SHORT COMMUNICATION

Higher rates of sex evolve under *K*-selection

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Abstract

The geographical distribution of sexual and related asexual species has been suggested to correlate with habitat stability; sexual species tend to be in stable habitats (*K*-selection), whereas related asexual taxa tend to be in unstable habitats (*r*-selection). We test whether this broad-scale pattern can be re-created at a microevolutionary scale by experimentally evolving populations of facultatively sexual rotifers under different ecological conditions. Consistent with the pattern in nature, we find that the rate of sex evolves to lower levels in the *r*-selected than in *K*-selection environments. We consider several different explanations for these results.

Introduction

Life history variation and its evolution are often interpreted with respect to *r*- and *K* selection (MacArthur & Wilson, 1967), and various traits are evolutionarily associated with *r*- and *K*-selection (Pianka, 1970). *K*-selection might favour slower development, greater competitive ability, delayed reproduction, higher survival rates, lower resource thresholds, leading to 'efficiency' (rather than productivity) and constant population sizes at or near carrying capacity of the environment. In contrast, *r*-selection might favour rapid development, higher maximal growth rates, lower survival rates, and early reproduction leading to 'productivity' and population sizes below the carrying capacity of the environment. Furthermore, the importance of survival vs. reproduction differs in populations under *K*- and *r*-selection (Pianka, 1970).

These types of life history traits also seem to vary between closely related species that differ in reproductive mode (i.e. sexual vs. asexual). Reproductive mode correlates with the distribution of *r*- and *K*-selection ('geographic parthenogenesis', (Vandel, 1928)): *r*-selection and asexual reproduction are found in variable and

unpredictable habitats (e.g. high altitudes and latitudes, xeric conditions, islands) in contrast to *K*-selection and sexual reproduction which are more often associated with stable habitats (Suomalainen, 1950; Ghiselin, 1974; Wiliams, 1975; Glesener & Tilman, 1978; Bell, 1982). Could this geographical parthenogenesis offer some insight into the great mystery of why sex is so prevalent?

There are at least three classes of reasons for why this pattern may exist. First, several of the classic 'ecological' explanations of sex may predict such a pattern. For example, the type of strong density-dependent selection required by the tangled bank hypothesis (Bell, 1982) may be more likely to occur in stable habitats. Similarly, the Red Queen hypothesis (Jaenike, 1978; Hamilton, 1980) may be more likely to apply in stable habitats because coevolution with parasites may be more likely to be a major selective force under these conditions.

The second class of reasons that could explain the observed pattern are special cases of the classic 'ecological' explanations. Several authors have argued that the infamous 'two-fold' cost may be reduced or, perhaps more accurately, more easily balanced in *K*-selected species (Abugov, 1985; Doncaster *et al.*, 2000; Lomnicki, 2001; Olofsson & Lundberg, 2007; Lively, 2010). The 'cost of males', (Maynard Smith, 1978) is with respect to reproduction. Abugov (1985) argued from life history theory principles that the two-fold cost of sex might be easier to pay with *K*-selection. The two-fold fecundity advantage of asexual reproduction is always a two-fold fitness advantage, regardless of whether it is in a *K*- or *r*-selected environment. However, a survival

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advantage is worth more under *K*-selection than under *r*-selection. Consequently, it is easier to balance the two-fold cost under *K*-selection if sexually derived genotypes have a survival advantage.

A third possibility is based on a simple mechanistic detail. In many taxa, sexual reproduction takes longer than asexual reproduction (Lewis, 1983; Burt, 2000). For instance, one round of sexual reproduction in the ciliate *Tetrahymena thermophila* takes the time of eight asexual divisions, summing up to a 256-fold cost of meiosis (Nanney, 1980). In environments where growth rates are high (*r*-selected habitats), the time required for sexual reproduction may impose a significant cost of sex. In *K*-selected environments, reproductive rate may be limited by resource uptake rather than cellular limits on development time so the 'time' cost associated with sexual reproduction may be largely irrelevant for fitness.

On the other hand, none of these explanations may be correct or even necessary. It is possible that the observed broad-scale pattern is completely spurious. For example, asexual taxa are often of higher ploidy and this factor may underlay the true reason for the pattern. Polyploid taxa often have higher (or different) tolerances to environmental stresses than do their diploid ancestors (see references in Otto & Whitton, 2000, p. 415). Nonetheless, the three ideas above all predict that sex should be more likely under *K*-selection than under *r*-selection. To our knowledge, this prediction has never been experimentally tested.

Here, we measure changes in the rate of sex in replicate populations of cyclic parthenogens evolving in two environments differing in *r-K* selection to test whether we can reproduce the broad-scale pattern observed in nature under controlled conditions. The two environments differ in terms of strength of selection for growth rates, with weaker *r*-selection in the *K*-environment. We emphasize that this experiment cannot distinguish between whether changes in rates of sex are due to selection on the genetic effects of sex (recombination and segregation) or other phenotypic correlates of sex in our experimental system. These phenotypic correlates of sex include differences in the length of time for sexual and asexual cycles as mentioned above as well as any physiological differences between progeny developing from sexual and asexual eggs. Nevertheless, our experiment allows us to test whether the relationship between reproductive mode and population stability observed at a broad taxonomic scale can be reproduced at the microevolutionary scale under controlled conditions without the confounding effects of ploidy differences.

Materials and methods

Experimental system

Rotifers of the genus *Brachionus* possess the capacity to switch between asexual and sexual reproduction (Gilbert, 1963). Asexual eggs are produced parthenogenetically by asexual (amicitc females) and amictic females hatch from these eggs. The switch to sexual reproduction (mixis) is induced by high densities of conspecifics and is mediated via quorum sensing (Aparici *et al.*, 2001; Gilbert, 2003; Stelzer & Snell, 2006; Fussmann *et al.*, 2007). Mixis induction is a variable genetic trait among clones (Stelzer & Snell, 2006; Fussmann *et al.*, 2007) and changes in the propensity for sexual reproduction within a population can be used to estimate selection for the rate of sex under different experimental or natural conditions (Aparici *et al.*, 2001; Carmona *et al.*, 2009; Becks & Agrawal, 2010). Once a female is induced to switch to sexual reproduction, she will produce mictic daughters (parthenogenetically), which themself produce males or, when the mictic females are fertilized, resting eggs. Under our laboratory conditions, resting eggs hatch spontaneously within one to five days, yielding amictic females. In this system, an asexual generation takes ~1.5 days, while the sexual cycle takes ~6 days (~1.5 for the production of mictic females and then ~4.5 days for sexually derived offspring to hatch and mature; note that there are two generations per sexual cycle by this accounting).

Rotifers for this experiment were taken from a laboratory stock population, which was founded in June 2009. Rotifers for the stock population were isolated from Lake Onondaga (NY, USA) in May 2009 and hatched in the laboratory (Becks & Agrawal, 2011). The stock population for this experiment showed genetic variation for the propensity to reproduce sexually, thus providing the necessary substrate for the evolution of sex (Becks & Agrawal, 2010).

We used replicated predator–prey systems with *Brachionus* feeding on the green algae *Monoraphidium minutum* (SAG 278-3, Algae Culture Collection University of Göttingen) in semicontinuous cultures. Each population was maintained in a 500 mL flask. For the '*r*-selected' populations, 40% of the volume was replaced every 2 days. For the '*K*-selected' populations, 10% of the volume was replaced every 2 days. Population sizes remained large throughout the experiment in both treatments (average population size > 5000 individuals). Fresh medium consisted of 5% of an inorganic medium to allow algae growth and supply rotifers with micronutrients. Ninety-five percentage of the fresh medium was conditioned medium from a high-density rotifer lab stock culture.

Our two selective regimes differ in where they are expected to fall on the *r-K* continuum of selection and the treatment labels reflect this; populations in the '*r*-selected' treatment are expected to experience stronger selection on growth rate and less selection on traits enhancing density-dependent competitive ability than populations in the '*K*-selected' treatment. However, it should be noted that neither treatment is likely to represent the end-point of the continuum, and we do not know how strong selection is, in either treatment,

on either density independent growth rate or density-dependent competitive ability. Nonetheless, it seems reasonable to assume the treatments will differ in *r-K* selection because of the conditions under which they are maintained.

We used conditioned medium to ensure that both life history treatments experienced a reasonably strong mixis stimulus (by design, populations in the *r*-selected environment had lower rotifer densities and densities might otherwise have been too low to induce mixis). Conditioned medium was prepared by repeated filtering through a 40 μm and 10 μm mesh. It was important to prevent introduction of any additional algae into to the experimental cultures to allow for constant conditions over the course of the experiment and across replicates. To minimize introduction of additional algae and if so, to detect it, rotifers of high-density rotifer lab stock culture were fed with low concentrations of the green algae *Chlamydomonas rheinhardtii* (CC-1009 wild-type strain from the Chlamydomonas Stock Centre) so that at time of filtration almost all algae cells were consumed. Any contamination with *Chlamydomonas,* which would have changed the composition of the algae population, would have been visibly obvious by the presence of *Chlamydomonas* cells in the experimental cultures. We did not see *Chlamydomonas* in the algae samples taken from the experimental populations.

There were 6 replicate populations of each selection regime. All rotifer cultures were kept at 25 ± 1 °C and 12-h light–dark cycle over the course of the experiment in culture tissue flasks (Sarsted) and flasks were moved randomly every second day on one shelf of the incubator. Rotifer (females, males, eggs, resting eggs) and algae (fixed with tincture of iodine; 0.25 mg iodine in 100 mL of 95% ethanol) population densities were recorded together with replacement of the medium. The experiment was maintained for over 90 days. As asexual reproduction can begin about 1 day after hatching, 90 days of evolution represents a reasonably large number of generations (30 (when entirely sexual) to 60 generations (when entirely asexual)).

Mixis induction and growth rates

Propensity for sexual reproduction was measured at the beginning of the experiment as well as after 30, 60 and 90 days of evolution in a common environment. For the assay, 30 individual rotifers (clones) of each replicate population were isolated and transferred individually to 10 mL of culture medium (1×10^6 *Monoraphidium* cells per mL) to remove environmental effects due to differences in treatment and replicate. For each clone, one neonate of the third generation after isolation was transferred to a single well containing 1 mL of culture medium (1×10^6 *Monoraphidium* cells per mL). Rotifers were

allowed to grow and were monitored every 24 h until the first male occurred. Then, density of first male occurrence was used as an estimate for propensity for sexual reproduction (Aparici *et al.*, 2001). A clone that starts producing males at a lower density is considered to have a higher propensity for sex. This allows us to estimate variation and changes in the mixis trait in a common environment independent of conditions in the experimental populations.

Per capita growth rates were also calculated from these assays by measuring the change in density over a single day ($r = [\ln (N_t) - \ln (N_0)]/1$). We used the change in density over the first day of the assay to ensure that all growth rates were measured under similar food concentrations. Clones that had produced males during this time were excluded from this analysis (most clones did not produce males at the first day: *r*-selection: Day 0: 166 of 180 tested across replicates, Day 30: 161 of 180, Day 60: 174 of 180, Day 90: 160 of 180; *K*-selection: Day 0: 164 of 180, Day 30: 174 of 180, Day 60: 177 of 180, Day 90: 164 of 180). Analysing growth rate over two days produced a qualitatively similar result (clones that did not produce males at the second day: *r*-selection: Day 60: 169 of 180, Day 90: 162 of 180; *K*-selection: Day 60: 174 of 180, Day 90: 161 of 180).

Growth rate and propensity for sex are measured from the same data set so caution is needed in interpreting the results. However, there are two reasons why we believe they are not confounded. First, propensity for sex is measured as the density at which males are induced rather than the time to produce males, so the two measures should not be autocorrelated. With these measures, a genotype with a high growth rate is not automatically constrained to have a high propensity for sex (or *vice versa*). Conversely, two genotypes could differ in growth rate but have the same propensity for sex. Second, our measures of growth rate are based on Day 1 growth only, which is long before males are induced in most cases (and the few cases where males are induced on Day 1 are excluded, as noted above).

Data analysis

Per capita growth rates and density of first male occurrence were analysed using generalized mixed models with treatment as fixed and replicated population as random effects for each day separately (GLMM; with poisson error structure for the density of first male occurrence; analyses were preformed in R using the lmer4 package (Bates & Maechler, 2009; R Development Core Team, 2009)). The percentage of amictic eggs between the unstable and stable environments were compared using generalized mixed model (GLMM with quasibinomial error structure, restricted to days 60–90).

Results

Populations in both environments reached stable populations densities after ~6 weeks with populations converging to densities of approximately 20 females in the K-selected environments or 10 females per mL and in r-selected environments (Fig. 1a). Maximum *per capita* growth rates as measured in a common environment evolved to higher rates under r-selection than under K-selection (day 90: GLMM: $\chi^2 = 8.08$, d.f. = 1, $P = 0.004$, Fig. 1b; for growth rate day 0–2: GLMM: $\chi^2 = 4.64$, d.f. = 1, $P = 0.03$). These results confirm that our selection regimes affect density as well as life history evolution as expected.

The propensity for sex declined over time in both treatments demonstrated by the increase over time in the threshold density required for inducing sex in the mixis assay (Fig. 2a). The sex-inducing threshold density reached significantly higher densities in the K-selected habitats (Fig. 2a), thus indicating a lower propensity for sex (GLMM: day 0: n.s., $\chi^2 = 0.42$, d.f. = 1, $P = 0.52$, day 30: $\chi^2 = 3.85$, d.f. = 1, $P = 0.0497$, day 60: n.s., $\chi^2 = 1.50$, d.f. = 1, $P = 0.22$, day 90: $\chi^2 = 4.69$, d.f. = 1, $P = 0.03$). The difference between the two life-history treatments is also reflected in the percentage of asexually derived offspring over time (Fig. 2b). The fraction of amictically produced eggs within the evolving populations approached a reasonably stable level around day 60 under K-selection. Considering the time after reaching this equilibrium-like state (days 60–90), significantly higher fractions of amictic eggs were produced in the r-selected habitat than in the habitat with K-selection (GLMM: $\chi^2 = 6.58$, d.f. = 1, $P = 0.01$; Fig. 2b). This latter observation is likely due in part to the density differences between the treatments (higher density is known to induce more sex (Gilbert, 1963)). However, the individual mixis assays in the common environment (Fig. 2a) suggest that there are also evolved differences contributing to this pattern.

Discussion

Here, we show how two treatments affecting population ecology exhibited markedly different evolutionary responses in experimental rotifer populations: the rate of sex evolved to lower levels in the r-selected environment (Fig. 2) accompanied by selection for higher maximum *per capita* growth rates (Fig. 1b). This experimentally recapitulates the observed broad-scale pattern of the distribution of asexual and sexual species with sexual species in more stable environments and asexual species in less stable environments (Glesener & Tilman, 1978; Lynch, 1984; Bierzychudek, 1985; Peck *et al.*, 1998; Kearney, 2003).

Our experiment was not designed to discriminate among the three hypothesized explanations for the broad-scale pattern that we outlined in the Introduction. However, it seems unlikely that our result is due to classic ecological hypotheses. Clearly, the Red Queen is unimportant here as no parasites were present. The Tangled Bank hypothesis requires a diversity of exploitable resources and such resources seems unlikely to exist in our simple lab cultures (rotifers could eat only a single type of algae). For both of these hypotheses, environmental stability is not the selective force favouring sexual reproduction. Instead, differences in stability alter the strength of the selective force (interaction with the parasite/predator or the intraspecific competitor). Thus, we
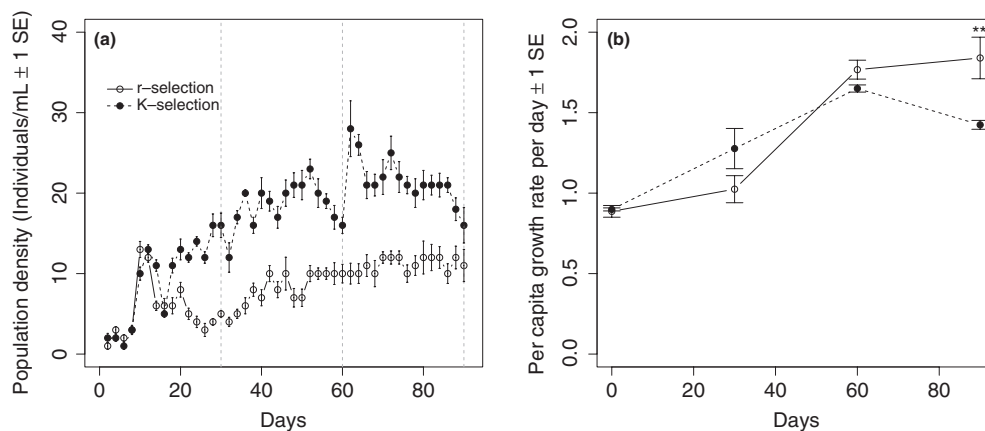

Fig. 1 Population densities of the rotifer *Brachionus calyciflorus* under r-selection and K-selection (a) and *per capita* growth rate (b). Replicated populations ($n = 6$) of *Brachionus* grew for 90 days in semicontinuous algae-rotifer systems with either 10% (K-selection) or 40% replacement (r-selection) of the population with fresh medium. Populations in K-selected habitats equilibrate at higher densities than those in r-selected habitats (a). *Per capita* growth rates of rotifers measured in a common environment (for day 0 to day 1) evolved to significant higher values in the r-selection treatment at the end of the experiment (b) (GLMM: day 0: n.s., $\chi^2 = 0.02$, d.f. = 1, $P = 0.88$, day 30: n.s., $\chi^2 = 2.88$, d.f. = 1, $P = 0.09$, day 60: n.s., $\chi^2 = 3.83$, d.f. = 1, $P = 0.0504$, day 90: GLMM: $\chi^2 = 8.08$, d.f. = 1, $P = 0.004**$). Dashed lines mark the time points when *per capita* growth rates and propensity for sex was measured (Fig. 2a).
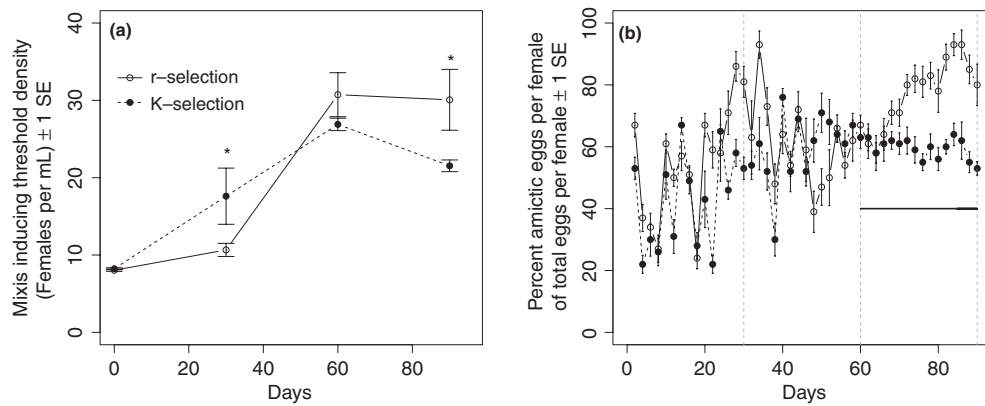
Fig. 2 Evolution of the propensity for sex in replicate populations in *r*-selective and *K*-selective environments. (a) The propensity for sex was measured under common assay conditions as the threshold density required for inducing sexual reproduction. *K*-selection resulted in lower threshold densities (day 90: GLMM: $\chi^2 = 4.69$, d.f. = 1, $P = 0.03*$) indicating higher propensity for sex in these populations. (b) The percentage of amictic eggs of all eggs produced *in situ*. By the time population dynamics appear reasonably stable (after Day 60), *K*-selected populations evolved higher rates of sex (a) and are producing a greater fraction of sexual eggs *in situ* (b: GLMM: $\chi^2 = 6.58$, d.f. = 1, $P = 0.01$).

suspect that our results reflect differences in the net cost of sex between *r*-selection and *K*-selection that exist for a more direct reason. This could be because the relative importance of reproduction vs. survival differs between unstable and stable environments (Charnov *et al.*, 1981; Abugov, 1985; Doncaster *et al.*, 2000; Lomnicki, 2001; Olofsson & Lundberg, 2007; Lively, 2010). A simple alternative is that the delay in generation time with sex is more strongly disfavoured under unstable conditions (e.g. mictic eggs take longer to hatch than amictic eggs, 1–5 days vs.1 day).

It is worth considering two potential reasons that could explain our experimental results that may not apply to the broad-scale pattern. For both life-history conditions, the rate of sex evolved towards low levels, showing that an overall cost of sex is present under these laboratory conditions. It is possible that selection against sex was equally strong under both ecological regimes but that the longer effective generation time under *r*-selection slows the rate of evolution as measured in days. However, inspection of the time course of evolution (Fig. 2) does not appear to support this interpretation as the propensity for sex seems to evolve faster, at least initially, under *K*-selection.

In most of our analysis, we focused on what happens in the latter half of the experiment when populations are close to demographic equilibrium. At this point, there is less sex under *r*-selection. However, one curious observation is that sex initially declines more slowly under *r*-selection (before eventually reaching a lower level than under *K*-selection). The difference between what happens early in the experiment and what happens later might be due to a different force affecting sex. The selection regimes used in this experiment are identical to neither the stock conditions nor the natural environment. Thus, there may be differing degrees of

potential for adaptation between the two selection regimes. Adaptation has been hypothesized to select for sex (Fisher, 1930 (reprinted by Dover, 1958); Muller, 1932; Felsenstein & Yokoyama, 1976; Burt, 2000; Barton & Otto, 2005) and has been shown to select for sex in other experiments using this species (Becks & Agrawal, 2012). There may have been more selection for sex in the more novel environment and during the first weeks of the experiments, because sex is most advantageous when the rate of adaptation is highest. *A priori*, the *r*-selected environment seems more different from the stock conditions than the *K*-selected environment. In the *r*-selected environment, the very high rate of medium replacement ensured fresher conditions (less waste products), higher food abundance and lower density than under standard (ancestral) conditions. These relatively novel conditions may have created a large potential for adaptation in the *r*-selected environment.

For both conditions, the rate of sex evolved towards low levels, showing that an overall cost of sex is present under these laboratory conditions. Identifying why the cost of sex differs between unstable and stable environments is (still) an important challenge for the future.

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