplains of the Rio Grande and in adjacent riparian areas. In central New Mexico, they continue sympatric but without *C. velox*, and farther south the same three join the southern dominant species, *C. uniparens*. While they are not exclusively confined to the Rio Grande Valley, their abundance along the river sheds doubt on the current belief that each of these species tend to be common in specialized areas, such as *C. tesselatus* in rocky canyons, but some populations are not restricted to such habitats. In fact, if any one salient feature characterizes the geographic distributions of these various species, it is their tendency to be floodplain dwellers. Naturally, a larger river such as the Rio Grande courses through highly diversified habitats, but the community of its floodplain and its principal tributaries remain relatively uniform, at least throughout the area in New Mexico between Española and Las Cruces (*39*).

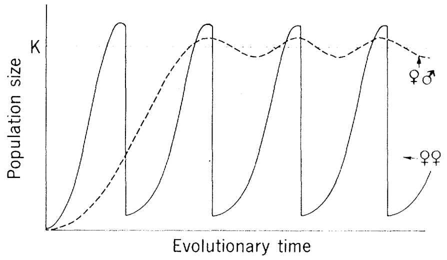


Fig. 2. Theoretical curves representing the difference between bisexual (dotted lines) and unisexual (solid line) population fluctuations in nature. The beginning of each curve up to line *K* (carrying capacity) represents the growth rate during invasion of new habitats. Thereafter bisexual populations fluctuate close to *K* whereas the unisexuals fluctuate radically, overshooting *K* between catastrophies due to high rate of increase, and catapulting to low level during catastrophies.

With the exception of the distributions of *C. tesselatus* (*19*) and *C. neomexicanus* (*40*), all others are inferred rather than based on actual localities. The general rule used for describing ranges is to shade all areas between collection sites. This is convenient for showing general distribution but gives a distorted view of actual micro distributions. For instance, the range of *C. tesselatus* is shown continuous from southeastern Colorado to Chihuahua, Mexico, covering all of the area between the Rio Grande and the Pecos (*2*, *41*). On the other hand, when only actual collecting localities are plotted, its range generally assumes a riverine distribution (Fig. 3). Axtell (*40*) has established the same pattern for *C. neomexicanus* (Fig. 4).

As judged from their present distributions and their morphological and geographical distinctness, every major drainage basin in southwestern North America appears to have played a role in the evolution of at least one parthenogenetic *Cnemidophorus* species. The single known exception to the occurrence of parthenogenesis within this tight complex in North America is the newly discovered species *C. laredoensis* described by McKinney (*42*) from the lower Rio Grande in Laredo, Texas. Whether or not flooding has been instrumental in the evolution of these parthenogenetic lizards is, of course, conjectural. Theoretically, catastrophic floods could produce large areas temporarily devoid of bisexual *Cnemidophorus*, and parthenogenesis could develop along the floodplains, provided that such flooding occurred with sufficient regularity to produce a more or less continuous vacuum.

As to climate, New Mexico has the second highest thunderstorm frequency in the United States, and, because of the rough terrain and sparse vegetation, these storms are the cause of numerous sporadic flash floods and major flooding throughout the state. Years in which there were high flood discharges in major New Mexico river basins are as follows: for the Rio Grande Basin, 1904, 1905, 1929, 1935, 1941; for the Pecos Basin, 1904, 1905, 1915, 1916, 1937, 1941, 1942, 1966; for the Canadian Basin, 1904, 1913, 1937, 1965; for the San Juan Basin, 1909, 1911, 1927, 1929, 1942; for the Gila River, 1941, 1965 (*43*). Major flooding in the Rio Grande Basin has now been largely controlled by channelization and construction of several reservoirs along its course, explaining the absence of major floods after 1941, and perhaps the disappearance of some parthenogenetic populations (*36*).

While these various unisexual species are commonly found in the perpetually disturbed floodplains of rivers, streams, and washes, they also occupy climax communities, but usually where bisexual species are absent. The bisexual *C. inornatus*, however, is an exception since it occurs sympatrically with several of the unisexuals in disturbed sites, behaving essentially as a unisexual species. Conversely, the bisexual *C. tigris* is almost exclusively restricted to adjacent climax communities characterized by sandy soils. In certain localities of southern New Mexico, for instance, it occurs abundantly in mixed mesquite-creosote associations, but is virtually absent from adjacent pure stands of creosote growing in gravelly soils. In this same area, the unisexual *C. uniparens* occupies the creosote formation to the west and the riparian zone to the east, isolating *C. tigris* in the middle (*39*). *Cnemidophorus tigris* has never been observed in purely riparian habitats, except where these are penetrated by extensions of the mesquite-creosote association (*36*). Exactly why *C. tigris* occupies such specific habitats in this area is not known. Edaphic conditions appear to be important, but these may be secondary to the denser and more complex plant associations they support, which may further reflect food abundance and dietary preferences. Outside of this general vicinity, however, *C. tigris* is the dominant *Cnemidophorus* inhabiting all of the North American deserts.

Undoubtedly, the most lucid example of a riparian distribution is that of *C. lemniscatus* in the Amazonas River. According to Vanzolini (*17*), only unisexual populations occur along the river, elsewhere *C. lemniscatus* is bisexual. While its distribution along the main course of the Amazonas has not been well studied, Vanzolini believes that *C. lemniscatus* is using the river to expand its range upstream, where it has established populations in urban and periurban environments adjacent to the river. Adequate sampling will probably reveal a uniform riparian distribution from which adjacent towns draw their unisexual populations. Similar evidence of a riparian distribution apparently exists for the recently described unisexual lizard *Leposoma percarinatum* (*44*) from the Guianan region of northern South America.

Glaciation and Parthenogenesis in Lizards

Darevsky (*8*), and more recently, Uzzell and Darevsky (*45*) have published maps of distribution for both the parthenogenetic and bisexual species of the *Lacerta* complex, giving precise information on sympatric relationships for these various species. The *Lacerta* complex consists of four bisexuals and four unisexuals, all occurring more or less sympatrically in the general area of Lake Sevan in the Caucasus Mountains of Armenia, U.S.S.R. Recognizing that parthenogenesis in many invertebrates is associated with areas affected by glaciation, Darevsky (*8*) similarly concluded that such conditions led to the origin of parthenogenesis in *Lacerta*, "under the extreme conditions of the Würm maximum, these species found refuge in rocky areas. In such refuges, populations . . . which had become parthenogenetic survived, whereas the bisexual populations either died out or were pushed to the south under the influence of the glacier." However, elsewhere Uzzell and Darevsky argued against this hypothesis (*45*), suggesting that the present occupancy by *Lacerta* of more extreme habitats may not represent an escape from competition with their parental species. These investigators proposed, instead, that parthenogenesis evolved in "ancient" times when conditions were more arid, but they did not explain how! Presently, the parthenogenetic *Lacerta* occupy rocky habitats (hence, the name rock lizard) and in this feature they resemble the North American *C. tesselatus*.

On the basis of Darevsky's (*8*) detailed geographical maps, three of these unisexual species, *L. armeniaca, L. rostombekovi*, and *L. dahli*, occur mainly along streams in headwaters of the Kuras River. *Lacerta unisexualis* is also found along streams; it is also found in headwaters of the Arak River and around the shores of Lake Sevan. In general, all of the unisexual species are sympatric in the high area dividing both drainages, whereas the bisexuals each occupy more or less distinct ranges in the surrounding lower areas. Since the high areas now occupied by the unisexuals correspond precisely to recent glaciation and those of the bisexuals do not, Darevsky's original hypothesis that bisexuals were pushed out appears correct. Another interpretation, however, is that repeated glacial advances and retreats created areas devoid of bisexuals in which parthenogenesis could proliferate during the milder climates of interglacial periods. According to this model, both unisexuals and bisexuals initially invaded these newly created areas; but the unisexuals, because of their higher reproductive rate, filled them more rapidly and eventually restricted the bisexuals to the periphery of the glaciated areas. As glaciation decreased, the unisexuals invaded higher and higher areas devoid of the bisexuals, which followed behind, keeping pace with the invasion of peripheral climax communities into the glacial free areas. Thus, their present occurrence may not necessarily reflect a relictual refuge from the Würm, but, rather, invasion after the end of the last glacial period. This process may still be in progress, in which case continued encroachment by the bisexuals will ultimately eliminate the unisexuals, unless another glacial period commences prior to their extinction. As shall become apparent below, ecological evidence from some of the most extensively studied parthenogenetic invertebrates lends support to the importance of glaciation on unisexuality in *Lacerta*.

Glaciation and Parthenogenesis in Invertebrates

Many investigators of invertebrate parthenogenesis recognized that glaciation has been the ecological force selecting for parthenogenesis in certain species. According to Suomaleinen (*6*), "glacial conditions during the ice age in Europe have considerably influenced the distribution of the various weevil races." The distribution of animal parthenogenesis in northern climates was first noted by Vandel (*3*) during studies with the isopod *Trichoniscus elisabethae*. According to White (*7, 46*), Vandel assumed that this was because the triploid parthenogenetic form is more hardy. But the more "likely explanation in this case is that the parthenogenetic forms have found it easier to expand their ranges just because every individual was capable of founding a local colony of the species, and because there was no reproductive wastage, however small or scattered the population" (*7*).

Seiler (*47*) found that parthenogenetic populations of the moth *Solenobia triquetrella* in Switzerland inhabit mainly areas previously covered by the Würm glaciation, whereas the bisexual races occupy the nonglaciated areas. According to Suomaleinen, parthenogenetic races of the weevil *Otirrhyncus dubius* have "spread to the areas which were later freed from the ice and occur in regions which during the Würm ice age were covered with the glaciers" (*6*). Another species, *Saga pedo*, also occupies the most northern distribution of this genus as well as being its only parthenogenetic species (*48*). According to White (*7*), its range is now very discontinuous and *S. pedo* is on the verge of extinction. Apparently, past glaciated habitats that prompted its origin are now being replaced by climax communities to which it is not adapted, and that are occupied by competing, congeneric bisexuals. Similar northern distributions have been noted in the parthenogenetic flies *Lonchoptera dubia* (*49*), *Ochthiphila polystigma* (*49*), and *Cnephia mutata* (*50*).

The large number of observations on invertebrate parthenogenesis reveals not only a relictual pattern in the unisexuals, but also that much yet needs to be known about the ecology, taxonomy, and cytogenetics of these unisexual-bisexual complexes to correctly interpret their origin, parental relationships, and geographical distributions. 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.

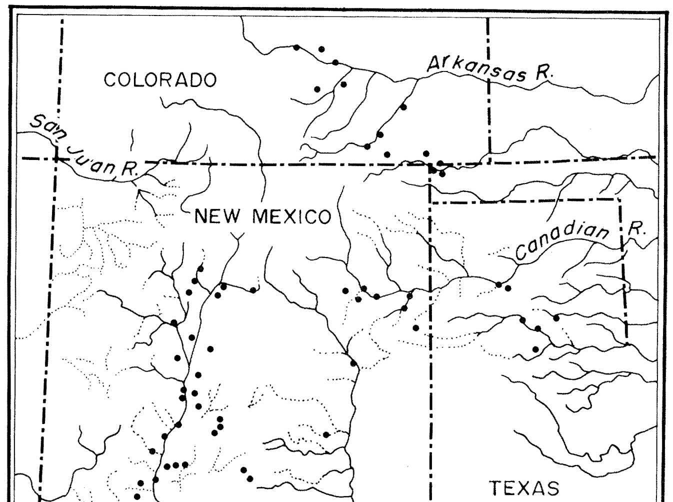
Fire Disclimax and Parthenogenesis

Theoretically, natural burning (fire cycles) could have similar effects to those of drought, flooding, and glaciation in creating new or disclimax conditions favorable for the origin and maintenance of parthenogenesis. Indeed, some workers believe that without fires certain formations, such as grasslands and savannas, might not exist at all, as these would eventually be replaced by species that are not fire resistant (*11, 33, 34*). As with the other catastrophic factors considered, the validity of fires as agents in promoting parthenogenesis may be tested by finding parthenogenetic species in natural fire zones. To my knowledge, there is only one animal species providing such evidence, although others may eventually be discovered. According to White (*46*) the Australian parthenogenetic grasshopper *Morabo virgo* inhabits only areas previously devastated by fires. "We have searched extensive areas of mallee vegetation . . . without finding *M. virgo* (except at the single locality 3 miles east of Roto). This whole area was devastated by fire in the summer of 1957–58. . . . Obviously it is a doomed species in an evolutionary blind alley. We cannot say how many colonies still survive. The fact that it is a summer species renders its population liable to extermination by bush fires."

Another alternative may be that the evolutionary survival of *M. virgo* actually depends on fire disclimaxes, which provide the essential refuge preventing contact with related bisexual species. The wingless condition was undoubtedly acquired from its bisexual progenitors, since winglessness is a common phenomenon among many insects, but I do not know whether wingless bisexual species of *Morabo* occur in the vicinity of *M. virgo*'s distribution. What then is the correlation between low vagility and parthenogenesis in potentially highly vagile organisms, such as winged insects? Winged bisexuals could easily recolonize newly available habitats, thereby eliminating them as potential sources for the propagation of parthenogenetic clones. On the other hand, a wingless condition in the bisexuals would favor the development of parthenogenesis because it would permit the unisexuals to invade and colonize new habitats faster than the bisexuals. Hence, one might expect the wingless condition in other groups to be associated with parthenogenesis in similar habitats periodically devoid of bisexuals. Surprisingly, the majority of parthenogenetic weevil (beetles) species are wingless and inhabit post-glaciated habitats (*51*).

Beach Dwelling and Parthenogenesis

Two species of parthenogenetic lizards, *Cnemidophorus cozumela* and *C. rodecki*, are known from the Yucatan



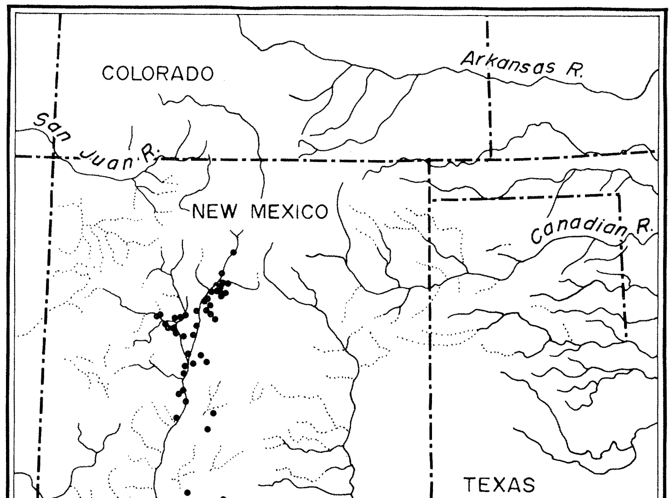


Fig. 3 (left). Riparian distribution of *Cnemidophorus tesselatus* (*19*). Spots indicate actual localities. Modifications from Zweifel (*19*) exclude shading showing conjectural range, and include more drainages. Fig. 4 (right). Riparian distribution of *Cnemidophorus neomexicanus*. Spots indicate actual localities. Modification from Axtell (*40*) excludes shading showing conjectural range and include more drainages.

Peninsula of Mexico (*52*). Both are found only along beaches and on nearby offshore islands, except for a single population found around Lake Petén, Guatemala. According to Fritts (*52*), most individuals occur on the open beach and, despite extensive searching, were not found inside adjacent forests. "The possibility of finding inland populations other than those at Lago de Petén is remote in view of the seemingly uniform high forest in the eastern half of the Yucatan Peninsula." Why these species inhabit primarily open beaches is not clear, but their presence "only at localities where one of the parental forms is not found" (*52*) suggests that these parthenogenetic species evolved on the beaches where they could propagate in isolation (*6*) from the bisexuals. Such a situation, however, does not reveal why the bisexuals do not invade the beach and vice versa. Perhaps beaches here bear flooding similarities with the riparian communities alluded to previously. The Yucatan Peninsula not only receives heavy rainfalls during the rainy season, but is also subject to coastal inundation from frequent tropical storms and hurricanes. High tides could effect the same results on these beaches as inundation by river flooding on riparian communities.

A form of beach dwelling around inland lakes is apparently characteristic of several parthenogenetic lizard species, but the factors responsible for maintenance of open habitats presumably devoid of bisexuals in such situations are not known. The only known populations of *C. cozumela* that do not dwell on beaches are found around Lake Petén, Guatemala. Also, the newly discovered unisexual species *Lepidophyma flavimaculatum* (*53*) occurs in the vicinity of Lake Gatún in Costa Rica. A conspicuous example of perilacustrine habitation is the previously mentioned *Lacerta unisexualis*, which occurs abundantly around Lake Sevan (*8*). *Cnemidophorus neomexicanus* also shows distinct lake-dwelling tendencies. In fact, wherever it occurs at any considerable distance from the Rio Grande Valley, it is usually in association with extinct lake beds. According to Axtell (*40*), in its southern distribution, *C. neomexicanus* "becomes increasingly associated with various sized basins of local internal drainage where flat surfaces and fine detrital sediments indicate the past presence of shallow ephemeral lakes. Populations have been found associated with lacustrine beds" in several basins of New Mexico and Texas. Possibly during wetter Pleistocene or post-Pleistocene times these basins drained into the Rio Grande Valley, providing corridors for migration into their present relictual lacustrine habitats. Theoretically, major fluctuations in lake levels due to frequent drought could produce extensive open habitats favorable to the origin and existence of parthenogenesis, but it has not been clearly ascertained whether the above species (besides *C. neomexicanus*) actually occupy the lake beds. For instance, *L. unisexualis* may occur on rocky cliffs surrounding Lake Sevan, rather than on the ground.

Islands and Parthenogenesis

Three species of gecko lizards are known to be parthenogenetic. These are *Lepidodactylus lugubris* (*14*), *Gehyra variegata* (*13*), and *Hemidactylus garnoti* (*12*). All are principally insular, but, if they are wide ranging, they may also occur in certain mainland areas. *Gehyra variegata* is known from the Bonin Islands of Japan, and the remaining are widely distributed throughout the South Pacific. Since these geckos are all arboreal and tropical, there is no a priori reason to suspect that their existence relies on disclimax conditions. What is it then about islands that tends to promote parthenogenesis, and conversely what is it about parthenogenesis that is favored on islands. The answer to both questions may be related to colonizing ability. Without discussing the many complications of zoogeography, one can reasonably argue that the chances of reaching and colonizing small distant land masses are greater if the colonizer can reproduce without a member of the opposite sex, for it dispenses with the need to have both sexes reach the same place simultaneously. Terrestrial species can reduce these hazards in two ways, both involving elimination of males. One is to have prolonged sperm storage, as, for instance, in reptiles (*54*), and the other is simply to reproduce by parthenogenesis. The former may not be related to insular conditions since sperm storage may have evolved in response to other conditions in the mainland. Parthenogenesis, in contrast, may have a dual origin in response to either mainland or insular conditions. If evolved in the mainland, the trait would simply be perpetuated on the colonized island, insular conditions therefore being secondary to the source of origin. Parthenogenesis, however, could also evolve directly on islands, since especially any latent parthenogenetic tendencies could develop in the absence of intra- and interspecific contacts. While parthenogenesis may be more common on islands than we recognize at present, the ultimate source of origin (whether primary or secondary) may be difficult to ascertain. For instance, the teiid lizard *Gymnophthalmus underwoodi* is parthenogenetic on the islands of Trinidad and Barbados, which are so close to mainland Venezuela that their parthenogenetic populations could easily have come from the mainland. This may also be the case in the islands of Cozumel and Mujeres off the Yucatan Peninsula. Both islands have parthenogenetic *Cnemidophorus* species, which are also found on the adjacent mainland. However, *G. underwoodi* has not been reported from mainland Venezuela. The probability exists, nevertheless, that colonizing ability may not be related to island parthenogenesis. In view of our understanding of insular conditions and geology, various natural disturbances such as severe storms, subsidence and emergence, and volcanism may provide disclimax habitats favorable for the origin of parthenogenesis from insular bisexual species. Of course, both of the above possibilities may be interrelated.

Generalities of the Model

Theoretically, any species could develop parthenogenesis. Why then is it common only in certain types? Why, for example, are lizards parthenogenetic and not mammals and birds? Why are only certain types of lizards parthenogenetic and not others that are found side by side with the unisexuals, as for instance *Sceloporus*, *Uta*, *Holbrookia*, *Phrynosoma*, and *Crotaphytus* found sympatrically with unisexual *Cnemidophorus*. Cytogenetic factors are undoubtedly important. In turkeys, despite intensive selective breeding for parthenogenesis, only *ww* males have ever been produced (*56*). Another probable genetic factor controlling the production of parthenogenesis is the frequency of homozygous lethals. Since spontaneous diploidization automatically duplicates every chromosome, homozygous lethals would result in any egg having a lethal gene in the heterozygous state. Hence, the probability of parthenogenesis arising in any particular species may depend on the frequency of such genes, which may further depend on the relative degree of inbreeding; the more inbred the population, the greater the elimination of homozygous lethals and the greater the probability of parthenogenetic development. Other factors, unrelated to the cytogenetic and genetic ones, may also be important in determining the types of species that may develop parthenogenesis. Highly territorial forms, such as the lizards *Uta* and *Scelo-*

porus, may expand too slowly to take advantage of temporary vacuums, whereas species like *Cnemidophorus* with loose, wide-ranging territories, may be better suited to fill them rapidly. In this connection, terrestrial species might have a dispersal advantage over more sedentary tree- or rock- dwelling forms. It does not seem likely, however, that parthenogenesis could evolve in highly vagile organisms such as birds and large mammals, as these could easily recolonize the relatively narrow areas in which parthenogenesis usually evolves. Hence, mode of transportation may also be important.

Recent evidence from histocompatibility studies (*37–38*) 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. Presumably, in these early stages of unisexual evolution, new areas open to either reproductive mode would tend to be filled with bisexuals, until emergence and propagation of a unisexual clone. Subsequently, unisexuals would begin dominating in density as a result of their higher intrinsic rate of increase. Later, as they became more dominant, selection would promote clones more or less specially adapted to survive either in the unique communities of perpetually disturbed areas or in areas not inhabited by the bisexual species. In time, the unisexuals would tend to supplant the bisexuals, not only because of their rapid ability to colonize but also because of their specialization. Hence, both would tend to be mutually exclusive, each remaining dominant and superior in its own habitat. The unisexuals could then spread from their source of origin into similar areas not occupied by the unisexuals. Conversely, termination of the physical or climatic conditions promoting and maintaining recurrent disclimax ecologies would eventually cause extinction of parthenogenesis as a result of reinvasion of the local climax communities.

This article represents an extension of an earlier idea proposing that parthenogenesis may evolve spontaneously rather than directly by hybridization, as is currently believed by most workers on vertebrate parthenogenesis (*1*). Since publication of this idea in 1974, the controversy between the hybridization and spontaneous modes of origin has not been further clarified, although belief in the hybrid theory has apparently been strengthened by those who previously upheld it (*56*). Since such a controversy bears intimately on the ecological origins of parthenogenesis, I feel justified in briefly revisiting it in the hope of amplifying our understanding of this most complex biological problem. According to Stebbins (*5*):

> the usual close association between apomixis, on the one hand, and polyploidy, interspecific hybridization, and polymorphy, on the other, must be explained on an indirect rather than a direct basis. . . . The first hypothesis developed to explain apomixis was that of Ernst (1918), who believed that it is caused by hybridization between species. Nevertheless, there is no evidence at all that hybridization by itself can induce apomixis. Hybrids between different sexual species . . . have in no instance shown any clear indication of apomictic reproduction, even though their parental species may be closely related to known apomictic forms. . . . A number of hybridizations have now been performed between sexual types and related facultative or obligate apomicts in the same genus. Segregation in later generations from these crosses has shown in every case that apomixis of the species is genetically controlled.

Since the idea that hybridization directly gives rise to parthenogenesis was borrowed by zoologists from botanists, future workers on animal parthenogenesis, in particular the vertebrate camp, should bear in mind Stebbins' caution.

Summary

The available evidence on the ecological factors favoring the existence and origin of natural parthenogenesis is evaluated. Analysis of the geographical distributions of the well-known cases of animal parthenogenesis in nature reveals (i) that most of these species exist in natural disclimax communities and (ii) that within these communities they exist in isolation from closely related congeneric species. 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. Furthermore, the two unique features allowing parthenogenetic species to invade and occupy open habitats faster than bisexuals are (i) a double intrinsic rate of increase and (ii) the ability of one individual to establish a new colony.

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