

Resource competition between genetically varied and genetically uniform populations of *Daphnia pulex* (Leydig): does sexual reproduction confer a short-term ecological advantage?

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Small competitive advantages may suffice to compensate for a large disadvantage in intrinsic growth capacity. This well-known principle from ecology has recently been applied to the enduring question of how sexual reproduction can persist in the face of invasion by female-only parthenogens. Small competitive advantages resulting directly from sexual reproduction are predicted to cancel a two-fold disadvantage in intrinsic growth capacity caused by males (which do not themselves produce offspring) comprising half the sexual population. In this paper we test the principal assumption of this theory, that the genetic variation produced by sexual reproduction confers a competitive advantage over self-identical asexual invaders. We set up competition between a diverse clonal assembly of *Daphnia pulex* and genetically uniform populations from single clones. At young ages, the population comprising genetically varied *Daphnia* had significantly higher birth rates in competition with populations of genetically uniform *Daphnia* than in competition with itself, indicating competitive release and a Lotka–Volterra competition coefficient $\alpha_{12} < 1$. No such difference was apparent under conditions of greater food stress, possibly due to individuals channelling more energy into survival, or for old-aged populations, possibly as a result of reduced selective pressures for high reproduction in old females. Mean birth rates differed between the clones at all ages in the presence of competition, providing evidence of variation in life history traits between clones. A Lotka–Volterra model predicted empirical estimates of $\alpha_{12} = 0.896$ (genetically uniform on varied) and $\alpha_{21} = 1.010$ (varied on uniform), which permits immediate coexistence of a sexual population of *D. pulex* even with an asexual lineage having twice the intrinsic growth capacity. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 111–123.

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INTRODUCTION

Why sex prevails in nature remains one of the great puzzles of evolution. Sex has an immediate cost relative to asexual reproduction, since males only express their contribution to population growth through females. With no males to sustain, asexual mutants can double their relative representation in the population in successive generations. This is the widely accepted ‘two-fold cost of males’ for anisogamous spe-

cies in which half the population comprises males (Williams, 1975; Maynard Smith, 1978). Recent theoretical studies by Doncaster, Pound & Cox (2000), Kerszberg (2000), Pound, Doncaster & Cox (2002) and Pound, Cox & Doncaster (2004) have shown that the presence of males can incur a considerably less than two-fold cost on population growth for sexual populations at density dependent carrying capacity. Small advantages in competition for the sexual population are sufficient to halt the invasion of asexual mutants. The asexual competitors then exert a weaker inhibitory effect on the carrying capacity of the sexual population than they exert on their own carrying capacity

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through intraspecific competition. The stable outcome is coexistence on a depleted resource base, both locally and regionally (Doncaster *et al.*, 2000, 2003). Under these ecological conditions we expect the sexual population eventually to drive out the asexual competitor by virtue of the longer-term benefits to its inherent genetic variation (e.g. Kondrashov, 1993; Pound *et al.*, 2004). This is a general treatment of ideas present in earlier models of 'sib-competition' (the 'Tangled Bank' of Bell, 1982) and niche differentiation (the 'Frozen Niche Variation Hypothesis' of Vrijenhoek, 1979). The recent theory differs from those models by calibrating the competition between sexual and asexual types against competition within each type, using the conceptual framework of classical Lotka–Volterra dynamics (see Pound *et al.*, 2002; in response to West & Peters, 2000).

The objective of this paper is to test the underlying assumption of Lotka–Volterra models for competition between sexual and asexual forms, that genetic diversity confers a competitive advantage. We experimentally measured the birth rate achieved by a genetically variable population of *Daphnia pulex* (Leydig) in competition with a genetically uniform population, and compared this to the birth rate under intraspecific competition alone. By using *D. pulex* during asexual phases of their life-cycle, we were able to measure competitive impacts on population growth rates due to differences in genetic variation without introducing confounding influences of male presence.

THEORETICAL CONTEXT

Doncaster *et al.* (2000) and Pound *et al.* (2002) analysed the cost of sex using Lotka–Volterra equations for two competing species with populations of sizes N_1 and N_2 . The classical equations for rates of change in numbers over time (\dot{N}_1 and \dot{N}_2) were extended to distinguish intrinsic rates of death d_i from birth b_i :

$$\begin{aligned}\dot{N}_1 &= b_1 \left[1 - \frac{N_1 + \alpha_{12} N_2}{K_1} \right] N_1 - d_1 N_1 \\ \dot{N}_2 &= b_2 \left[1 - \frac{N_2 + \alpha_{21} N_1}{K_2} \right] N_2 - d_2 N_2\end{aligned}\quad (1)$$

The parameters K_i represent the carrying capacity of each population in isolation from the other and before deaths. The competition coefficients α_{ij} describe the per capita impact of species j on the population growth rate of species i , relative to the impact from intraspecific competition of species i on itself. Thus $\alpha_{12} = 1$ means that Species 2 has the same impact on Species 1 through interspecific competition as Species 1 has on itself through intraspecific competition. Although density-dependent impacts are modelled on the birth term in equation 1, the dynamics are not changed by applying them to the death term, or to survival up to and

including the first fecund age in a population with age-structured fecundity (Doncaster, 2003).

Setting both rate equations (1) to zero yields equilibrium solutions N_1^* , N_2^* . The conditions for invasion by individuals of each species are then:

$$\begin{aligned}N_1^* > 0 \text{ if: } & \alpha_{12} K_2 \left(1 - \frac{d_2}{b_2} \right) < K_1 \left(1 - \frac{d_1}{b_1} \right) \\ N_2^* > 0 \text{ if: } & \alpha_{21} K_1 \left(1 - \frac{d_1}{b_1} \right) < K_2 \left(1 - \frac{d_2}{b_2} \right)\end{aligned}\quad (2)$$

The component in parentheses either side of each condition is the intrinsic component of carrying capacity; the product of extrinsic and intrinsic components: $K_i(1-d_i/b_i)$ is the net carrying capacity of species i in the absence of the other species. It is the distinction of independent birth and death terms in equations (1) that allows us to model explicitly the dynamics of a sexual Species 1 competing with an asexual Species 2. In effect, we confer an identical intrinsic per capita birth rate on sexual females as on asexual individuals, and a zero birth rate on males which are deemed to constitute half the sexual population; thus $b_2 = 2b_1$. If the two types differ only in this respect, we can expect $d_1 = d_2$. Species 2 therefore has twice the intrinsic growth capacity and consequently a larger net carrying capacity. The net carrying capacity is not twice as large, however, as assumed by earlier models (e.g. Case & Taper, 1986; Koella, 1988; Gaggiotti, 1994). Its decelerating relationship to growth capacity has been explored in detail in Pound *et al.* (2002).

For a sexual species 1 with fast growth capacity, given by high b_1/d_1 (albeit half the value of b_2/d_2 for the asexual competitor 2), coexistence with a single clone is possible even with α_{12} close to unity (Doncaster *et al.*, 2000). This is an expression of the trade-off between competition and growth that is a well-known ecological principle permitting coexistence of slow growing but strong competitors with faster growing species (Nee & May, 1992; Doncaster, Pound & Cox, 2003). In the particular case of competitive advantages to the sexual population brought about by its having access to a wider resource base than any one clone, niche breadth has a complicated relation to b_i and K_i in equations (1). Versions of equations (1) expanded for niche breadth nevertheless demonstrate how a sexual population will withstand multiple clonal invasions, provided it retains at least a small resource refuge from the clones (Pound *et al.*, 2002). This is because clonal diversity tends to be associated with intense competition among the clones, with the result that they can prevent each other from establishing more effectively than they inhibit coexistence with the sexual population.

Our adaptation of the Lotka–Volterra model differs categorically from Tangled Bank models of sib-

competition (Bell, 1982), which consider influences of genetic variation on the intensity of competition among sexual siblings compared to competition among identical asexual siblings. Under sib-competition, advantages of sex are inferred from observing a higher growth rate for sexual populations with lower competition among siblings. In contrast, our Lotka–Volterra dynamics consider how genetic variation in a sexual population influences the impact of asexual on sexual competitors, relative to the impact that the sexual individuals have upon themselves. These two consequences of genetic variation, reducing intraspecific competition (sib models) and interspecific competition (Lotka–Volterra model), may co-occur but are not necessarily found together (e.g. Maynard Smith, 1989). The many empirical tests showing a less than two-fold difference in sib-competition (e.g. Schmitt & Erhardt, 1987; Kelley, 1989) leave untested models of interspecific competition which predict coexistence from more subtle differences in niche usage (Case & Taper, 1986; Koella, 1988; Gaggiotti, 1994; Doncaster *et al.*, 2000, 2003; Kerszberg, 2000; Pound *et al.*, 2002). These models are closer in concept to Vrijenhoek's (1979) Frozen Niche Variation hypothesis: that asexual lineages arise in a sexual population with genotypes frozen to those of the progenitor parent. Several empirical studies present evidence of limited genetic variation in asexual clones relative to sexual populations, constraining the clonal phenotype to a narrower ecological niche (Vrijenhoek, 1979; Hebert, Ward & Weider, 1988; Honeycutt & Wilkinson, 1989; Weeks, 1995; Jokela *et al.*, 1997a; Semlitsch, Hotz & Guex, 1997). The literature contains numerous examples of empirical studies on a range of taxa providing evidence that such niche differentiation may result in coexistence of sexual and asexual types (e.g. lizards: Case, 1990; enchytraeid worm: Christensen, Hvilsom & Pederson, 1992; crustaceans: Barata *et al.*, 1996; mollusc: Fox *et al.*, 1996; fish: Vrijenhoek & Pfeiler, 1997; insects: Becerra, Bricchette & Garcia, 1999; frogs: Negovetic *et al.*, 2001). None of these studies, however, have explicitly modelled the relative strengths of interspecific and intraspecific competition. In this study, in contrast, we are able to test a quantitative theoretical model by calibrating the strength of interspecific competition against intraspecific competition.

EXPERIMENTAL CONTEXT

The quantitative ecological model described by equations (1) and conditions (2) has yet to be tested experimentally in the context of competition between reproductive modes (but see Weeks, 1995 for qualitatively similar experiments). This paper reports first tests with *Daphnia pulex*, which has both obligately

and cyclically parthenogenetic forms in North American ponds (Hebert *et al.*, 1988). Laboratory experiments were designed to estimate competition coefficients α_{ij} from controlled observations of birth and death rates for populations alone and in competition with each other. We used cyclically parthenogenetic *D. pulex* as a model organism because its aquatic habit and rapid growth facilitate measuring competitive impacts, and its parthenogenetic (asexual) phase allows control over genetic variation. The *Daphnia* system suits Lotka–Volterra dynamics for this experimental timescale, involving continuous reproduction from the mixing of individuals and resources in a three-dimensional habitat. Several different clones were established in the laboratory by isolating individual females from natural populations. By allowing populations comprising several clones to compete against populations comprising single clones, we were able to measure directly the influence of genetic variation on competitive ability.

We tested two hypotheses: (a) net growth of a genetically varied population is higher in competition with a genetically uniform population than in competition with itself [$\alpha_{12} < 1$ in the first of equations (1)]; and (b) net growth of a genetically uniform population is higher in competition with a genetically varied population than in competition with itself [$\alpha_{21} < 1$ in the second of equations (1)]. By estimating the values of α_{12} and α_{21} we could then use the equilibrium conditions (2) to test whether coexistence would be possible in the presence of a two-fold cost of males (i.e. with $b_1 = 0.5 \cdot b_2$). This prediction assumes that the males are identical to females in all respects except the zero production of offspring. For example, it assumes that they have the same resource requirements as females, and that they neither reduce the fecundity of sexual females by harassment or inefficiency in finding mates, nor do they reduce the fecundity of asexual females by harassment. These and other constraints on the use of *Daphnia* as a model organism are evaluated in the Discussion.

REPRODUCTIVE BIOLOGY OF *DAPHNIA*

All-female populations of cyclically parthenogenetic *Daphnia* reproduce asexually until unfavourable conditions arise (for example over-crowding, reduced food or a change in temperature) and males are produced parthenogenetically. Sexual females then produce haploid eggs that are fertilized by these males, resulting in 'resting eggs' protected by the ephippium (modified carapace) that are able to withstand extreme conditions of freezing or desiccation. The resting eggs hatch upon resumption of favourable conditions, and so permit *Daphnia* populations to occupy temporary pond habitats.

Some species of *Daphnia*, including forms of *D. pulex*, have abandoned the sexual phase of their life-cycle in favour of obligate parthenogenesis. The arrival of obligate parthenogenetic lines has been suggested to result from the males produced by some obligate parthenogens transmitting a dominant gene for sex-limited meiosis suppression (Innes & Hebert, 1988). Evidence that these males can pass such genes to their progeny suggests that the gene could spread through a cyclically parthenogenetic population resulting in a genotypically diverse group of obligate parthenogens. It is reasonable to assume that this process is continuing and therefore that some obligate parthenogen clones have originated relatively recently (Innes & Hebert, 1988). These populations occur in Canada (Hebert *et al.*, 1988) and to a lesser extent further south (Lynch, Spitze & Crease, 1989). Obligate parthenogens have the same life stages as cyclical parthenogens, but without the fertilization of haploid eggs. They produce resting eggs that do not require fertilization and will hatch into genetically identical offspring.

METHODS

SYNCHRONIZATION OF CLONAL GENOTYPES

Ten random clonal genotypes were established from individual females collected from a temporary pond population (Long Point 8A) near Port Rowan in southwestern Ontario, Canada, in early May 2001. The 50 m² woodland pond is less than 1 m deep (Innes, 1997). Long Point 8A is inhabited by genetically diverse cyclically parthenogenetic *D. pulex* during April and May each year (Innes, Fox & Winsor, 2000) with polymorphic loci displaying Hardy–Weinberg equilibria (Innes, 1991). *Daphnia* were collected using a plankton net (mesh size 300 µm) towed immediately below the water surface, and sampling approximately 100 l. Clones were cultured from individual females carrying a brood. Each female was placed in a plastic cup with 80 ml zooplankton media (Lynch, Weider & Lampert, 1986) and fed *ad libitum* with algae-water from an aquarium culture system. Aquaria-cultured algae contain bacteria and inedible algae as well as edible algae (in this case predominantly *Scenedesmus quadricauda*). The cups were kept in a temperature-controlled cabinet set at 15 °C for a 20L : 4D h photoperiod to encourage good levels of health and reproduction. Neonates of the second-generation females were used in the experiment, all aged between 4 and 10 days old, and prereproductive maturity.

EXPERIMENTAL DESIGN

Plastic cups containing 120 ml zooplankton media were divided in two by a central mesh of 200 µm gauge, preventing passage of *Daphnia* but allowing

free mixing of their food (confirmed by a preliminary experiment). For the experimental treatments, ten immature females, all from the same clone, were placed on one side of the mesh (genetically uniform population), and one immature female from each of the ten clones on the other (genetically varied population) as shown in Figure 1. This treatment was repeated 20 times to allow each of the clones 1–10 to act as the genetically uniform population twice. For the ‘genetically varied’ control treatment (ten replicates), one female from each of the ten clones was placed each side of the cup. For the ‘genetically uniform’ control treatment, ten individuals from the same clone were placed each side of the cup. This treatment was replicated for each of clones 1–10. Cups were kept in a temperature-controlled cabinet, set at 15 °C for a 20 L : 4D h photoperiod. Reserve stocks of each of the ten clones were held in similar conditions.

FEEDING AND MONITORING

Conditions of limited food supply were sustained by providing all cups each day with $2.0\text{--}2.4 \times 10^6$ algal cells, or 100 000–120 000 cells per *Daphnia* (haemocytometer counts), divided into twice daily feeds for 9 days (*Daphnia* aged 4–20 days old). Preliminary

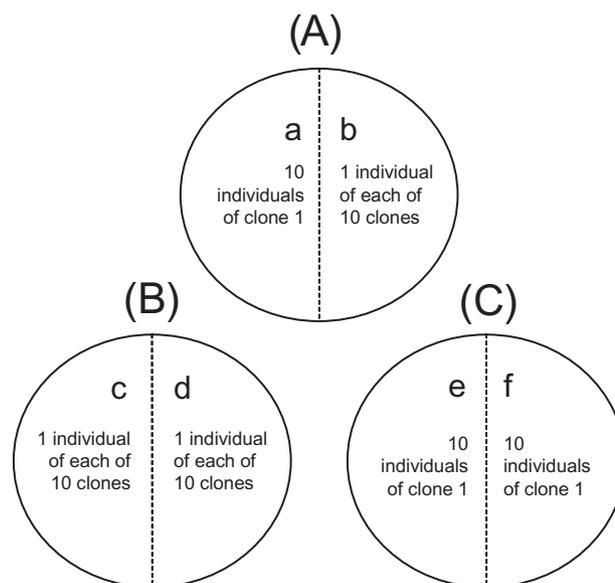


Figure 1. The experimental design. Cups were divided into two halves by a 200-µm mesh. A, experimental treatments in which a genetically varied population competed with genetically uniform populations (two replicates for each of clone 1 through 10, here showing clone 1). B, first control condition in which the genetically varied population competed against itself (ten replicates). C, second control condition in which genetically uniform populations competed against themselves (two replicates for each of Clone 1 through 10, here showing Clone 1).

feeding trials had established that this regime provided sufficient food for reproduction, with brood sizes of about ten per female per day, whilst clearly inducing some food stress, since well-fed females can produce on the order of 50 or more eggs per brood, but avoiding adult starvation. The food was administered by pipette and mixed into the media by swivelling the cup. For the next 9 days (days 10–18 of the experiment; *Daphnia* aged 13–29 days old), food supplies were reduced to $1.5\text{--}2.0 \times 10^6$ algal cells, or 75 000–100 000 cells per *Daphnia*, in order to test the hypothesis that with increased food stress, exploitative competition would reveal subtle competitive advantages. For the last 11 days of the experiment (days 19–29; *Daphnia* aged 24–40), the higher food allowance was resumed. Throughout the experiment, levels of zooplankton media were maintained at 120 ml, and any settled inedible algae or detritus removed. Cups were examined twice daily and newly released young immediately removed and counted, to prevent prolonged changes in population size. Reproductive success was measured in terms of the number of live young produced per adult per day. The competitive impacts of different treatments were measured from variation in this number, which could result from variation in brood size or in survival of offspring immediately *post partum* (since only live young were counted as contributing to population growth). Ehippial females were counted, and this allowed for a rough conversion to the number of ehippia released (total number of ehippial females per population every 4 days) and subsequently to reproductive units (1 ehippium = 9 reproductive units: Lynch, 1983; Korpelainen, 1992), in order to include the reproductive effort of these females in the analysis. Of the 200 test adults in the genetically uniform populations, 44 died during the experiment. Each of these individuals was immediately replaced with a fresh individual from the reserve stock of that clone. Reserve individuals were of the same age as the experimental individuals, and only non-brood carrying individuals were used in order to minimize differences in physiological state. Of the 200 test adults in the genetically varied populations, 20 died during the experiment. For each of these individuals, its genotype could not be identified and therefore it could not be replaced without changing the genetic variation by an unknowable amount. Instead, an individual from the other side of the cup (i.e. a random genetically uniform individual) was removed to balance the population sizes on either side. In the case of decreasing population sizes, food supply was reduced accordingly.

STATISTICAL ANALYSIS

The null hypothesis $H_0: \alpha_{12} = 1$ was tested with a one-way general linear model and planned contrasts (SAS

v. 6.12). The model analysed the hypothesis that the per capita birth rate of the genetically varied population depended on Treatment with 11 levels, accounting for the genetically uniform clones 1–10 and the single genetically varied control. The planned contrasts were made between the ten treatments of genetically varied-on-uniform and the one treatment of varied-on-varied. These contrasts are numerically equivalent to a two-factor general linear model that partitions the variation due to Treatment into a Competitor effect (genetically uniform vs. genetically varied) and a Clone effect (the ten clones nested within the genetically uniform Competitor):

$$\text{Births}_{\text{varied}} = \text{Competitor} + \text{Clone}(\text{Competitor}) \\ + \text{Replicate}'(\text{Clone}(\text{Competitor}))$$

The impact of the genetically uniform population was measured from the b side of the cup in Figure 1A, with two replicates for each of the ten treatments; the control impact of the genetically varied population was calculated from the mean value of the two sides of each cup in Figure 1B, with ten replicates.

The null hypothesis $H_0: \alpha_{21} = 1$ was tested with a two-factor analysis of variance (Minitab v. 13.1). The model analysed the hypothesis that the per capita birth rate of the genetically uniform population depended on an interaction of Competitor with Clone:

$$\text{Births}_{\text{uniform}} = \text{Competitor} + \text{Clone} + \text{Competitor} \\ \times \text{Clone} + \text{Replicate}'(\text{Competitor} \times \text{Clone})$$

with two levels of Competitor (genetically varied and genetically uniform) and ten levels of Clone (representing clones 1–10). The impact of the genetically varied population was measured from the a side of the cup in Figure 1A, with two replicates per Clone; the control impact of the genetically uniform population was calculated from the mean value of the two sides of each cup in Figure 1C, also with two replicates per Clone.

COMPETITION COEFFICIENTS

The intrinsic birth rate, b , of each clone was required in order to calculate competition coefficients. Estimates of b were obtained by culturing five females from each clone individually in plastic cups kept under optimal conditions with food and space provided *ad libitum*. All live offspring were removed immediately after release, and counted.

Carrying capacities, K_i , were estimated from the experimental controls of intraspecific competition alone, in which values were known for the population growth rate, N_i , the rate constants, b_i and d_i , and population size, N_i in the growth equations:

$$\begin{aligned}\dot{N}_1 &= b_1 \left[1 - \frac{N_1}{K_1} \right] N_1 - d_1 N_1 \\ \dot{N}_2 &= b_2 \left[1 - \frac{N_2}{K_2} \right] N_2 - d_2 N_2\end{aligned}\quad (3)$$

This model assumes the simplest form of density-dependent growth, given by a linear decline in births per capita with increasing density, and density-independent deaths. The predictions may be biased if density dependence is non-linear, although this appears unlikely for these laboratory populations of *Daphnia* which have dynamics controlled by their algal food and not by interactions with other components of the environment (as do many stable wild populations: McCauley & Murdoch, 1987; Gurney & Nisbet, 1998). Their algal food generally has self-limiting logistic growth in the absence of predation (e.g. Nisbet *et al.*, 1991), and *Daphnia* have a linear response of food intake to food availability up to saturation levels (a Type I functional response: Rigler, 1961), and of birth rate to food intake (Richman, 1958). Equations (3) use rates of instantaneous population growth (\dot{N}_i) that were obtained from continuous reproduction by a constant number of adults of known age. The design therefore avoided the complications of age structure and discrete reproductive events present in wild *Daphnia* populations, which require more sophisticated models (McCauley *et al.*, 1999). Although laboratory populations are susceptible to cycle (McCauley *et al.*, 1999), we assume that wild sexual populations produce males during a period when their carrying capacity is gradually declining as the environment deteriorates.

Competition coefficients were calculated from equations (1), given values of b_i , d_i , and K_i . For the genetically uniform populations deaths were replaced and therefore $d_2 = 0$. Competitive impacts between populations were assumed to have the same density dependent profile as the impacts within populations given by equations (3). Finally we tested the hypothesis that a genetically variable population with a sex ratio of 1M : 1F could coexist with a genetically uniform population of female-only parthenogens. Condition (2) was tested with lifetime estimates of b_2 , d_1 , d_2 provided by Paloheimo & Taylor (1987). We set $b_1 = 0.5 \cdot b_2$, on the parsimonious assumption that sexual populations invest equally in both sexes (Fisher's sex-ratio theory), and the presence of males has no other effect than to halve the intrinsic growth capacity of the sexual population.

RESULTS

At young ages (4–20 day-olds), the genetically varied *Daphnia* population had a higher mean birth rate in competition with all genetically uniform populations,

compared to competition with itself over the first 9 days of the experiment (Competitor contrast: $F_{1,19} = 15.44$, $P = 0.001$). Within the genetically uniform group, clones varied little in their competitive impact (4–20 day-olds, Clone contrast: $F_{9,19} = 0.48$, $P = 0.868$). Figure 2 illustrates the relatively lower impact of all the genetically uniform populations on the genetically varied population, from which we conclude $\alpha_{12} < 1$ for young individuals. No differences were observed for the second 9 days under food stress (13–29 day-olds, Competitor contrast: $F_{1,19} = 0.16$, $P = 0.690$; Clone contrast: $F_{9,19} = 0.87$, $P = 0.565$) or for the last 11 days after the period of food stress (24–40 days old, Competitor contrast: $F_{1,19} = 0.90$, $P = 0.345$; Clone contrast: $F_{9,19} = 0.52$, $P = 0.840$).

The genetically uniform populations of *Daphnia* showed no systematic difference in competition with the genetically varied population, compared to competition with themselves. The impact of the genetically varied population on birth rates depended on the clone that made up the uniform population only at old ages (24–40 day-olds over last 11 days, Competitor \times Clone interaction: $F_{9,20} = 4.68$, $P = 0.002$). Interspecific competition had no main effect on birth rates of genetically uniform populations either at young ages (4–20 days old over first 9 days of experiment, Competitor main effect: $F_{1,20} = 0.04$, $P = 0.839$), or under food stress (13–29 days old over days 10–18 of experiment, $F_{1,20} = 0.01$, $P = 0.917$), or at old ages (24–40 days old over last 11 days of experiment, $F_{1,20} = 0.03$, $P = 0.870$). Figure 3 illustrates the absence of an overall pattern with respect to competitor, from which we conclude $\alpha_{21} = 1$.

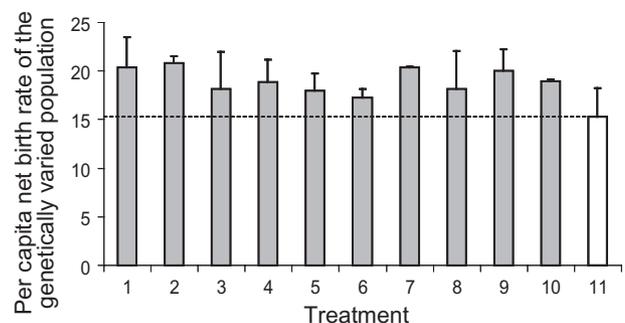


Figure 2. Birth rate of the genetically varied population over the first 9 days, in competition with genetically uniform populations (hashed bars), and with itself (clear bar). Values are young produced per individual by the genetically varied *Daphnia* population over the period (scaled per day), measured from the b side of the cup in Fig. 1A for competition with each clone (treatments 1–10 showing mean \pm SE of two replicates), and from the mean of both sides of the cup in Fig. 1B for competition with itself (treatment 11 showing mean \pm SE of ten replicates).

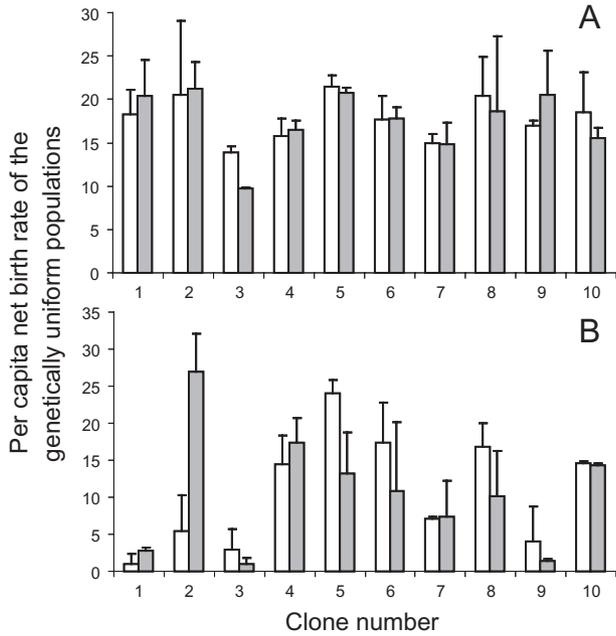


Figure 3. Birth rate of the genetically uniform populations when in competition with the genetically varied population (hashed bars) and in competition with themselves (clear bars) at (A) 4–20 and (B) 24–40 days old. Values are young produced per individual by each of the ten genetically uniform *Daphnia* populations over the period (scaled per day), measured from the a side of the cup in Fig. 1A for hashed bars (mean \pm SE of two replicates), and from the mean of both sides of the cup in Fig. 1C for clear bars (mean \pm SE of two replicates).

CLONAL VARIATION

Figure 3 shows a significant overall variation in birth rate between clones in the presence of competition, both at young (4–20 day-olds, Clone main effect: $F_{9,20} = 2.40$, $P = 0.049$) and old ages (24–40 day-olds, $F_{9,20} = 10.44$, $P < 0.001$), but not during food stress (13–29 days old, $F_{9,20} = 1.75$, $P = 0.143$). The mean number of young produced each sampling day differed for each of the clones throughout the experiment.

Figure 4 shows the difference in mean production of young between the ten clones when competing with other genetically uniform populations (continuous lines) and a genetically varied population (dashed lines). Most births occurred in the first 9-day period for most clones, while food stress from days 10–18 markedly reduced birth rates. Production of young displays short-term cycling, with the majority of young being produced every few days in all clones. There is no pattern of difference between clones competing against themselves and against a genetically varied population.

Table 1. Intrinsic birth rates of each of the ten clones, calculated per day from the mean number of young produced per isolated female over a 19-day period

Clone	Production per individual over 19 days (Mean \pm SE of 5 females)	Intrinsic birth rate, b (per individual per day)
LP8A 1–2	170.75 \pm 22.87	8.99
LP8A 1–5	213.20 \pm 17.40	11.22
LP8A 1–6	158.20 \pm 19.78	8.33
LP8A 1–8	173.00 \pm 7.03	9.11
LP8A 1–11	172.20 \pm 3.17	9.06
LP8A 1–16	205.60 \pm 13.55	10.82
LP8A 1–20	202.80 \pm 16.94	10.67
LP8A 1–21	191.20 \pm 20.66	10.06
LP8A 1–27	204.40 \pm 26.71	10.76
LP8A 2–1	176.00 \pm 7.40	9.26
Pooled	186.74 \pm 8.47	9.83

COMPETITION COEFFICIENTS

Table 1 shows estimates of intrinsic birth rates for each of the ten clones, representing the ten genetically uniform populations in the study. Mean production did not differ between clones ($F_{9,40} = 1.14$, $P = 0.359$). The combined average for the group provides an estimate of the intrinsic birth rate for the single genetically varied population created from these ten clones.

Table 2 shows the calculation of carrying capacities for genetically varied and genetically uniform populations from equations (3), using estimated rates b_i , d_i and N_i , for given N_i . With these estimates of K_i , competition coefficients were calculated from equations (1) as $\alpha_{12} = 0.896$ and $\alpha_{21} = 1.010$, as shown in Table 3. These values are conservative estimates since they apply to the full 29 days of the experiment, even though the value of α_{12} was consistently below unity only for the first 9 days (as described by Fig. 2). The values of the coefficients may be biased by the slightly higher value of d_1 that was obtained in competition compared to isolation (cf. Tables 2 and 3), and by these deaths forcing $N_i < 10$ over the course of the experiment since it was not possible to replace them. If the competition between populations was responsible for increasing the death rate per capita, however, as well as decreasing the birth rate, then the value of α_{12} given by the first of equations (1) in Table 3 is larger than the true value. The calculated values of K_1 and α_{12} , moreover, are relatively insensitive to d_1 , changing by $< 0.2\%$ for a ten-fold increase in its value.

Condition (2), testing for coexistence of sexual and asexual types, was quantified with the numbers N_i , K_i and the calculated parameter values for α_{ij} given in

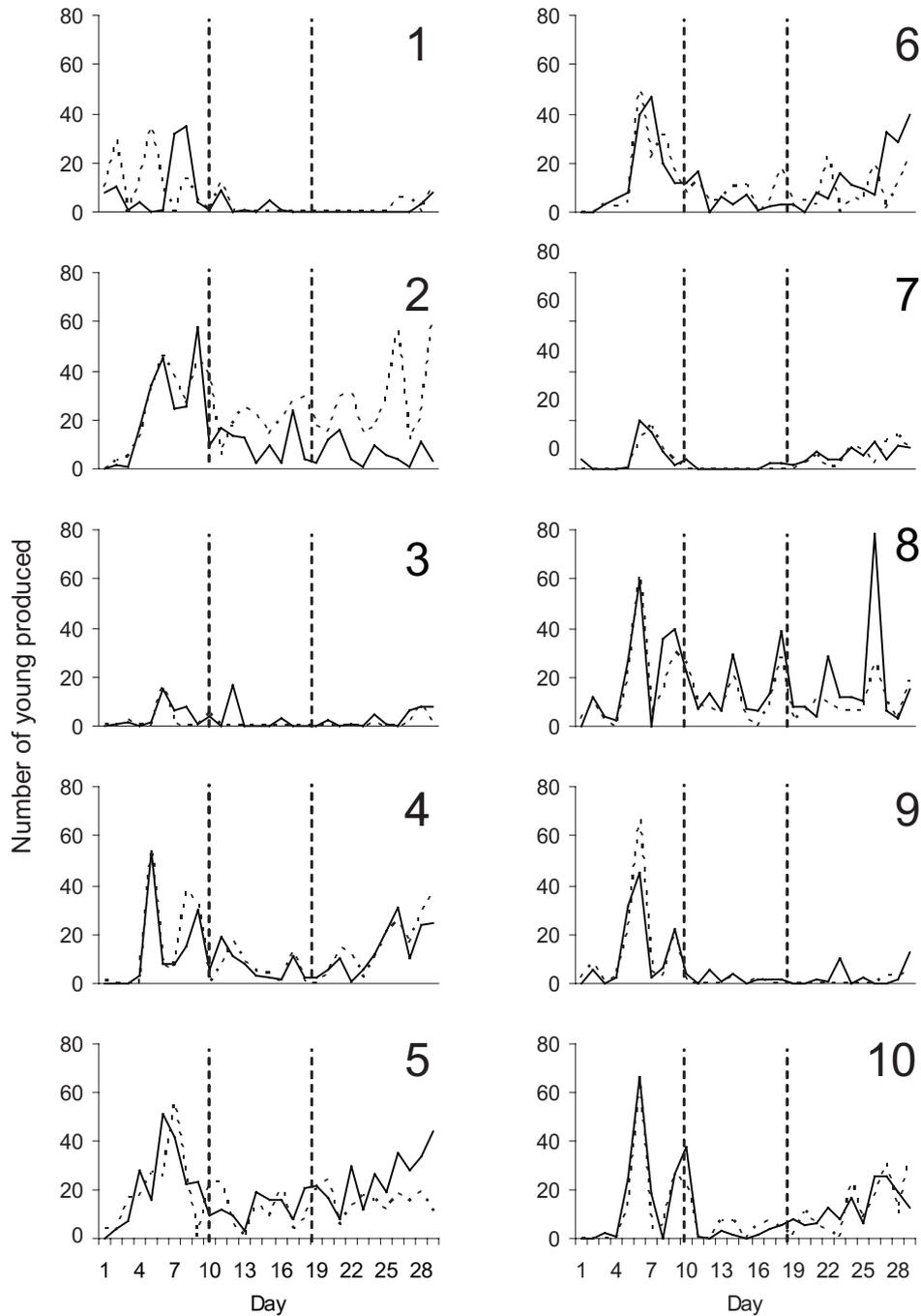


Figure 4. Young production per day by clones 1–10 when in competition with themselves (continuous line, mean of four replicates) and with the genetically varied population (dashed line, mean of two replicates). Period of food stress over days 10–18 is delimited by vertical broken lines.

Table 3, along with lifetime estimates of $b_2 = 0.194$, and $d_1, d_2 = 0.011$ per individual per day given by Pal-
oheimo & Taylor (1987). Setting $b_1 = 0.5 \cdot b_2$, the prediction for $N_1^* > 0$ was met, with $19.623 < 21.391$ in the first of conditions (2). The prediction for $N_2^* > 0$

was also met, with $21.605 < 21.901$ in the second of conditions (2). The first of conditions (2) was also satisfied by using end-of-experiment values for N_i (parenthetical values in Tables 2, 3), although the second was not. We therefore conclude that the observed

Table 2. Calculation of the pre-death carrying capacities, K_i , for the genetically varied ($i = 1$) and genetically uniform ($i = 2$) populations in isolation. Values were obtained from inputs into equations (3) of the empirical estimates of intrinsic birth and death rates per capita and population growth for given size. Parameter b_i = mean birth rate per capita per day (from Table 1); d_i = mean death rate per capita per day; \dot{N}_i = mean number of young produced per population per day over the 29 days of the experiment (population growth rate); N_i = number of individuals in population. The value of N_i in parentheses is the mean number by the end of the experiment, and using this in equations (3) gives the K_1 value in parentheses

	Genetically varied population in isolation		Genetically uniform populations in isolation	
	Parameter	Value	Parameter	Value
Inputs to equations (3)	b_1	9.830	b_2	9.830
	d_1	0.00179	d_2	0
	\dot{N}_1	33.590	\dot{N}_2	27.234
	N_1	20 [19.60]	N_2	20
	N_2	0	N_1	0
Output from equations (3)	K_1	24.127 [23.744]	K_2	23.217

Table 3. Calculation of the competition coefficients α_{12} and α_{21} for the populations experiencing interspecific competition. Values were obtained from inputs into equations (1) of the empirical estimates of intrinsic birth and death rates per capita and realized population growths for given sizes. Parameter definitions as Table 2. Values of N_i in parentheses are the mean numbers by the end of the experiment, and using these as inputs to equations (1) gives the α_{ij} values in parentheses

	Genetically varied population in isolation		Genetically uniform populations in isolation	
	Parameter	Value	Parameter	Value
Inputs to equations (1)	b_1	9.830	b_2	9.830
	d_1	0.00278	d_2	0
	\dot{N}_1	21.017	\dot{N}_2	13.210
	N_1	10 [9.52]	N_2	10 [9.52]
	N_2	10 [9.52]	N_1	10 [9.52]
	K_1	24.127 [23.744]	K_2	23.217
Output from equations (1)	α_{12}	0.896 [0.933]	α_{21}	1.010 [1.094]

competitive advantage conferred by genetic variation suffices to permit persistence of sexual populations with or against asexual invaders, even if the growth capacity of the sexual population is half that of the asexual competitors due to the presence of up to 50% males.

DISCUSSION

The principal result of the experiment is that genetic variation can contribute significantly to competitive

release in the presence of genetically uniform populations. Further work will be needed to elucidate the mechanism of competitive release, but we expect it is a combination of responses to the impure mix of edible and inedible algae and bacteria, expressed in the fertility of females and the survival of their newborn offspring (dead newborns were not counted among the live offspring from which we measured population growth). The different mean growth rates of the genotypes (Figs 3, 4) suggest that the heterogeneous food supply provided sufficient habitat variation against

which different genotypes could express variation in ecological advantages.

An even greater release from competition may occur in natural settings, presenting a 'tangled bank' of microhabitats to populations. Our calculations indicate that an estimated competitive impact even as high as $\alpha_{12} \approx 0.9$ can provide sufficient release to cancel the two-fold disadvantage in growth capacity that would be incurred by a sexual population comprising 50% males. This is a standard prediction for coexistence from Lotka–Volterra theory which, surprisingly, has never previously been tested on the question of maintenance of sex (Doncaster, *et al.*, 2000). Although we did not include males in our experiments, copepod males are known to express aggressive mating behaviour (Brewer, 1998). This may extend to harassment of asexual females in particular, since they gain no compensating benefit of mating, which would further increase the competitive advantage of the sexual population.

In regions where sexual and asexual populations of *D. pulex* coincide (Hebert *et al.*, 1988) we can at least expect that the genetic variation inherent to the sexual populations may cancel the immediate advantage to asexual populations of greater growth capacity, to allow coexistence. Sex then has time to express its longer-term advantages of genetic variation in meeting the demands of environmental change, resulting in eventual displacement of asexual invaders. Our calculations are based on the stringent assumption that males make up half of the sexual population. In cyclically parthenogenetic *Daphnia*, however, males may only be produced in response to deteriorating conditions, giving them a much less than two-fold impact on the growth capacity of the sexual population.

In heterogeneous habitats, such as the temporary ponds favoured by *Daphnia*, adapting to new environments is essential to long-term survival. Cyclical parthenogens confront seasonally changing environments by creating new genotypes in sexual recombination, and then multiply the favourable ones by parthenogenesis. Obligate parthenogens can only create genetic diversity in a stepwise accumulation of mutations. Moreover, they carry an ever-increasing load of recessive deleterious genes, with a finite population never having a load less than its least-loaded clone, and the resulting accumulation of deleterious mutations may limit their life span (Innes & Hebert, 1988; Innes, 1989). Evidence for this genetic load has been found in a decreased relative survival of offspring from self-mated clones (parthenogenesis) as compared to those from outcrossed clones (Innes, 1989).

Parthenogenesis is widely accepted to be advantageous, however, under conditions of uninhibited population growth, when an asexual population can double its representation each generation relative to

an otherwise identical sexual population. In addition, parthenogenesis allows any favourable genotype to be replicated without costs of meiosis in segregation and recombination load (Maynard-Smith, 1978). Once populations reach carrying capacity, our study has shown that these short-term advantages to parthenogenesis may be cancelled by small competitive advantages to a genetically variable sexual population.

Short-term advantages of sexual reproduction have also been recorded for other taxa. New World sexual populations of the brine shrimp *Artemia salina* out-competed sibling asexual populations at high food levels (Browne, 1980; Browne & Halanych, 1989). Amongst dipterans, genetically variable populations of *Drosophila melanogaster* evolving under natural selection developed more pupae than homogeneous populations whose larvae were unable to evolve (Becerra *et al.*, 1999). Similarly for coleopterans, Dunbrack, Coffin & Howe (1995) set two populations of *Tribolium castaneum* in competition, with the population prevented from responding to selection for competitive ability being eliminated within a few generations.

Although those experiments predate the quantitative framework for ecological costs of sex that we use here, they all suggest levels of competitive release that may permit coexistence of sexual with asexual types. Weeks (1995) tested fitness indicators of pseudogamous clones and out-crossed sexual strains of the fish *Poeciliopsis*, finding that sexual populations outperformed clones when held in isolation, but not under competition in mixed treatments. Ecological models of pseudogamy suggest that sperm-dependent parthenogenesis imposes a special set of selection pressures, whereby sperm-dependency can compensate for lower intrinsic growth with a superior intrinsic resource exploitation (Schley, Doncaster & Sluckin, 2004).

The competitive release that we observed for genetically variable *Daphnia* populations in competition with genetically uniform populations, giving $\alpha_{12} < 1$, arose only in the first part of the experiment for young competitors before food deprivation. The subsequently increased food stress may have stimulated females to channel their energy more into survival than fecundity. Browne (1980) observed a similarly reduced competitive ability in sexual populations of *Artemia salina* when held at low food availability. In our experiment, the absence of competitive release in older genetically variable *Daphnia* (24–40 days old) may be explained by reduced competitive effort at this stage. Older individuals may shift investment towards survival and away from fecundity.

In previous tests of sib-competition, several experimental studies found that the difference in growth between isolated populations of sexual and asexual types became less apparent at higher growing densi-

ties (e.g. Ellstrand & Antonovics, 1985; Kelley, 1989). Experimental studies of genetic mixtures in laboratory and agronomic settings have shown that their yield is not much greater than that of the average of their pure components, and is rarely greater than that of the best component (e.g. Bell, 1990; Weeks & Sassaman, 1990).

Although such studies showing a less than two-fold reduction in the impact of intraspecific competition within a genetically varied type, compared to intraspecific competition within a uniform clone, have provided evidence against the Tangled Bank model of sib-competition, they do not constitute evidence against interspecific competition as a mechanism for the maintenance of sex. The theory and experimental test described in this paper demonstrate how a very modest competitive release for a genetically variable population competing with a uniform clone can be sufficient to compensate for the two-fold disadvantage in intrinsic growth capacity that is the cost of obtaining genetic variation from male production. To our knowledge, no previous studies of the maintenance of sex have attempted to measure competitive release specifically in the form of a lower interspecific impact (from the clone) compared to the impact of intraspecific competition on the growth of the genetically variable population. Of the few other studies directly competing sexual or genetically variable types against asexual clones, however, most have found that the latter perform relatively poorly (e.g. review in Lynch, 1984a; also Michaels & Bazzaz, 1986) although this is not always the case (e.g. Jokela *et al.*, 1997b).

The choice of *D. pulex* as an empirical model for testing cost of sex theory has some potential disadvantages to set against the advantages of measurable genetic variation and testable competitive impacts. Although wild populations have long-term stability (Gurney & Nisbet, 1998; Murdoch *et al.*, 1998), they undergo seasonal changes in abundance and can cycle at least under laboratory conditions (McCauley *et al.*, 1999).

The experimental conditions that we imposed on our populations prevented any cycling of density that might occur in natural populations. Although we could have coupled the resource dynamics into our Lotka–Volterra equations in order to model population cycles around an equilibrium, this would not have changed the predictions of the experiment for competitive release at the equilibrium due to genetic variation. The diet of our experimental *Daphnia* contained a mix of edible and inedible algae, which is thought to reduce cycling at high nutrient levels (Murdoch *et al.*, 1998), and our lab cultures did not cycle over time when we allowed them to grow freely during another set of experiments. In sexual forms, males tend to be produced as environmental conditions deteriorate and the products of sexual reproduction hatch from diapausing eggs. Sexual and obligate asexual forms may

therefore compete out of phase with each other. Nevertheless, for the short period when sexual forms start to produce males, our experiment is designed to show whether genetic variation confers competitive advantage on a population at its carrying capacity.

Our experiment replicated the genetically uniform populations with ten different clones from a genetically variable population. It was once believed that clonal species had little or no genetic diversity (Williams, 1975), but more recent genetic analysis has shown much genetic diversity among clones in *D. pulex* (Weider, Beaton & Hebert, 1987), the prosobranch *Potamopyrgus antipodarum* (Dybdahl & Lively, 1995; Fox *et al.*, 1996) and the dandelion *Taraxacum officinale* (Lyman & Ellstrand, 1984). In addition Lynch (1984a) and Lynch *et al.* (1989) have demonstrated much genetic variation for life-history characters in *D. pulex*. Any associated interclonal differences in niche requirements or life history traits may affect average competitive impacts. In our experiment, birth rates differed significantly between clones, particularly at older ages, and the late-age birth rates of some clonal genotypes were improved by competition with the genetically varied population (Fig. 3B). The relative growth rates of clones will depend particularly on differences in age at first brood, size of first brood and size of subsequent broods. In obligately parthenogenetic *D. pulex*, such variation in life-history traits is likely to be derived both from mutation (Lynch, 1984b) and the polyphyletic origin of obligately parthenogenetic clones from the sexual cyclical parthenogens (Lynch *et al.*, 1989). *Daphnia* are known to exhibit age and maternal effects, although our experiment attempted to control for these by using similarly aged and experienced females in the starting populations.

Whether or not sexual reproduction can balance the two-fold cost of sex in competitive superiority will certainly depend upon the life-history traits of the genetically uniform population against which it is competing. The clonal genotypes of *D. pulex* that we used were derived from a single population of cyclical parthenogens. Obligate parthenogens from different ponds would be expected to have an even greater degree of variation in life history traits (for example, filtering efficiency) due to their spatial isolation over generations, and may therefore present a more formidable competitive challenge to sexual populations of *D. pulex*. Further experiments are in progress to test whether sexual populations of *D. pulex* can resist invasion by obligately parthenogenetic *D. pulex*.

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