Niche breadth in clonal and sexual fish (*Poeciliopsis*): a test of the frozen niche variation model

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Abstract: The evolution and subsequent maintenance of sex has been debated for many years, and there are numerous aspects that remain poorly understood. When comparing sexual with asexual reproduction, there are many more apparent benefits to being asexual than sexual. The frozen niche variation (FNV) model describes how asexual clones can arise from a sexual population and how the two reproductive types can coexist. Herein we compared three sympatric populations of sexual and asexual fish (one sexual population, *Poeciliopsis monacha*, and two clonal populations, *P. 2-monacha-lucida*) to test the assumption of the FNV model that sexual populations have a broader dietary niche (as measured by gut contents analysis) than clonal populations. Individual sexual fish had similar dietary breadth when compared with clonal individuals. However, dietary breadth for sexual populations as a whole was broader than for either clonal population, indicating differences in between-individual dietary choice. Our results support the primary assumption of the FNV model and thereby provide a possible explanation for the maintenance of sexual reproduction in this clonal–sexual complex.

Résumé : L'origine et le maintien de la sexualité font l'objet de débats depuis de nombreuses années et il y a plusieurs aspects de la question qui sont encore mal compris. Il semble y avoir beaucoup plus d'avantages à la reproduction asexuée qu'à la reproduction sexuée. L'hypothèse du gel de la variation de la niche (FNV, « Frozen Niche Variation ») illustre comment des clones asexués peuvent surgir de populations sexuées et comment les deux types de reproduction peuvent coexister. On trouvera ici une comparaison de trois populations sympatriques de poissons sexués et asexués (une population sexuée, *Poeciliopsis monacha*, et deux populations clonales, *P. 2-monacha-lucida*) qui vise à vérifier les présuppositions du modèle FNV selon lesquelles la niche alimentaire des populations sexuées (mesurée par l'analyse du contenu du tube digestif) est plus étendue que celle des populations clonales. Les individus sexués ont une étendue de niche alimentaire semblable à celle des individus clonaux. Cependant, l'étendue de la niche de la population sexuée considérée dans son ensemble est plus grande que celles de l'une ou de l'autre des populations clonales, ce qui indique qu'il y a des différences de choix alimentaires entre les individus. Nos résultats sont en accord avec la présupposition fondamentale du modèle FNV et ils fournissent donc une explication possible au maintien de la reproduction sexuée dans ce complexe sexué–clonal.

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Introduction

The evolution of sex has intrigued scientists for many years, stimulating the generation of numerous arguments and theories about the origin and maintenance of sex (Williams 1975; Bell 1982; Kondrashov 1993). Asexually reproducing individuals require less energy, time, and resources than sexually reproducing individuals and can thus produce twice the number of offspring (Williams 1975). However, sexual repro-

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duction is still commonplace despite these apparently overwhelming advantages to asexual reproduction (Bell 1982).

There is an array of theories about the benefits to sex (Kondrashov 1993) but only two have gained widespread acceptance: the mutation accumulation hypothesis, wherein an asexual lineage slowly "melts down" because of its inability to purge deleterious mutations (Muller 1964; Kondrashov 1988; Lynch and Gabriel 1990), and the Red Queen hypothesis, wherein sexuality is advantageous for avoidance of rapidly evolving parasites and viruses (Bell 1982; Hamilton et al. 1990). Of the two, the Red Queen hypothesis has had the greatest empirical support (Dybdahl and Lively 1995; Jokela et al. 1997; Johnson 2000).

Although the Red Queen hypothesis has generally broad acceptance, one well-studied unisexual–sexual species complex, the topminnow *Poeciliopsis*, is not well explained by this model (Weeks 1996) but remains best explained by a third hypothesis: the frozen niche variation (FNV) model (Vrijenhoek 1979, 1984, 1994). In this model, sexuals are assumed to have a wider niche breadth than the clones, which should then translate to lower inter-individual competition among sexuals compared with that among clones (Bell

1982; Case and Taper 1986; Weeks 1993). Assuming such a difference in relative niche breadth, a sexual population can avoid replacement by a few clones by being able to use resources unavailable to the clones. In this model, genotypes are assumed to be "frozen" into clones by hybridization events between two closely related sexual species (Vrijenhoek 1979, 1984) or by random mutations within a single sexual population (Weeks 1993). Over time, there is assumed to be a constant extinction and rebirth of different clonal populations, and consequently, the clones are assumed to arise from polyphyletic origins (Vrijenhoek 1979, 1984). If the creation of viable clones is low enough, the random extinction of these clones is great enough, and the sexuals' niche is sufficiently broader than that of the clones, then the sexual populations can resist replacement even though they incur the twofold cost of sex (Weeks 1993). In many respects, the FNV model is similar to the Tangled Bank model, as outlined in Bell (1982; see also Case and Taper 1986).

Many of the assumptions and predictions of the FNV model have been successfully tested and confirmed (Vrijenhoek 1994). The recurrent production of clones has abundant empirical support in natural asexual populations (Uzzell 1964; Dybdahl and Lively 1995; Johnson and Bragg 1999). The assumption that the sexual ancestor(s) have considerable genetic variability for ecologically relevant traits, thereby allowing the freezing of ecologically distinct clones, has been thoroughly addressed using clonal and sexual populations of *Poeciliopsis*. Wetherington et al. (1989) found considerable among-individual genetic variation for size at birth, juvenile growth, and early reproduction among "hemiclones" that were artificially produced from two *Poeciliopsis monacha* populations. Schenck and Vrijenhoek (1986, 1989) found both spatial and dietary differences among sexual and clonal populations of two unisexual biotypes of *Poeciliopsis* in their native streams. Weeks et al. (1992) described differences in feeding behavior between two naturally co-occurring hemiclones and their sexual progenitors, which corresponded with natural differences in diets in field-caught fish.

The prediction that genotypic differences in ecologically relevant traits leads to niche partitioning in clonal and sexual populations has had mixed support. Vrijenhoek (1979) has shown that sexuals constitute a smaller proportion of *Poeciliopsis* populations in streams where clonal diversity is high relative to monoclonal streams, which is consistent with the notion that the clones are usurping a higher proportion of the "niche space" in populations where their combined resource breadth is largest. Semlitsch et al. (1997) found that mixed clonal populations performed better than single clonal populations of the hybridogenetic frog *Rana esculenta* in artificial ponds. However, Weeks (1995) found no evidence of niche partitioning in clonal and sexual populations of *Poeciliopsis* raised under high-density treatments in the laboratory. One possible explanation for this lack of partitioning is that the laboratory environment was not heterogeneous enough to allow significant niche partitioning (Weeks 1995). Nonetheless, the combined evidence suggests that genetically determined, ecologically relevant phenotypic differences among clonal lineages and between clones and sexuals are likely to facilitate coexistence between clonal and sexual populations, as predicted by the FNV model.

One of the critical assumptions of the FNV model is that sexuals should have a broader niche than a single clone (Vrijenhoek 1979, 1984, 1994). To date, this assumption has not been directly tested in the *Poeciliopsis* species complex (Vrijenhoek 1994). Herein we report the results of a dietary study of sexual and clonal *Poeciliopsis* collected from natural populations. We partition total dietary breadth into within- and between-individual components to test the assumption that sexual *Poeciliopsis* have a greater between-individual dietary breadth than coexisting clones.

Materials and methods

Fish strains and collection locations

Three *Poeciliopsis* (Atheriniformes: Poeciliidae) strains were analyzed in this experiment: an outcrossed sexual strain (*P. monacha* Miller) and two associated unisexual, triploid strains (*P. 2-monacha-lucida* MML/I and MML/II, hereafter referred to as Clone 1 and Clone 2, respectively; Vrijenhoek et al. 1977). The triploid *Poeciliopsis* reproduce gynogenetically, a strictly clonal mode of reproduction whereby the entire triploid genome is faithfully replicated among generations (Schultz 1969). Although sperm from a sexual species is required to activate embryogenesis in the triploid ova, paternal genes make no contribution to the genotype of the offspring (Schultz 1967; Cimino 1972; Vrijenhoek 1972). For further information on this reproductive complex, see Schultz (1969).

A total of 427 fish (80 Clone 1, 33 Clone 2, and 314 *P. monacha*) were collected from pools in the Arroyo de los Platanos region of the Rio Fuerte, Sonora, Mexico (26°30′N, 108°30′W; see Moore and Eisenbrey (1979) for further details of the region), during May 1990. During this time of year, the stream dries into small, isolated pools that are either completely isolated or are interconnected by only small rivulets of water. This isolation results in a number of pools that are essentially "closed systems," with only a slight amount of migration among pools (Moore and Eisenbrey 1979). Nine of the most isolated of these pools were chosen to maximize the likelihood that the fish measured from each pool were likely experiencing conditions in that pool rather than being migrants from nearby pools. The pools were aligned in a linear array, with Pool 1 at the head of the stream and Pool 9 about 1 km downstream. The intervening pools were scattered along this length, with at most several hundred metres separating one pool from the next (Weeks 1996). The number of fish of each strain collected at each pool was as follows: Pool 1, 18 Clone 1 and 32 *P. monacha*; Pool 2, 8 Clone 1 and 40 *P. monacha*; Pool 3, 12 Clone 1, 7 Clone 2, and 16 *P. monacha*; Pool 4, 10 Clone 1 and 40 *P. monacha*; Pool 5, 10 Clone 1, 8 Clone 2, and 32 *P. monacha*; Pool 6, 1 Clone 1 and 48 *P. monacha*; Pool 7, 4 Clone 1 and 40 *P. monacha*; Pool 8, 8 Clone 1 and 42 *P. monacha*; Pool 9, 9 Clone 1, 18 Clone 2, and 24 *P. monacha*. Because we wished to compare only pools with coexisting strains, we removed Pool 6 from the analyses, thus allowing a total of 378 fish (79 Clone 1, 33 Clone 2, and 266 *P. monacha*) to be analyzed in this study.

The fish analyzed in this comparison were previously used to compare clonal and sexual strains differing in external parasitism (Weeks 1996). In that experiment, the ovaries were removed for a comparison of reproductive health among parasitized and nonparasitized fish. In that project, care was taken to keep the intestinal tract intact. These fish were then stored individually in vials with 70% ethanol until the recent examinations were conducted on their intact intestinal tracts. Sexual type and clonal identity were determined in a previous study (Weeks 1996) via starch–gel electrophoresis of muscle tissue.

Table 1. Percentage of dietary items averaged across individuals and pools.

Dietary item	Clone 1	Clone 2	*P. monacha*
Algae	4.5	6.4	9.4
Other plants	3.4	1.7	4.6
Detritus	78.4	72.5	72.3
Nematodes	2.2	3.9	0.2
Trichopterans	1.4	1.4	2.5
Ephemeropteras	2.7	7.1	3.4
Chironomids	1.8	2.4	1.8
Other invertebrates	2.8	0.9	2.4
Adult fish scales	0.0	0.0	0.6
Whole *Poeciliopsis* juveniles	1.8	1.8	1.1
Terrestrial invertebrates	0.8	1.8	0.8
Aquatic invertebrates	0.3	0.2	0.9

Table 2. ANOVA of the natural log of within-individual dietary breadth (B) for all three fish strains.

Source	df	Sum of squares	F ratio	P value
Pools	7	7.271	14.773	0.0001
Fish strain	2	0.013	0.093	0.9112
Error	368	25.876		

Fig. 1. Within-individual dietary breadth (B) for the three fish strains averaged across pools. Error bars indicate two standard errors of the mean. Numbers above error bars are sample sizes.

Analysis of gut contents

Dietary analyses were conducted on females only (see Weeks 1996). A dissecting scope (Olympus SZH (Olympus of America, Inc., Mellville, N.Y.)) equipped with an ocular micrometer was used to examine the intestinal tracts of these fish. When the appropriate magnification was determined, the micrometer scale was calibrated to a metric scale. The length of the whole intestinal tract was measured and recorded and then was partitioned into sections of 100 μm. If the ending section was less than 50 μm, it was left attached to the previous 100-μm section. If the ending section was greater than 50 μm, it was analyzed as a separate section. All sections were opened and the contents were examined. The items found were then placed into one of 12 categories and given a proportion based on the volume of the intestinal tract occupied by that item in that 100 μm section of the intestinal tract. When all sections were examined, a weighted total proportion was computed for each dietary item. Thus, data consisted of the categories of food items consumed and their relative proportion (p) in the diet of each fish.

Statistical analyses

Within- and between-individual dietary breadth was estimated following the procedures outlined in Case (1990). The within-individual measures (B) were calculated using the Simpson Index (Simpson 1949). This measure was calculated for each fish within each strain and in each of the nine pools and is simply the inverse of the sum of the squared proportions (p) of all items consumed by an individual (i.e., $[\Sigma p_i^2]^{-1}$, where $i = 1$ to x and $x =$ total number of food items consumed; Case 1990). Natural log-transformed B values were normally distributed and thus were analyzed using parametric methods. B values were analyzed in a blocked one-way analysis of variance, using pools as the block and fish strains as the main effect (SAS 1985).

The between-individual dietary overlap values (α) were calculated using the proportion of the diet of a particular food item consumed by two fish of the strain in question, adjusted for the within-individual dietary breadth, B (Case 1990). Each individual fish within a strain was compared with all others in that strain using the following overlap calculation:
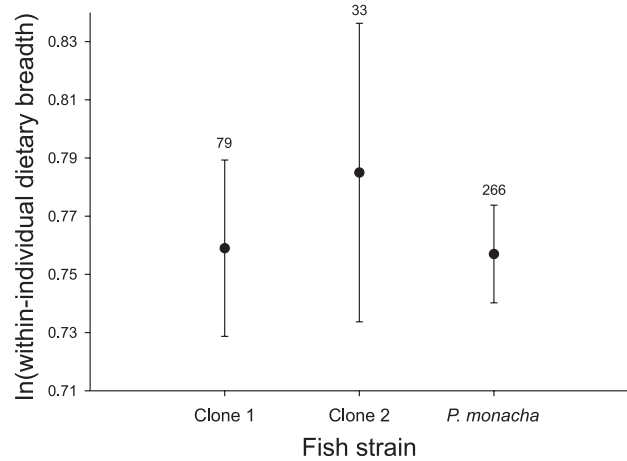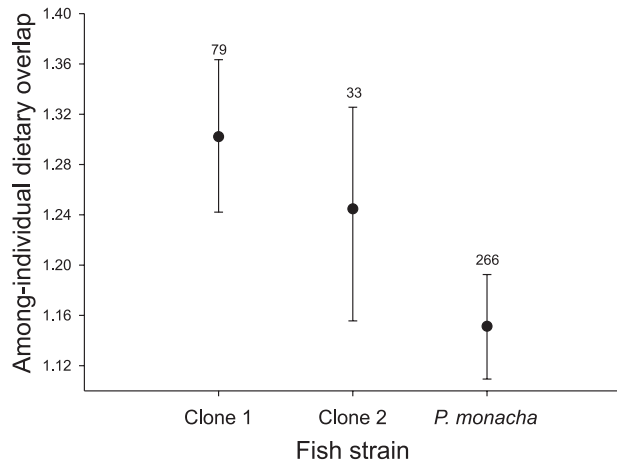
$$(1) \qquad \alpha_{l,j,k} = B_{j,k} \Sigma p_{i,j,k} p_{i,l,k}$$

The above calculation measures the dietary overlap of individual l with individual j in fish strain k by comparing the sum of the products of all i food items consumed (Case 1990). For example, in a population of 10 individuals, there would be 9 α's calculated per individual, for a total of 90 α's in the sampled population. Given this multiple set of calculations per individual, the α's are not conducive to parametric analyses (see Case 1990). Therefore, the overlap values generated using Case's procedure were compared using 95% confidence intervals generated using a bootstrapping procedure to produce a distribution of estimates for each fish strain (1000 runs; see Dixon 1993). Between-individual overlaps were constructed both within pools (for Clone 1 and *P. monacha*) and for all strains grouped across pools.

Results

Dietary items consumed by the three fish strains were grouped into the following categories for dietary comparisons: aquatic algae (Algae), other plant material (Plants), nematodes, Trichopteran larva, Ephemeropteran larve, Chironomid larva, *Poeciliopsis* spp. juveniles, terrestrial invertebrates (spiders, mites, grasshoppers, Odonata, Diptera, Coleoptera), fish scales (from *Poeciliopsis* adults), aquatic invertebrates (Isopods, Copepods, Amphipods, snails), other invertebrates (any unidentified invertebrates), and detritus (unidentified organic matter). In all three fish strains, detritus was the most abundant food item found in the intestinal tracts (Table 1). Plant material (especially algae) and aquatic insects were the next most abundant food items. All other food items were generally uncommon (<5% of diet).

The within-individual dietary breadth did not differ among any of the three fish strains (Table 2, Fig. 1), indicating that all three strains had similarly diverse diets within an individual (i.e., all were similar on a specialist to generalist scale). There were significant pool-to-pool differences in diet, with fish in some pools having much more diverse diets than those in other pools. A comparison of within-individual dietary breadth of only Clone 1 and *P. monacha* revealed that

Fig. 2. Between-individual dietary overlap for the three fish strains averaged across pools. Error bars indicate the 95% confidence interval of each mean (calculated by bootstrapping; see text for further information). Numbers above error bars are sample sizes.

Table 3. Average between-individual dietary overlap for coexisting clones and sexuals by pool.

Pool	Clone 1	*P. monacha*
1	1.42 (1.32, 1.51)	**1.51** (1.42, 1.57)
2*	**1.37** (1.28, 1.47)	1.08 (0.91, 1.23)
3	**1.45** (1.31, 1.59)	1.41 (1.32, 1.49)
4	1.16 (1.01, 1.30)	**1.20** (1.11, 1.29)
5	**1.33** (1.08, 1.51)	1.23 (1.12, 1.31)
7*	**1.33** (1.28, 1.38)	1.24 (1.19, 1.28)
8*	**1.40** (1.30, 1.51)	1.01 (0.91, 1.10)
9	1.01 (0.84, 1.19)	**1.04** (0.85, 1.18)
Average	**1.30** (1.24, 1.36)	1.17 (1.13, 1.21)

Note: 95% confidence intervals are shown in parentheses. Larger values between strains are in bold. Pools in which the two strains differ significantly (at $P < 0.05$) are indicated by asterisks (*).

the interaction of pools and fish strain was not significant ($F_{7,329} = 0.424$; $P > 0.85$), suggesting that although diets differed among pools, the lack of a difference in within-individual dietary breadth between Clone 1 and the sexual strain was consistent across pools. Such a test could not be conducted for all three strains as Clone 2 was found in only a subset of all nine pools.

Comparisons of between-individual dietary overlap revealed a much different pattern (Fig. 2). The sexual strain (*P. monacha*) had a significantly lower between-individual dietary overlap compared with Clone 1 when averaged across pools (Fig. 2). *Poeciliopsis monacha* also had lower overlap (but not significantly so) compared with Clone 2 across pools. Although Clone 2 was lower than Clone 1 in between-individual overlap, their 95% confidence intervals overlapped widely (Fig. 2), suggesting that this difference was not significant.

A comparison of the between-individual dietary overlap data for Clone 1 and *P. monacha* within pools showed the same trend, with *P. monacha* having lower dietary overlap than Clone 1 in five of eight pools examined. Only three of these eight comparisons revealed significant differences among strains, with all three showing lower between-individual dietary overlap for *P. monacha* than for Clone 1 (Table 3).

Discussion

The coexistence of a limited number of clones and sexuals can occur if the sexuals have a broader niche breadth relative to the combined niche breadth of the clonal population (Vrijenhoek 1984; Bell 1982; Case and Taper 1986). For this to be true generally, individual clonal strains must have a narrower niche breadth than coexisting sexuals (Case 1990). In cases where clones are continually frozen from the sexual population (Vrijenhoek 1979), clonal extinction is required in addition to the broader niche breadth for the sexuals to persist (Weeks 1993). Clonal and sexual fish in the genus *Poeciliopsis* have been thoroughly studied in attempts to un-

derstand what conditions promote coexistence (reviewed in Vrijenhoek 1994). However, to date, no study has directly compared relative dietary breadth between sexual and clonal types in this clonal–sexual species complex.

The results obtained herein support the assumption that sexual *Poeciliopsis* have a broader dietary breadth than do two coexisting clones. The dietary items consumed were similar to those reported in previous studies (Schenck and Vrijenhoek 1989; Weeks et al. 1992) in that detritus, algae, and aquatic insects were the major component of the diet of all three fish strains. One major difference is that a number of whole juvenile *Poeciliopsis* were found in the diets of all three strains in the current study, whereas only adult fish scales were found in previous field-collected specimens (Schenck and Vrijenhoek 1989). Cannibalism has been previously reported in the laboratory for these fish strains (Weeks and Gaggiotti 1993; R.C. Vrijenhoek, Monterey Bay Aquarium Research Institute, 7700 Sandholt Road, Moss Landing, CA 95039-9644, personal communication), but this is the first documented example of cannibalism from their native habitat. Overall, we found equivalent levels of within-individual dietary breadth when we compared diets among strains, indicating that all three fish strains were similar in their level of within-individual dietary generalization.

Conversely, when we compared between-individual dietary overlap, the sexuals were found to have less dietary overlap than the clones, indicating that each clonal strain consumed a less diverse range of food than the sexuals. The combined within- and between-individual comparisons imply that although the sexual individuals are not dietary generalists, they each choose to eat slightly different food items. Thus, the combined diets of all sexuals lead to a more diverse diet as a population than observed within the two clonal populations. If such dietary choices are partially genetically determined, then they suggest that the genetic diversity of the sexual population translates into a wider array of food items consumed by the sexuals than by either clone. This greater dietary breadth in the between-individual dietary component but no difference in the within-individual dietary component is exactly the pattern assumed by the FNV model (Vrijenhoek 1979, 1984). If sexuals were to have a greater overall dietary breadth merely because of being greater individual food generalists, competition among sexuals would

be similar to that among clones. If this occurred, then the reproductive advantage of the clones would drive the sexuals to extinction (Vrijenhoek 1979, 1984). These findings thus provide strong confirmatory evidence that the niche-partitioning predicted by the FNV model can provide the necessary conditions allowing clonal and sexual coexistence in this species complex.

Additional, although only circumstantial, evidence suggests that genotypic diversity translating to dietary breadth can be found by comparing the niche breadths of Clones 1 and 2. Moore and Eisenbrey (1979) found that Clone 2 is made up of four minor subtypes (identified by tissue grafting), whereas Clone 1 is truly a single clone. If these grafting subtypes also differ in dietary or behavioral characters, then they might be expected to have a wider between-individual niche breadth than any single clone. It is interesting to note that Clone 2 has an intermediate between-individual dietary overlap relative to Clone 1 and *P. monacha*. Because differences in dietary overlap between Clones 1 and 2 were not significant, we cannot assert that the more genetically diverse Clone 2 indeed has a broader diet than Clone 1. Nevertheless, the relative ranks of the three fish strains is exactly that assumed by the FNV model (Vrijenhoek 1979, 1984), with the monoclonal population having the narrowest diet, followed by the polyclonal population (Clone 2), with the sexual population having the broadest diet.

The only other system so far studied for dietary breadth is the clonal–sexual lizard *Cnemidophorous*. Case (1990) did a detailed dietary comparison of clonal and sexual *Cnemidophorous* in Arizona and found the same pattern as we describe here: clonal lizards had a narrower between-individual dietary overlap compared with coexisting sexual lizards, whereas there was no difference in dietary breadth found within-individuals (i.e., individual sexuals were not greater generalists than the clones). Case (1990) also interpreted this as evidence that the between-individual dietary breadth was due to genetically determined dietary differences among sexuals, as assumed in the FNV model (Vrijenhoek 1979, 1984). In a separate study, Paulissen et al. (1988) found that polyclonal populations of *Cnemidophorus* had increased dietary breadth relative to monoclonal populations, although they did not partition dietary breadth into within- and between-individual components. Therefore, the current results on *Poeciliopsis* are consistent with the only other tests of relative dietary breadth in clonal–sexual hybrid vertebrates.

Some of the dietary differences documented in this study might be partially due to behavioral differences. Schenck and Vrijenhoek (1986, 1989) found that Clones 1 and 2 tended to frequent areas where there was current and that the sexuals preferred still waters. This spatial niche partitioning could cause some of the variation in dietary choice found in the present study. Different aquatic and terrestrial insect prey may occur in these different parts of the pool because of current and air movement.

A comparison of between-individual dietary overlap of Clone 1 and the sexual fish of each pond was made to see how overlaps values compared from pool to pool. We found that three of eight ponds showed significant differences in between-individual dietary overlap, with the sexual fish having less overlap than Clone 1 fish. Two additional ponds

showed trends in that direction. Thus, the greater dietary diversity for the sexuals is not merely due to combining fish caught in different pools (which may have different prey items) but is a true reflection of a wider dietary breadth both within and among pools.

The FNV model asserts that sexual reproduction is advantageous in heterogeneous environments because individuals have slightly different ecological requirements (Vrijenhoek 1979, 1984). Each clonal population has its own, narrow requirements, thereby allowing sexuals and clones to coexist (see also Bell 1982; Case and Taper 1986). This study reports evidence in favor of the FNV model: sexuals have a wider niche breadth than either coexisting clone in a naturally heterogeneous environment. Such a reduced niche overlap should mean less competition between individuals for food, which might allow the sexuals to "pay back" some of the twofold cost of sex (Vrijenhoek 1984; Bell 1982; Case and Taper 1986). This study, however, has not addressed the issue of relative niche overlap of multiple clones with a sexual species but merely has shown that individual clones have a reduced niche breadth relative to a coexisting sexual species. The FNV model cannot allow sexuals to coexist with a large number of clones because the combined niche breadth of a large clonal assemblage can eclipse that of the sexuals (Vrijenhoek 1979, 1984; Weeks 1993). It is perhaps for this reason that many of the apparently stable *Poeciliopsis* assemblages have been among a sexual species and only a handful of differing clones (Vrijenhoek 1984, 1994).

Acknowledgements

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