Chapter 6
Geographical Parthenogenesis: General Purpose Genotypes and Frozen Niche Variation

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> *"It is not entirely clear, however, how forms whose genetic system must be very inflexible manage to become adapted to new environments when they* do *get transported to them: the apparent ecological versatility in* space *seems to be at variance with their lack of ecological versatility in* time*" (Original italics; MJD White, 1973, p. 748).*

Abstract Clonally reproducing all-female lineages of plants and animals are often more frequent at higher latitudes and altitudes, on islands, and in disturbed habitats. Attempts to explain this pattern, known as geographical parthenogenesis, generally treat the parthenogens as fugitive species that occupy marginal environments to escape competition with their sexual relatives. These ideas often fail to consider the early competitive interactions with immediate sexual ancestors, which shape alternative paths that newly formed clonal lineages might follow. Here we review the history and evidence for two hypotheses concerning the evolution of niche breadth in asexual species – the "general-purpose genotype" (GPG) and "frozen niche-variation" (FNV) models. The two models are often portrayed as mutually exclusive, respectively viewing clonal lineages as generalists versus specialists. Nonetheless, they are complex syllogisms that share common assumptions regarding the likely origins of clonal diversity and the strength of interclonal selection in shaping the ecological breadth of asexual populations. Both models find support in ecological and phylogeographic studies of a wide range of organisms, and sometimes generalist and specialist traits (e.g., physiological tolerance, microspatial preference, seasonal abundance, food habits, etc.) are found together in an asexual organism. Ultimately, persistent natural clones should be viewed as microspecies in ecological models that consider spatial and temporal heterogeneity rather than multi-locus genotypes in simplistic population models.

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I. Schön et al. (eds.), *Lost Sex*, DOI 10.1007/978-90-481-2770-2_6,

6.1 Introduction

All-female reproduction offers twice the generative potential of biparental sex, but strictly asexual species are rare in the plant and animal kingdoms. The overwhelming prevalence of biparental sex is paradoxical, given the cost of producing males and risks associated with finding and obtaining mates. With few exceptions, biparental sex persists in taxa that can produce all-female clones (Williams 1975); therefore, everything else is not equal between sexual and asexual lineages. Considerable discussion has focused on identifying immediate benefits that can compensate for the demographic costs of sex (West et al. 1999; West and Peters 2000). Comparative studies have focused on ecological circumstances that might favor asexual lineages, because exceptions to the 'rule of sex' can provide insight into reasons for the rule (Vrijenhoek 1989a). Geographical parthenogenesis is one such an exception (see also Chapter 8). Vandel (1928, 1940) first recognized that parthenogenetic arthropods tend to have wider and more northern distributions than their sexual relatives in Europe. Since his initial observations based mostly on comparisons of glaciated versus non-glaciated distributions, many other examples have been reported of parthenogens being more prevalent at higher altitudes, in anthropogenically disturbed environments, at the margins of a species range, on islands versus the mainland, and in successional versus climax communities (Glesener and Tilman 1978; Bell 1982; Lynch 1984; Parker 2002).

With these diverse examples, a number of hypotheses have been proposed to explain geographical parthenogenesis: (1) all-female reproduction provides superior colonizing ability and reproductive assurance (Baker 1965; Tomlinson 1966); (2) biotic uncertainty favors genotypically diverse sexuals in species-packed central environments (Glesener and Tilman 1978; Hamilton et al. 1981); (3) destabilizing hybridization favors displacement of parthenogens from the sexual range (Lynch 1984; cf. Paulissen et al. 1988); (4) heterozygosity assurance due to cloning favors asexual lineages in subdivided metapopulations (Vrijenhoek 1985; Haag and Ebert 2004); and so forth. As opposed to hypotheses that parthenogens simply escape from competition with their immediate sexual ancestors, we consider two commonly invoked hypotheses that focus on selection pressures occurring while parthenogenetic clones first arise from their sexual progenitors.

The "general-purpose genotype" (GPG) and "frozen niche-variation" (FNV) hypotheses appear at first glance to be mutually exclusive explanations for the success of parthenogenetic lineages. The GPG model proposes that individual clones (see Chapter 9 on clone definition) have broader environmental tolerances than their sexual relatives, whereas the FNV model proposes that individual clones are specialists. We consider selective pressures that might favor generalist versus specialist clones in central versus marginal environments and examine mechanisms for clonal origin that might shape interclonal selection. Finally, we address the possibility that these hypotheses are not mutually exclusive. Hereafter, we use the term parthenogenesis for all-female clonal reproduction in a broad sense. We restrict the term thelytoky for obligate parthenogenesis that does not require sperm. Gynogenesis and hybridogenesis, on the other hand, are sperm-dependant forms parthenogenesis

(Beukeboom and Vrijenhoek 1998). Gynogens are strictly clonal and require sperm only to initiate embryogenesis. Hybridogens are hemiclonal and incorporate sperm and express paternal genes, but transmit only the maternal genome to ova (for examples, see Chapters 16, 19 and 20).

6.1.1 Adaptation at the Margins

To consider factors that might contribute to geographic parthenogenesis, we must first review some conditions that are expected to occur on the edge of a species range. Mayr (1954) was among the first to indicate that adaptation to marginal environments might be limited by gene flow from central populations. This idea implies that the genetic composition of marginal populations differs in some way from populations at the center of a species range, and that gene flow contributes to outbreeding depression (Wallace 1959). Partially isolated marginal populations are expected to exhibit reduced genetic diversity due to population fluctuations, genetic drift and possibly directional selection for local adaptations (da Cuhna et al. 1950; Carson 1968). Nevertheless, adaptive gains may be swamped by episodic gene flow, unless marginal populations evolve means to increase their isolation (García-Ramos and Kirkpatrick 1997). Therefore, selfing, parthenogenesis and chromosomal rearrangements that impede recombination will be favored in marginal populations by closing the genome to introgression (Wallace 1959). Selection that favors genetic diversity and effective recombination in central populations is replaced by selection that favors closure of the genome at the periphery of a species range (Stalker 1954; Templeton 1982).

The dynamics of marginal populations have been considered in several attempts to explain geographical parthenogenesis. Metapopulation simulations by Ladle et al. (1993) suggest that dispersal advantages and Red Queen processes (see also Chapter 7) might favor the accumulation of parthenogens in low-density marginal habitats to which they escaped during a parasite-free stage in the life cycle. Peck et al. (1998) modeled parthenogenesis along a gradient in annual reproductive output that decreased with latitude. In their simulations excess immigration from more productive southern populations diluted the open genomes of locally adapted, northern, sexual populations. In contrast, locally adapted clones were protected from dilution and tended to accumulate in the north due in part to their dispersal advantages. However, Horne and Martens (1999) argue that the absence of sexual freshwater ostracods in northern Europe is not just a consequence of the superior colonization abilities of clones. Fossil evidence indicates that sexual ostracods also inhabited northern Europe during post-glacial times and were replaced as climates gradually became more stable. Consequently, they argue that modern climatic stability favored the replacement of sexual lineages by competitively superior clones. Though these arguments were intended to explain geographical parthenogenesis, they do not explore the nature of clonal competitive superiority, and thus do not exclude aspects of either the GPG or FNV models.

A putatively “new” idea about geographical parthenogenesis was recently outlined by Haag and Ebert (2004). Sexual populations inhabiting subdivided marginal habitats are subject to metapopulation processes that should lead to genetic drift and contribute to inbreeding depression. Apomixis, however, protects clones from inbreeding depression associated with founder events. This potential benefit of parthenogenesis was clearly articulated in earlier publications (Vrijenhoek and Lerman 1982; Vrijenhoek 1985; Niklasson and Parker 1994) and called “heterozygosity assurance” (Beukeboom and Vrijenhoek 1998; Vrijenhoek 1998b; Kearney and Shine 2004). Evidence for the temporary benefits of heterozygosity assurance is clearly documented in studies of sexual and clonal forms of *Poeciliopsis* (Vrijenhoek and Lerman 1982; Vrijenhoek 1989b; Lively et al. 1990).

6.2 General Purpose Genotype (GPG)

Vandel (1928) first associated broad environmental tolerance with geographical parthenogenesis. He reported that parthenogenetic races of the terrestrial isopod, *Trichoniscus*, are distributed in cooler and drier habitats than their sexual relatives. White (1973), who studied the wingless Australian grasshopper *Warramaba*, also associated parthenogenesis with broadly tolerant genotypes, noting that "Natural selection may possibly tend to favor genotypes that are especially plastic, phenotypically, in the case of thelytokous populations (replacing genetic polymorphism by physiological adaptation).

The concept of a general-purpose genotype was defined by Baker (1965) to describe the life history syndrome associated with weedy species of plants. He defined it as a genotype characterized by the ability to grow in a multitude of climates and edaphic situations, i.e. a genotype with broad environmental tolerance. Baker’s original description was explicitly comparative: colonizing species of weeds were more tolerant of physical stresses, more plastic in flowering phenology, more likely to have vigorous vegetative growth, and more likely to be self-compatible or apomictic than their closest non-colonizing relatives.

Soon after, allozyme studies revealed that many parthenogenetic taxa are composed of multiple clones (Solbrig 1971; Hebert 1974; Lokki et al. 1975, 1976; Parker and Selander 1976; Saura et al. 1976a, b; Vrijenhoek et al. 1977, 1978). How did these findings bear on the concept of a GPG?

A simple model (Fig. 6.1) for the evolution of GPGs was articulated by Parker et al. (1977). While selection in sexual populations acts primarily on individual genes with small additive effects, selection among clones acts on epistatic interactions within composite genotypes. The continuous generation of new clones from sexual ancestors would favor the persistence of clones that can survive in all environments – i.e. genotypes with broad ecological tolerance. The key idea in this model was that the geometric mean of fitness (replacement rate) had to be greater than zero for clonal lineages to persist. It was not necessary that a successful clone should have the highest fitness in all environments, only that it can survive in the most environments. Lynch (1983) advanced a similar argument, but the model

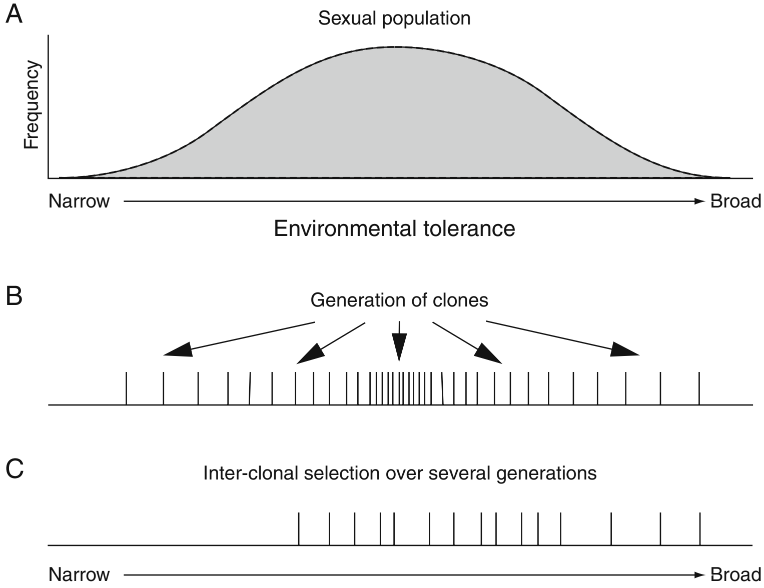

Fig. 6.1 The origin of general purpose genotypes in colonizing parthenogenetic taxa (adapted from Niklasson 1995). **(a)** A sexual population that varies in the range of tolerances (*narrow* to *broad*) that individual genotypes have for a particular form of environmental stress. **(b)** A range of genotypes is frozen among clones produced by the sexual ancestor. **(c)** Natural selection over several generations fixes clones with wider than average tolerance

focused on mutations within clonal lineages as the primary source variation (Lynch 1985; Lynch and Gabriel 1987) rather than multiple origins of clones from sexual progenitors. The race to improve fitness within a clonal lineage may be compromised over the long term, however, by mutational meltdown (Lynch et al. 1993). Multiple origins of clones from genetically variable sexual ancestors, on the other hand, have been demonstrated experimentally to create new genotypic combinations that exhibit considerable fitness variance and opportunities for interclonal selection (Annest and Templeton 1978; Wetherington et al. 1989b). Templeton (1982) emphasized a radical shift in the unit of selection that accompanies clonal origins – from individual genes in sexual progenitors to whole genomes in clonal populations – which could result in distinct evolutionary trajectories for closely related parthenogenetic and sexual lineages under identical environmental conditions. Multiple origins of clones from genetically variable sexual ancestors are now well established for many asexual taxa (White 1978; Parker 1979; Vrijenhoek 1979; Suomalainen et al. 1987; Hebert et al. 1989; Moritz et al. 1989). Occasionally "hopeful monsters" (*sensu* Goldschmidt 1940) with wide environmental tolerances may arise among new clones. Consequently, the capacity of parthenogens to generate robust and flexible physiologies "cheats the system," because polyphyletic clones generated by recombination in the immediate sexual ancestors creates the variation on which inter-clonal selection acts to produce GPGs.

6.2.1 Elevated Ploidy and Hybridity

Elevated ploidy and hybridity both have been invoked as rapid means to evolve broadly tolerant genotypes, but these genetic phenomena are often confounded in parthenogens, making it difficult to disentangle their contributions to fitness (Parker and Niklasson 2000; Lundmark and Saura 2006). Vandel (1940) suggested that geographical parthenogenesis was a direct consequence of selection for larger and more robust polyploids in extreme environments. Polyploid races of the terrestrial isopod, *Trichoniscus*, are distributed in cooler and drier habitats than their diploid sexual relatives (Vandel 1928). Polyploid races of the curculionid weevil, *Otiorrynchus*, are more cold tolerant than their smaller sexual relatives (Lindroth 1954). Apparently, the larger body sizes of polyploids allow them to occupy more extreme environments in the north of Europe, but many of these polyploids also are hybrids, so heterosis might be involved. A few appear to be autopolyploids, however, lending credence to Vandel's idea that elevated polyploidy alone may be a sufficient explanation for geographical parthenogenesis (Lundmark and Saura 2006).

Kearney (2005) argued that selection for the stabilization of hybrid genotypes is more important than polyploidy or all-female reproduction per se. Essentially all parthenogenetic vertebrates and many parthenogenetic insects are inter-specific or inter-populational hybrids; thus clonal reproduction has been viewed as a means for preserving heterotic or intermediate genotypes (White 1970; Schultz 1971). Elevated heterozygosity is evident in many parthenogenetic animals (reviewed in Vrijenhoek 1990), and the physiological breadth of some unisexual-hybrid fish (*Poeciliopsis monacha-lucida* and *Phoxinus eos-neogaeus*) and a frog (*Rana esculenta* = *R. ridibunda-lessonae*) was interpreted by several researchers as evidence for heterosis (Bulger and Schultz 1979; Tunner and Nopp 1979; Schlosser et al. 1998). Nevertheless, experimental studies with *Poeciliopsis monacha-lucida* did not reveal evidence for "spontaneous heterosis" in laboratory-synthesized hybrids (Wetherington et al. 1987). However, enhanced larval growth rates and size at metamorphosis in laboratory-synthesized *Rana ridibunda-lessonae* hybrids was interpreted as evidence for heterosis (Hotz et al. 1999). It is difficult to generalize from so few experimental studies. More studies are obviously needed, but caution should be exercised in interpreting the results from such studies, because enhanced performance of hybrids for some life history and somatic traits does not necessarily translate into enhanced fitness (euheterosis) – witness the sterile mule.

Parthenogenesis has also been viewed as a means to preserve hybrid phenotypes that are optimally adapted to transitional habitats (ecotones) between the ranges of the sexual progenitors (Wright and Lowe 1968; Moore 1977). Hybrid intermediacy differs from the heterosis hypothesis, because it does not view hybrids as superior; instead, it views hybrids as inferior competitors within the ranges of their progenitors. Thus, parthenoforms are thought to persist as ecological fugitives that escape competition by occupying marginal habitats, which are likely to be intermediate for hybrids (Moore 1984). The geographical distribution of allodiploid and allotriploid *Poeciliopsis* within and between river systems is broadly consistent with this view (Moore et al. 1970; Thibault 1978). Nonetheless, the hybrid intermediacy hypothesis fails to account for stable coexistence of multiple clones in geographically intermediate habitats (see Moore 1984 for a discussion of this issue).

6.2.2 Evidence for General Purpose Genotypes

Evidence for and against the GPG model comes from two sources: (1) field and experimental studies that compare parthenogenetic taxa with their closest sexual relatives (summarized in Table 6.1); and (2) comparative population genetic and phylogeographic studies of parthenogenetic taxa that focus mainly on local differentiation versus wide geographic ranges of clones (summarized in Table 6.2). We present cases that illustrate the range of conclusions derived from different taxa and from varying criteria used to define generalist versus specialist clones. Many of the cited authors produced earlier papers on this subject, which can be accessed from the papers we cite.

Experimental and observational studies (Table 6.1) offer mixed support for the GPG model. Acute tolerance to stress and performance across a range of environments (breadth of tolerance) are both criteria for GPG's (Baker 1965). Ideally, direct ecological or physiological comparisons should be made between parthenogens and their closest sexual relatives, but in some cases (*Artemia*, *Octolasion*, *Sitobion*) this was not possible, due to the lack of a known sexual ancestor. In some comparisons, males were found to be less tolerant, but sexual and parthenogenetic females races showed no consistent differences (*Pycnoscelus*, *Nemasoma*). The studies on *Antennaria* illustrate one of the most powerful experimental designs to test the GPG hypothesis. Ramets of sexual and apomictic genotypes were reared under several temperature and desiccation regimes, and performance was plotted against mean performance of all the genotypes in these environments. This method of joint-regression (Bierzychudek 1989; Michaels and Bazzaz 1989) is optimal for testing the GPG model, but it requires replicated sexual genotypes, which limits the design to plants and a few animal groups in which researchers can experimentally clone sexually produced genotypes. Genotypes that show a "flatter" response to environmental sources of variance than the mean of all genotypes can then be argued to be "generalists".

Two problems often occur with claims that geographically widespread parthenogens are GPGs (Table 6.2). First, parthenogens should be examined genetically to determine whether their distribution is comprised of many independent clonal genotypes or a single clonal lineage. The second problem lies in the evolutionary ages of clonal lineages. A geographically widespread clone might have evolved very recently to occupy a narrow but universally available niche and depend on human transport or habitat disruption (Vrijenhoek 1979). Many of the cases in Table 6.2 involve aphid pests of crop plants (see also Chapter 25). These pests have spread with human assistance, even to new continents, during the last few hundred years. In these cases, wide distributions of particular clones could be random consequences of serendipitous introductions (cf. Fenton et al. 1998; Delmotte et al. 2002;

Table 6.1 Experimental and observational evidence for and against the general purpose genotype hypothesis in parthenogenetic taxa

Order: family	Taxon	Mode[a]	Character	Evid[b]	Comments	References
Annelida						
Haplotaxida Lumbricidae	*Octolasion tyrtaeum*	P	Distribution across soil types and forest types	+	Two dominant clones distributed in all habitats. Frequencies not correlated with soil texture or pH. Rare clones at a few localities. No evidence for differentiation between dominant clones	Jaenike et al. (1980)[c]
Arthropoda						
Anostraca Artemiidae	*Artemia pathenogenetica*	P	Salinity and thermal tolerance	–	Thelytokes have narrower tolerance than sexual species for salinity and temperature. Differences between 2N and 4N thelytokes from the same population. Sexual ancestors are unknown	Browne and Wanigasekera (2000)
Cladocera Daphniidae	*Daphnia pulex*	P	Salinity and thermal tolerance	±	Permanent ponds have reduced clonal diversity implying selection for generalist clones. No significant differences between obligate clones and sexually produced clones in sensitivity to salinity stress. Sexuals less sensitive to thermal stress	Lynch (1983) and Weider (1993)
Acariformes Penthaleidae	*Penthaleus major*	P	Spatial distribution	–	Clonal diversity decreases toward population margin, but no evidence that a general-purpose clone increases in frequency at margins	Robinson et al. (2002)
Julida Nemasomatidae	*Nemasoma varicorne*	P	Desiccation resistance	–/?	Males of sexual race less tolerant than females. Differences between sexual and clonal females inconclusive	Enghoff (1976) and Hoy Jensen et al. (2002)
Coleoptera Curculionidae	*Otiorrhynchus dubius*	P	Thermal tolerance	+	3N thelytokes are larger and more cold tolerant than 2N sexuals	Lindroth (1954)
Dictyoptera Blaberidae	*Pycnoscelus surinamensis*	P	Life history traits and desiccation resistance	–	Fertility and viability differences among clones consistent with FNV hypothesis. Sexual *P. indicus* males less tolerant than females. Highly tolerant sexual race in lab for over 30 years	Niklasson and Parker (1994), Parker and Niklasson (1995) and Gade and Parker (1997)

Table 6.1 (continued)

Order: family	Taxon	Mode[a]	Character	Evid[b]	Comments	References
Hemiptera Aphididae	*Myzus persicae*	P	Host plant associations and performance	±	Predominant clones do not segregate by host plants in Scotland. No difference in geometrical mean fitness between obligate and cyclical parthenogens across experimental host plants	Fenton et al. (1998), Vorburger et al. (2003a)
	Sitobion avenae	P	Host plant performance	+	Two dominant clones on all host plants in two successive years in France. Agricultural practices may have favored generalist clones	Haack et al. (2000)[c]
Ostracoda Cyprididae	*Heterocypris incongruens*	M	Salinity and thermal tolerance	–	Four clones identified across two Belgian population samples. No evidence for GPG clones, but may be consistent with FNV model	Van Doninck et al. (2002)
Darwinulidae	*Darwinula stevensoni*	P	Salinity and thermal tolerance	+	Several clones from European sites have broad tolerance to environmental stresses, though some differences exist among geographical clones	Van Doninck et al. (2002)
	Penthesilenula brasiliensis	P	Salinity and thermal tolerance	+	Widespread species with broad salinity tolerance	Van Doninck et al. (2003)
	P. aotearoa	P	Salinity and thermal tolerance	–	Limited distribution and salinity tolerance	Van Doninck et al. (2003)
	Vestalenula molopoensis	P	Salinity and thermal tolerance	–	Limited distribution and salinity tolerance	Van Doninck et al. (2002)
Chordata						
Anura Ranidae	*Rana esculenta*	H	Asymmetric competition, GxE interactions	±	Crowding and competition affect hybridogenetic *R. esculenta* less than sexual *R. lessonae*, but fitness of individual hemiclones is strongly habitat dependent	Semlitsch (1993) and Semlitsch et al. (1997)
Cypriniformes Cyprinidae	*Phoxinus eos-neogeneus*	G/H	Spatial distribution, tolerance of hypoxia	±	Widespread single clone outperforms related sexuals under hypoxic conditions, leading to partial niche segregation. Situation is complicated by 2N/3N mosaicism	Elder and Schlosser (1995), Schlosser et al. (1998), and Doeringsfeld et al. (2004)

Table 6.1 (continued)

Order: family	Taxon	Mode[a]	Character	Evid[b]	Comments	References
Cyprinodontiformes Poeciliidae	*Poeciliopsis monacha-lucida* complex	H/G	Thermal tolerance	±	2N hemiclones exceed parental sexual forms, but 3N gynogenetic clones vary among one another in survival of thermal stresses	Bulger and Schultz (1979)
	P. monacha-occidentalis	H	Thermal tolerance	–	Hybridogens do not exceed parental sexual species for thermal tolerance	Bulger and Schultz (1982)
Squamata Teiidae	*Aspidoscelis tesselatus*	P	Physiological	–	Parthenogens do not exceed sexual relatives for burst speeds and endurance	Cullum (1997)
Gekkonidae	*Heteronotia binoei*	P	Physiological, reproductive, geographical	–	Parthenogens do not exceed sexual relatives for burst speeds but have greater endurance. Parthenogens more cold tolerant but have greater water loss, a higher standard metabolic rate, and lower fecundity than sexuals. Geographic range of parthenogens is broader than sexuals but "environmental niche" may be narrower	Kearney and Porter (2004), Kearney and Shine (2005) and Kearney et al. (2005)
Mollusca						
Neotaenioglossa Hydrobiidae	*Potamopyrgus antipodarum*	P	Salinity tolerance, feeding rate, growth and reproduction	±	Introduced European populations exhibit wide tolerance and relatively constant fitness ranks across a range of environments. No sexuals present	Jacobsen and Forbes (1997) and Dybdahl and Kane (2005)
Magnoliaphyta						
Asterales Asteraceae	*Antennaria parlinii*	A	Light and nutrient gradients	±	Apomicts respond more evenly across range of nutrients, but sexuals better at some treatments	Michaels and Bazzaz (1989)
	A. parvifolia	A	Desiccation and thermal tolerance	+	Apomicts less sensitive to variation in environmental conditions than sexuals	Bierzychudek (1989)
	Erigeron annuus	A	Competition and shading	–	Apomict performed no better across experimental treatments than sexual relative *E. philadelphicus*	Kenny (1996)

[a] Reproductive mode: A = apomictic; G = gynogenesis; H = hybridogenesis; P = thelytoky or obligate parthenogenesis; M = mixed sexual and apomictic parthenogenesis.

[b] Evidence: + is positive; – is negative; and ? is equivocal.

[c] No direct comparisons made with a sexual ancestor (see text).

Table 6.2 Phylogeographic evidence for and against the GPG hypothesis for parthenogenetic taxa

Order: family	Taxon	Mode[a]	Marker(s)	Evid[b]	Comments	References
Arthropoda						
Hemiptera Aphididae	*Diuraphis noxia*	P	Microsatellites	–	No widespread clones across 38 localities in Iran. High population structure, with $F_{ST} = 0.23$	Dolatti et al. (2005)
	Myzus persicae	P	Microsatellites	+	Two clones among obligate parthenogens in Victoria, Australia. Low population structure, with $F_{ST} = 0.021$	Vorburger et al. (2003b)
	Rhopalosiphum padi	P	Allozymes, microsatellites	+/?	Widespread clones persist over 4 years in S. France. Clones sampled from various host plants, but no data on host range	Delmotte et al. (2002)
	Sitobion miscanthi, *S. fragariae*	P	Microsatellites, SSCP	+/?	Both geographic partitioning and widespread clones in New Zealand	Wilson et al. (1999)
	*S.*miscanthi, *S. fragariae*	P	Microsatellites	+	Single dominant clones within 4 chromosomal races of *S. miscanthi,*one clone of *S. fragariaei* in Australia	Sunnucks et al. (1996)
Julida Nemasomatidae	*Nemasoma varicorne*	P	AFLPs	+	Single monophyletic clone in Denmark, England and Poland; >30% sequence divergence from closest potential sexual ancestor (see text)	Hoy Jensen et al. (2002)
Ostracoda Cyprididae	*Heterocypris incongruens*	M	Allozymes	+/?	Multiple clones are found, but a single clone dominates 66% of the localities (mostly rice fields) sampled in N. Italy. Is widespread clone a rice field specialist?	Rossi et al. (2006)
Darwinulidae	*Darwinula stevensoni*	P	mtDNA, ITS1	+	Ancient worldwide asexual species with a single ITS1 sequence but 3.8% mtDNA sequence divergence among lineages. Lives in wide range of aquatic habitats	Schön et al. (1998)
	Microdarwinula zimmeri	P	Clonal diversity not reported	+/?	Associated with mosses on four continents	Van Doninck et al. (2003)

Table 6.2 (continued)

Order: family	Taxon	Mode[a]	Marker(s)	Evid[b]	Comments	References
	Penthesilenula brasiliensis	P	Clonal diversity not reported	+/?	Found on four continents in springs, ponds and lakes.	Van Doninck et al. (2003)
	P. aotearoa	P	Clonal diversity not reported	–	Only known from type locality in Brazil	Van Doninck et al. (2003)
	Vestalenula molopoensis	P	Clonal diversity not reported	–	Restricted to dolomite springs in S. Africa	Van Doninck et al. (2003)
Chordata						
Squamata Teiidae	*Aspidoscelis tesselata*	P	Allozymes	+	One multi-locus 2N genotype at 12 of 18 localities ranging across 1000 km	Parker and Selander (1976)
			Skin grafts	+	One histocompatibility clone across nearly entire range of the 2N race	Maslin (1967)
Mollusca						
Neotaenioglossa Thiaridae	*Melanoides tuberculata*	P	mtDNA	+	Two haplotypes co-occur in all freshwater habitats on French Polynesian Islands	Myers et al. (2000)
Cnidaria						
Actiniaria Edwardsiidae	*Nematostella vectensis*	P	RAPDs, AFLPs	±	Single dominant clone (= 61% of population) in S.E. England, but regional population structure in New England, USA	Pearson et al. (2002) and Darling et al. (2004)

[a] Reproductive mode: A = apomictic; G = gynogenesis; H = hybridogenesis; P = thelytoky or obligate parthenogenesis; M = mixed sexual and apomictic parthenogenesis.
[b] Evidence: + is positive; – is negative; and ? is equivocal.

Vorburger et al. 2003b). Other cases involving "natural" post-Pleistocene dispersals provide more convincing evidence for the long-term persistence of one or a few clonal genotypes (Hoy Jensen et al. 2002). However, wide distributions of individual clones (superclones according to Vorburger et al. 2003b) following recent colonization events suggests that these clones have characteristics of GPGs, because they must have survived temporal fluctuations between generations to be dispersed over such wide areas.

The GPG model for geographic parthenogenesis has considerable appeal, but mixed support in the literature. Given the various ways in which parthenogenesis evolves (hybridization, polyploidization, spontaneously, by infection, etc.) and the differing ages of parthenogenetic lineages, it is not surprising that a diversity of patterns can be found. The prevalence of polyploid and hybrid genotypes among parthenogens does not negate the generality of this model. It only suggests that multiple processes in addition to post-formational mutations can generate the fitness variation that allows natural selection to fix GPG's, but the same is true for specialist genotypes under the FNV model (below). In this sense polyploidy and hybridization should be viewed as sources of variation that can drive the phenotypic evolution of asexual populations, rather than the *raison d'être* of parthenogenesis (cf. Kearney 2005, 2006; Lundmark 2006). Regardless of the ways in which broadly tolerant genotypes may evolve, clonal reproduction provides the additional benefit of reducing fitness costs associated with meiosis and the production of "unbalanced genomes" (Parker and Niklasson 2000).

6.3 Frozen Niche-Variation (FNV)

When organisms colonize open habitats with low species diversity, they often expand their phenotypic distribution and niche breadth, a phenomenon called "ecological release" (MacArthur and Wilson 1967). Sexual reproduction impedes disruptive selection and niche diversification, because recombination forces offspring distributions to regress to the population mean. Selfing, assortative mating, limited dispersal, and chromosomal rearrangements are ways to counteract antagonistic recombination and foster diversification in sexual species (Wallace 1959; Maynard Smith 1962; Antonovics 1968). Parthenogenesis completely eliminates recombination; therefore, White (1970) suggested that new parthenogenetic lineages might be adapted to new ecological niches. Roughgarden (1972, p. 684) concluded from a modeling study that "an asexually reproducing population is capable of very rapid ecological release, . . . an important reason why asexual populations should be good colonists." The model partitions niche width into within- and between-phenotype components that contain (1) the breadth of resources used by each phenotype, and (2) the variety of phenotypes in the population. Given an adequate source of clonal variation, an asexual population should rapidly attain an optimal phenotypic distribution, because the between-phenotype component of niche width "is more malleable to the force of natural selection than in sexual populations" (Roughgarden 1972, p. 712).

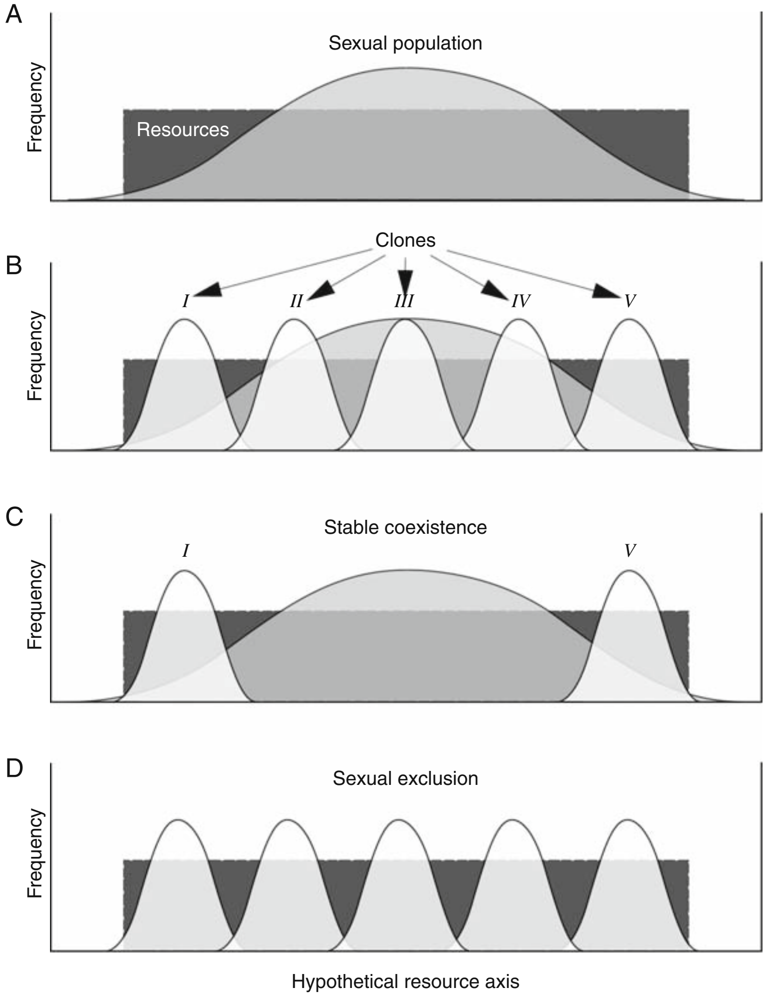

Fig. 6.2 Frozen Niche variation and asymmetric competition between new clones and their sexual progenitors. **(a)** A sexual population (*broad curve*) exhibits genetic variation for the utilization efficiency of a natural resource that is evenly distributed (*dotted line*). **(b)** A range of genotypes is frozen among clones produced by the sexual ancestor. **(c)** Natural selection rapidly eliminates clones that substantially overlap one-another and the centrally distributed sexual phenotypes, leading to stable coexistence if rate of clonal origins is not too high. **(d)** Too high a rate of clonal formation will eclipse resource use by the sexual ancestor and lead to its extinction

The Frozen Niche Variation model (Vrijenhoek 1979, 1984) was directly stimulated by Roughgarden's (1972) ideas and a need to explain the stable coexistence of *Poeciliopsis* fish clones in spatially heterogeneous desert streams (Vrijenhoek 1978). The model, as illustrated in Fig. 6.2, involves three stages: (1) multiple clones arising from genetically variable sexual ancestors provide frozen genotypic variation; (2) interclonal selection eliminates clones that significantly overlap the niches of established clones and the sexual progenitors; and (3) selection fixes an array of specialized clones that efficiently partition underutilized resources. A few specialized clones should be able coexist with a broad-niched sexual ancestor as long as the rate of clonal synthesis is not too high; however, " a broad panel of efficient specialist clones could competitively exclude the sexual host..." (Vrijenhoek 1979, p. 792).

Bell's (1982) Tangled Bank model led to a similar conclusion, but his goal was broader – to explain the maintenance of sex rather than the coexistence of clones. The idea stems from Weisman's (1889) view that the diversity generated by sex increases ecological efficiency. Phenotypic differences among sexual genotypes should decrease competition among siblings (Williams and Mitton 1973) and thereby increase the breadth of resources exploited by the population as a whole (Ghiselin 1974). The Tangled Bank model incorporated ideas about the maintenance of genetic diversity in multi-niche environments (Levene 1953; Strobeck 1974). Individual genotypes are regulated by density-dependent factors and imperfect competition within their respective subniches; therefore, rare genotypes suffer the least competition and fitness becomes frequency-dependent. Sexual recombination makes each individual unique and therefore rare and favored. Bell (1982, p. 131) concluded that a single specialized "clone cannot displace the sexual population from the whole of its ecological range ... [but] If the number of clones were as great as the number of sexual genotypes the sexual population would have no refuge ..." His conclusion was anticipated by empirical studies that showed how clonal diversity of *Poeciliopsis* hybridogens correlated with increased abundance of asexual fish relative to the sexual fish (Vrijenhoek 1979); however, a similar association has not been observed in hybridogenetic waterfrogs (Hotz et al. 1994).

Theoretical analyses have explored many aspects of the Tangled Bank and FNV models in fine- vs. course-grained environments and in temporally stable vs. fluctuating environments. Asymmetric competition - in which clones have a greater inhibitory effect on identical clone-mates than on genetically diverse sexual individuals – tends to facilitate coexistence, as long as the sexuals maintain a broader overall niche than that of the combined clones (Ghiselin 1974; Bell 1982; Case and Taper 1986; Koella 1988; Gaggiotti 1994; Lomnicki 2001). Clones lost due to genetic drift or temporal fluctuations in fitness can be replaced with new clones arising from the sexual ancestors, but the rate of clone-formation will influence the persistence time of sexuals and lead to their exclusion if clone-formation is too frequent (Vrijenhoek 1979; Bell 1982).

Computer simulations revealed that invasive clones initially exploit marginal resources, where competition from sexual relatives is weak, but eventually new clones exclude the sexuals from the center of the resource distribution, unless clone-formation is infrequent (Weeks 1993). Invading parthenogens should succeed best in ecologically marginal habitats where inter-specific interactions are weak, which is completely consistent with observations of geographical parthenogenesis (Gaggiotti 1994). Nonetheless, intraspecific competition under high density can prevent clones from realizing their two-fold advantage (Doncaster et al. 2000). Thus, competition with a reproductively isolated sexual species or among distinct clonal genotypes should be considered forms of inter-specific competition (Lomnicki 2001), and basic Lotka-Volterra dynamics apply. So again, we return to the critical role that asymmetrical competition plays in determining the window for coexistence among clones and their sexual progenitors, or among distinct clones (Pound et al. 2002). Treating clones as ecological microspecies with distinct life histories and niches results in different outcomes than the simpler models that assume "all else is equal" between completely replaceable sexual and clonal genotypes, consequently the persistence of sex may require much smaller advantages than previously thought (Tagg et al. 2005b).

6.3.1 Evidence for Frozen Niche Variation

Few experimental studies have tested the first premise of the FNV model – that ecologically relevant genotypic variation can be frozen among new clones when they arise. Schultz (1973) first demonstrated that different trophic morphologies could be frozen among hemiclones of *Poeciliopsis monacha-lucida* that he synthesized in the laboratory via crosses of *P. monacha* × *P. lucida*. Subsequent studies with additional synthetic *P. monacha-lucida* hemiclones demonstrated the capacity to freeze genotypic variation in life-history and reproductive traits (Wetherington et al. 1989b; Lima et al. 1996; Lima 2005) and in predatory behavior (Lima and Vrijenhoek 1996). Similar experiments might also be conducted with laboratory-synthesized strains of hybridogenetic *Rana esculenta* (see for example Hotz et al. 1999), with the pseudogamous leaf hopper *Muellerianella 2-fairmairei-brevipennis* (Drosopoulis 1978), and with tychoparthenogenetic *Drosophila mercatorum* (Annest and Templeton 1978). Laboratory clones generated from cyclically parthenogenetic aphids, cladocerans and rotifers might also be studied in this light, but we are not aware of such studies to date.

The second FNV premise – that inter-clonal selection weeds out new clones that substantially overlap the niche of established clones and the sexual ancestors – is harder to test. Stringent selection eliminates most newly formed tychoparthenogenetic clones of *Drosophila mercatorum* (Annest and Templeton 1978), but this results mostly from fitness penalties associated with complete homozygosity of these automictic strains. Unisexual-hybrid clones may also suffer fitness penalties due to genetic and developmental incompatibilities between the combining genomes (Vrijenhoek 1989a). More than half of the laboratory-synthesized *Poeciliopsis monacha-lucida* hemiclones mentioned previously had poor survival abilities, limited reproductive potential, and reduced developmental stability (Wetherington et al. 1987, 1989b). Nonetheless, a few of these strains performed as well as natural *P. monacha-lucida* strains, and the differences in life history, reproductive, behavioral, and trophic characters among these strains illustrate the scope for inter-clonal selection. Newly synthesized triploid-hybrid clones of *Taraxacum* closely resemble diploid sexuals in leaf size and phenology, which suggests that selection has shifted the ecological characteristics of natural triploid apomicts (de Kovel and de Jong 2000).

Indirect evidence for inter-clonal selection is found in seasonal shifts in the frequencies of cladoceran, ostracod and insect clones (Table 6.3). Generally, obligate parthenogenetic populations of these arthropods show lower clonal diversity than cyclical populations (Hebert 1974; Tomiuk and Wöhrman 1981; Llewellyn et al. 2003), which can be interpreted as evidence that inter-clonal selection has eliminated less fit and ecologically redundant clones. Extant clones in nature "can only be a minute fraction of those that have participated in the contest. The competitive exclusion principle should apply in the extreme... Occasionally [a new clone] succeeds and crowds out one or more of the older clones, wholly or partly. Thereafter the prevailing clones represent an even more select array." (Williams 1975, p. 29).

Many studies have shown that coexisting clones are not ecologically identical (Table 6.3), starting with the classical example in apomictic North American *Taraxacum* (Solbrig and Simpson 1974, 1977). Coexisting dandelion clones flourish under different disturbance regimes. One clone (A) was the majority type in disturbed fields and another clone (D) performed best in undisturbed fields. *Taraxacum* is more complex in Europe (see also Chapter 22), however, where higher clonal diversity results from hybridization between triploid apomicts and diploid sexuals (see Menken et al. 1995; de Kovel and de Jong 2000). Many of the studies listed in Table 6.3 were interpreted as support for the FNV model, whereas other studies sought to compare phenotypic distributions or niche breadths between closely related sexual and asexual forms. Asymmetric competition between narrow clones and ecologically broad sexual relatives has been reported for *Poeciliopsis*, *Aspidoscelis (Cnemidophorus), Rana* and *Alsophila*. Differences in trophic morphology, feeding behavior and diet exist among *Poeciliopsis* and *Aspidoscelis* clones, and life history differences exist among clones of *Heterocypris*, *Poeciliopsis*, *Rana* and *Taraxacum* clones. Host plant associations differ among *Brevipalpus*, *Uroleucon* and *Alsophila*. Clones segregate spatially along environmental gradients in *Lumbricillus*, *Penthaleus, Artemia*, *Trichoniscus*, *Poeciliopsis*, *Aspidoscelis*, *Lepidodactylus*, *Potamopyrgus,* and *Asplanchna*, and different clones exhibit unique tolerances to hypoxic and thermal stress in *Daphnia*, *Poeciliopsis*, *Rana*, and *Lepidodactylus*. Finally, temporal frequencies vary among clones of *Daphnia*, *Heterocypris*, *Dipsa*, *Trichoniscus*, and *Asplanchna*.

6.4 Evolution of Generalist Versus Specialist Clones

None of the geographically widespread clones listed as GPGs in Table 6.2 are sperm-dependent hybridogens or gynogens. True parthenogens can escape direct competition with their sexual progenitors, and their ability to disperse and colonize new habitats is greatly facilitated by not having to produce males or find mates. Consequently, some researchers view parthenogens as "weedy" species (sensu Baker 1965) –i.e., inferior competitors that can only thrive as fugitives in marginal or disturbed habitats where competition with sexual relatives is minimal (Lowe and Wright 1966; Cuellar 1977). A generalist should be favored under these conditions

Table 6.3 Experimental and observational evidence for and against the FNV hypothesis for parthenogenetic taxa

Family	Taxon	Mode[a]	Characters	Evid.[b]	Comments	References
Annelida Haplotaxida Enchytraeidae	*Lumbricillus lineatus*	G	Spatial segregation	+	Clonal genotypes segregate along salinity gradients in the littoral zone of Danish fjords	Christensen (1980)
Arthropoda Acariformes Penthaleidae	*Penthaleus major*	P	Spatial and temporal segregation	+	Environmental heterogeneity effects relative fitness of clonal genotypes. Intense selection maintains clonal diversity	Weeks and Hoffmann (1998)
Tenuipalpidae	*Brevipalpus phoenicis*	P	Host plant associations	+	Clones are specialized. Fitness reduced when clones moved to alternative host plants	Groot et al. (2005)
Anostraca Artemiidae	*Artemia salina* complex	P	Life history, physiology, spatial segregation	+	Extremely high clonal diversity. Sexuals are not known. Clones differ in key life history traits and segregate along salinity gradients	Browne and Hoopes (1990) and Barata et al. (1996)
Cladocera Daphniidae	*Daphnia magna*	P	Temporal distribution, physiology	+	Seasonal changes in clone frequencies; thermal differentiation. Individual clones constrained to narrower niche	Hebert (1974), Hebert and Crease (1980), Carvalho (1987) and Hebert et al. (1988)
	D. obtusa	P	Competitive abilities, experimental evidence	+	Genetically diverse clones have competitive advantage when invading a genetically uniform population	Tagg et al. (2005a)
	D. pulex	P	Temporal and spatial segregation, physiology	+	Physiological differences and spatial segregation among clones. Seasonal changes in clone frequencies. Higher clonal diversity in temporary ponds may favor specialized genotypes	Lynch (1983), Weider and Hebert (1987), Weider (1989) and Weider (1993)
			Competitive abilities, experimental evidence	+	Genetically diverse clones experience competitive release (higher birth rates) when competing with uniform population vs. competing with themselves	Tagg et al. (2005b)
	D. pulicaria	M	Spatial and temporal segregation	+	Habitat partitioning and microhabitat specialization of clones in response to fish predation	Hembre and Megard (2006)

Table 6.3 (continued)

Family	Taxon	Mode[a]	Characters	Evid.[b]	Comments	References
Ostracoda Cyprididae	*Heterocypris incongruens*	M	Temporal distribution, life history	+	Recurrent frequency shifts among clones that differ in growth rates, survival and reproductive characteristics	Rossi and Menozzi (1993)
Coleoptera Curculionidae	*Ips acuminatus dubius*	G	Spatial segregation	+	Niche differentiation between gynogens and sexual hosts	Løyning (2000)
Diptera Lonchopteridae	*Dipsa bifurcata*	P	Temporal distribution	+	Seasonal changes in clone frequencies are synchronous among populations	Niklasson et al. (2004)
	Loncoptera dubia	P	Temporal distribution	+	Seasonal changes in clone frequencies	Ochman et al. (1980)
Lepidoptera Geometridae	*Alsophila pometaria*	G	Asymmetric competition, host plant associations	+	High clonal diversity. Sexuals present. Individual clones have narrower niche than sexuals. Dominant clones associated with particular tree stands	Mitter et al. (1979), Futuyma et al. (1981), Futuyma et al. (1984) and Harshman and Futuyma (1985)
Hemiptera Aphididae	*Uroleucon rudbeckiae*	P	Host plant associations	+	Fitness of clones varies across host-plant species and across host plant phenotypes	Service and Lenski (1982) and Service (1984)
Isopoda Trichoniscidae	*Trichoniscus pusillus*	P	Temporal and spatial segregation, physiology	+	Temporal changes in clone frequencies. Clones differ in moisture tolerance and distribution along moisture gradients	Christensen (1979), Christensen and Noer (1986) and Christensen et al. (1988)
Chordata						
Anura Ranidae	*Rana esculenta*	H	Asymmetric competition, life history, thermal physiology, GxE interactions	±	Life history and thermal differences among hemiclones. GxE interactions among hemiclones. Hemiclonal mixtures outperform single clones in competition experiments. No correlation between clonal diversity and abundance relative to sexuals	Hotz et al. (1994), Rist et al. (1996) and Negovetic et al. (2001)
Caudata Ambystomidae	*Ambystoma jeffersonianum* complex	G	Asymmetric competition	+	Larvae of gynogenetic triploids more adversely affected by competition with sexuals than vice versa	Wilbur (1971)

Table 6.3 (continued)

Family	Taxon	Mode[a]	Characters	Evid.[b]	Comments	References
Atheriniformes Atherinidae	*Menidia clarkhubbsi*	G	Spatial segregation	+	3N gynogens and 2N sexuals may segregate partially on salinity gradients. Differences among 3N clones not assessed	Echelle and Echelle (1997)
Cypriniformes Cyprinidae	*Squalius alburnoides*	H/G	Spatial segregation, morphology, diets	±	3N females in shallower, high velocity, water than 2N sexuals. Differences among clones not assessed, but ploidy levels appear to have same dietary niches	Martins et al. (1998) and Gomes-Ferreira et al. (2005)
Cyprinodontiformes Poeciliidae	*Poeciliopsis monacha-lucida*	H	Spatial segregation, life history, GxE interactions behavior, diet	+	Coexisting hybridogenetic hemiclones differ in trophic and aggressive behavior, diets, disease resistance, microhabitat use, and growth rates	Schenck and Vrijenhoek (1986), Schultz and Fielding (1989), Wetherington et al. (1989a), Weeks et al. (1992) and Leberg and Vrijenhoek (1994)
			Competition experiments	±	Mixed clones outperform single clones in competition with sexuals. Sexuals have wider niche than single clones but not greater than clonal mixture	Weeks (1995)
	P. 2 *monacha-lucida*	G	Asymmetric competition, physiology, diet, spatial segregation	+	3N clones segregate along stream gradients, and differ in survival of thermal and hypoxic stresses. Within-phenotype component of dietary breadth narrower in clones than sexual relatives	Vrijenhoek (1978), Vrijenhoek and Pfeiler (1997) and Gray and Weeks (2001)
Squamata Teiidae	*Aspidoscelis tesselatus*	P	Asymmetric competition, spatial distribution	+	Clones segregate into different habitats. Removal experiments indicate that sexuals have small inhibitory effect on asexuals but not *vice versa*	Scudday (1973) and Price (1986)
	A. sonorae	P	Asymmetric competition, diet	+	Sexual, *A. tigris*, has greater between-individual variation in diet than parthenogens. Both have similar within-individual diet breadth	Case (1990)

Table 6.3 (continued)

Family	Taxon	Mode[a]	Characters	Evid.[b]	Comments	References
Gekkonidae	*Lepidodactylus lugubris*	P	Spatial segregation, physiology	+	Clones differ in thermal preferences and geographical distribution	Bolger and Case (1994) and Radtkey et al. (1995)
Mollusca Neotaenioglossa Hydrobiidae	*Potamopyrgus antipodarum*	P	Spatial distribution, morphology, life history	+	High diversity of 3N clones. Sexuals present. Individual clones express narrower phenotypic variation than sexuals. Clones differ in size, morphology and life history traits. Common clones typically found in one habitat	Fox et al. (1995), Jokela et al. (1997) and Jokela et al. (2003)
Platyhelminthes Tricladida Planariidae	*Schmidtia polychroa*	G	Spatial segregation	+	Weak niche differentiation between sexuals and parthenogens in Italian lake	Weinzierl et al. (1999)
Rotifera Ploima Asplanchnidae	*Asplanchna brightwelli* and *A. girodi*	P	Temporal and spatial segregation, life history	+	Experimental evidence for strong interclonal competition between clones adapted to environments separated in time and space	Snell (1979)
Magnoliaphyta Asterales Asteraceae	*Taraxacum officinal*e	A	Life history, GxE interactions	+	Dominant N. American clones differ in competitive and reproductive abilities. Coexistence related to environmental disturbance	Solbrig (1971), Solbrig and Simpson (1974) and Vavrek et al. (1996)
	Erigeron annuus	A	GxE interactions		Differential performance of clones across environments	Stratton (1994)
Myrtales Onagraceae	*Oenothera lanciniata*	H	Asymmetric competition	+	Clonal diversity is higher when asexuals do not compete locally with sexuals	Ellstrand and Roose (1987)

[a] Reproductive mode: A = apomictic; G = gynogenesis; H = hybridogenesis; P = thelytoky or obligate parthenogenesis; M = mixed sexual and apomictic parthenogenesis.

[b] Evidence: + is positive; - is negative; and ? is equivocal.

because fugitives experience a wide range of marginal conditions while dispersing (Parker et al. 1977), and because no premium exists on competitive abilities (Lowe and Wright 1966).

Sperm-dependant parthenogens, on the other hand, must live with a closely related sexual host that is likely to be similar ecologically (reviewed in Beukeboom and Vrijenhoek 1998). Unless the unisexual form is constrained by a unique carrying capacity or by mating behaviors that limit its reproductive potential, the all-female form should eliminate its sexual host and thereby ensure its own demise (Clanton 1934; Moore 1975; Kawecki 1988). Coexistence is greatly facilitated by resource partitioning that diminishes direct competition between the sexual parasite and its host (Stenseth et al. 1985; Kirkendall and Stenseth 1990; Schley et al. 2004). Therefore, it is not surprising that essentially all of the sperm-dependant parthenogens listed in Tables 6.1 and 6.3 exhibit some degree of niche separation from their sexual hosts. Of course, many of the listed examples are hybrids, which may partially shift the ecological niche away from the progenitor it uses as a sexual host. Additionally, many of these sperm-dependant parthenogens (Table 6.3) exhibit evidence for phenotypic variation and resource partitioning among coexisting clones. Strong conspecific mate preferences by males of the sexual host limits sperm availability (Moore and McKay 1971). If sexual mating preferences regulate unisexuals below their carrying capacity, clones would compete for sperm rather than food and spatial resources. Such conditions might favor clonal generalists, but this does not appear to be the case for *Poeciliopsis* where multiple clones negatively impact the sexual population by occupying a wider range of subniches (Vrijenhoek 1979). Sperm-dependence and limitation are not necessary conditions for operation of the FNV model because many true parthenogens also have coexisting specialist clones (Table 6.3).

Sources of clonal variation may also play a role in determining the evolutionary trajectories of asexual populations. Spontaneous mutations affecting life history characters can accumulate in clonal lineages, but each new mutation must express itself against a genetic background that has a history of favorable selection, and thus phenotype effects may be limited (Lynch 1985). The within-phenotype component of niche breadth might slowly evolve in this way, but point mutations are not likely to be as effective as frozen variation in affecting changes in the between-phenotype component (Roughgarden 1972). Polyploidization, on the other hand, should be able to affect both components instantaneously as a result of genome duplications and subsequently as a result of genome reorganization and reduction. Hybrid origins, which produced all known chordate and many arthropod clones, adds another dimension to inter-clonal variation, because genomic interactions and dominance will play strong roles in generating phenotypic variation (Wetherington et al. 1989b). Finally, hybridization and polyploidy together have the capacity to create a tremendous variety of genotypes and corresponding phenotypes. Multiple origins of clones provides sufficient variation to drive both the FNV and GPG models (Parker et al. 1977). To the extent that variation exists in the sexual ancestors for the within-phenotype component of niche breadth, newly arising clones might also freeze differences in their tolerance to environmental conditions (Vrijenhoek

1979). Polyphyletic origins of clones simply increase the scope for natural selection among clones, but the trajectory taken by an asexual population will depend mostly on the competitive regime it encounters. Hard selection that is density- and frequency-independent should favor the evolution of GPGs in regions of low intra- and inter-specific competition; whereas soft selection that is density- and frequency-dependent should favor specialist clones in regions of high competition (Kenny 1996).

6.4.1 GPG and FNV Are Not Mutually Exclusive

Attempts to contrast the FNV and GPG models as mutually exclusive hypotheses ignore the complex interplay between spatial and temporal sources of variation in fitness. Simple contrasts of these models often cast the GPG model as focused only on factors that dampen temporal fluctuations in fitness, and the FNV model as focused only on spatial variance. Yet environments can vary in space and time, and different clones possess complex multivariate phenotypes that respond differentially to these sources of variance in fitness; thus, it is possible to have a clone with narrow trophic preferences and wide thermal tolerances, or *vice versa* (Vrijenhoek 1979, 1998a). A problem with many models for the maintenance of clonal diversity in time and space results from an extrapolation of genetic models to the ecology of clones (Tomiuk et al. 2004). Genetic models reveal that it is difficult to maintain allelic diversity under temporal variation in fitness, unless fitnesses are precisely balanced (Haldane and Jayakar 1963; Hedrick et al. 1976). Spatial heterogeneity is generally more conducive to maintaining diversity (Levene 1953; Strobeck 1970). Nonetheless, seasonal differences in fitness do appear to contribute to the maintenance of clonal diversity in *Taraxacum officinale* (Vavrek et al. 1996) and *Dipsa bifurcata* (Niklasson et al. 2004). Different clones of these organisms appear to be favored during different seasons, which can have profound effects on growth rates and diets that are affected by seasonal temperatures and food availability. As spatial and temporal fluctuations can both affect fitness variation, each clone should be considered a reproductively isolated microspecies with unique demographic properties (birth and death rates, diapause, immigration rates, etc.). Consequently, ecological models (e.g., Chesson 1985; Hedrick 1995; Pound et al. 2002) are likely to be more realistic than simple genetic models for explaining the coexistence of clones and the maintenance of sexual and asexual lineages.

Does the FNV model require recurrent origins of new clones? The *Poeciliopsis* example suggests that the opportunity for recurrent clonal origins drives the demographic success of hybridogenetic populations (Vrijenhoek 1979, 1984). Apparently this is not the case for *Rana esculenta*, as no correlation exists between clonal diversity and abundance (Hotz et al. 1994), but this problem should be addressed in other taxa. Nonetheless, essentially all the well-documented cases of ecological diversification among clones (Table 6.3) involve taxa that have extant sexual progenitors or cyclical progenitors. Elimination of the sexual progenitors or escape from their genetic influence reduces the sources of variation to mutation, which may be insufficient to drive rapid clonal differentiation.

6.5 Conclusions

The FNV and GPG models share a number of features. First, clonal diversity can be frozen during multiple origins of clones from genetically variable sexual ancestors. Second, newly formed clones will likely differ from one another in niche breadth, and depending on the competitive regime, inter-clonal selection will fix generalist or specialist genotypes by expanding the within- or between-phenotype components, respectively (Roughgarden 1972). The competitive regimes faced by new clones will likely be influenced by the ability of clones to escape competition from their sexual progenitors (sperm-dependence versus independence) and by the rate at which new clones are formed (mutation versus recurrent frozen variation). Although the GPG and FNV models are often portrayed as mutually exclusive hypotheses, this view is simplistic because the models, as originally stated, focused on different aspects of environmental variation in time and space. Now, the distinction between environmental heterogeneity in time and space has begun to blur as more robust ecological models are applied to these problems (Chesson 1985; Hedrick 1995). Finally, these ideas must be reconsidered in the light of “pluralistic” models for the maintenance of sex (e.g. West et al. 1999; Pound et al. 2004). Both generalist and specialist genotypes must survive rapidly evolving parasites, mutational deterioration, and an ever-changing environment. It is hard to imagine how genuinely ancient clones can persist with such multifarious threats, but apparently some have (Schön et al. 1998; Mark Welch and Meselson 2000). For the rest, it appears that the recurrent freezing of new clonal genotypes from extant sexual ancestors provides the diversity that allows asexual taxa to refresh their genotypes, spread to new locations and occupy new niches.

Acknowledgments The authors wish to thank the C. Patrick Doncaster and the editors for helpful suggestions and clarifications.

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