

**Figure 5** Ternary diagram showing relative lengths of the three non-ungual phalanges of pedal digit III in living birds and fossil archosaurs expressed as a percentage of the summed lengths of the three phalanges. For example, the phalangeal proportions of the grasping digit III of a swift (*Chaetura cinereiventris*), represented by the inverted triangle (identified as C) closest to the apex of the diagram, are, from first to third phalanges: 19, 21, and 60%. Conversely, the phalangeal proportions of the fully terrestrial, and highly cursorial, rhea (*Rhea americana*), represented by the open circle closest to the base of the diagram (R), are 54, 32, and 14%. We include data from studies of 32 climbing, perching, or raptorial birds (3 woodpeckers, a toucan, a colie, 4 parrots, 2 cuckoos, a hoatzin, 4 owls, 6 falconiforms, an oilbird, a hornbill, a swift, and 7 perching passeriforms), all of which possess grasping feet. Data from studies of 22 terrestrial birds (4 raites, a tinamou, 3 penguins, 4 galliforms, 2 herons, a stork, an ibis, 3 charadriiforms, a sand grouse, a cuckoo (*Geococcyx californicus*, the roadrunner), and a falconiform (*Sagittarius serpentarius*, the secretary bird labelled S) are included. Ten theropods and one ornithomimid are the dinosaurs included. Two specimens of the early fossil bird *Archaeopteryx* are represented by filled circles and two primitive dinosauriforms are represented by open crosses (*Marasuchus*, upper left, and *Lagerpeton*). The lower cluster of three pterosaurs (stars) includes (lowest to highest stars) *D. macronyx*, *D. weintraubi*, and *Peteinosaurus zambellii*; the upper cluster includes (left to right) *Rhamphorhynchus muensteri*, *R. longicauda*, and *Anurognathus ammoni*. The pterosaur points lie on or close to a cluster of five non-terrestrial falconiforms (the most dorsal, above *A. ammoni*, being the osprey, *Pandion haliaetus*).

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## Explaining the geographic distributions of sexual and asexual populations

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Examination of the geographic distributions of sexual organisms and their asexual, or parthenogenetic, competitors reveals certain consistent patterns. These patterns are called geographic parthenogenesis<sup>1–8</sup>. For example, if we compare sexual organisms with closely related asexuals, we find that, in the Northern Hemisphere, there is a strong tendency for the asexuals to occur further to the north. One researcher to document this pattern is Bierzychudek, who examined 43 cases (drawn from 10 genera) where the geographic distributions of a sexual plant and a closely related asexual are known<sup>4</sup>. In 76% of these cases, the asexual plant's range was more northerly than the range of the sexual. Some of the remaining cases probably fit with this pattern, but more data must be obtained before this suggestion can be confirmed. Asexuals also tend to occur at high altitudes, and in marginal, resource-poor environments<sup>1–8</sup>. We have constructed a mathematical model of a habitat that stretches from south to north in the Northern Hemisphere. Our computer simulations based on this model support the idea that a single basic process may account for much of what is known about geographic parthenogenesis. This process involves the movement of individuals from areas in which they are well adapted to areas where they are poorly adapted.

Details of our model are given in Box 1. We assume that the hypothetical organisms living in the habitat are obligately sexual hermaphrodites. Each adult produces a large number of offspring through 'female effort' (for example, by producing seeds or eggs), and mating is random within local areas. We also assume that the growing season is longer as one moves further south, and so, over the course of a generation, adults in southern regions produce more offspring through female effort than do adults in northern regions. Within a local area, the expected number of offspring produced by female effort is the same for all adults.

After the production of offspring the adults die, and the juveniles are subject to viability selection. A given juvenile's chance of surviving this stage depends on its phenotype, and on the local environment within which it is born. The optimal phenotype varies from one location to another. We assume that phenotype is entirely determined by genotype. Offspring phenotypes are normally distributed around the mean of the phenotypes of their parents (this is the 'infinitesimal model'<sup>9</sup>).

After viability selection, some juveniles migrate to other regions.

The direction and distance that a juvenile migrates are chosen at random. We assume that the local population density of adults that can be sustained by the available resources is the same everywhere within the habitat. Thus, after migration, randomly selected juveniles die at such a rate as to equalize the population density in all areas. The remaining juveniles mature to adulthood, and give birth to the next generation.

Most multicellular asexual organisms are thought to have been derived, in the relatively recent past, from sexual ancestors<sup>7,10</sup>. We therefore considered a situation where the habitat is occupied initially by an obligately sexual population at equilibrium. We then selected an adult at random from this population, and assumed that this adult has a newly arisen mutation that makes her entirely asexual, and that causes her to produce only asexual offspring. Thus the initial mutant and all of her descendants reproduce exclusively through female effort. The expected fertility of an asexual adult is assumed to be proportional to the expected number of offspring produced by female effort by sexual adults in the same region. Let  $K$

represent this latter quantity in a particular region. We assume that asexual adults in the same region produce an average of  $\Theta K$  offspring each, where  $\Theta > 0$ ; the value of  $\Theta$  is the same for all asexual adults.

In general, we can expect to find that sexuals and asexuals living in the same region will not have equal fertility (that is, we can expect  $\Theta \neq 1$ ). Asexuals do not have to find mates, and so they may be more efficient than sexuals, leading to  $\Theta > 1$ . However, asexuality can produce problems, such as a high rate of mortality from deleterious mutations and a high level of susceptibility to parasites<sup>7,10-20</sup>. Factors such as these may lead to depressed fertility in asexuals (so  $\Theta < 1$ ). For each simulation trial, we chose the value of  $\Theta$  at random. (The other parameters of the model were also chosen at random, as described in Box 1).

We assume that all descendants of the initial asexual mutant have the same phenotype as their ancestor until a mutation occurs among them that changes the phenotype. We refer to this collection of phenotypically identical descendants as a clone. The number of

## Box 1

For the purposes of the simulations, it is convenient to 'discretize' both the environment and the possible phenotypes. The environment was divided into an infinite number of areas, numbered sequentially from  $-\infty$  in the far south to  $\infty$  in the far north. The population is inviable in all areas except for those numbered  $1, 2, \dots, \Omega$  (see below for details). For the main set of simulations,  $\Omega = 11$ . However, we experimented with larger values of  $\Omega$ , and this had no qualitative effect on the results.

Let the expected number of offspring produced by a sexual adult through female effort in the southern-most habitable area (area number 1) be denoted by  $K_1$ . The same statistic in area  $i$  is denoted by  $K_i$ . We assume that  $K_i$  is given by  $K_i = K_1[1 - (2i - 2)/(\Omega - 3)]$  for  $1 \leq i \leq \Omega$ . Thus fertility undergoes a three-fold decrease from the most southern to the most northern habitable area.

We assume that phenotypes are discrete, and the possible phenotypic values (denoted by  $z$ ) range sequentially by integers from  $-\infty$  to  $\infty$ . If the mean phenotypic value of a pair of parents is given by  $\bar{z}$ , the probability that the phenotype of a particular offspring takes on an integer value  $i$  namely  $V(i|\bar{z})$  is given by the following 'discretized' normal distribution:  $V(i|\bar{z}) = Q \exp(- (i - \bar{z})^2 / \beta_z)$ , where  $\beta_z$  is a positive constant. Here,  $Q$  is chosen to ensure that  $\sum_{z=-\infty}^{\infty} V(i|\bar{z}) = 1$ .

After birth, viability selection occurs. In any given area  $i$ , the probability that an individual with phenotype  $z$  will survive viability selection is denoted by  $W(i, z)$ . For  $1 \leq i \leq \Omega$ ,  $W(i, z)$  is given by the traditional 'non-optimal' function:  $W(i, z) = \exp(- (z - i)^2 / \beta_v)$ , where  $\beta_v > 0$ . Thus the optimum phenotype in a given area  $i$  is given by  $z = i$ . We assume that  $W(i, z) = 0$  for  $i \leq 0$  or  $i > \Omega$ .

During the migration phase, the probability that an individual living in area  $i$  migrates to area  $j$ , namely  $M(i, j)$  is given by  $M(i, j) = \tanh(1/[2\beta_m]) \exp(- |i - j|/\beta_m)$ , where  $\beta_m > 0$ . Thus the probability that an individual remains in the area where it was born is given by  $\tanh(1/[2\beta_m])$ . The average absolute distance (in terms of values of  $i$ ) that an individual moves is  $1/\sinh(1/\beta_m)$ . The probability that an individual in area  $i$  will migrate beyond  $x = 1$  or  $x = \Omega$  is equal to  $\exp(- \Omega/[2\beta_m]) \cosh([2i - \Omega - 1]/[2\beta_m]) / \cosh(1/[2\beta_m])$ .

We began simulations with a sexual population in which phenotypes  $z = 1, z = 2, \dots, z = \Omega$  were present in areas  $1, 2, \dots, \Omega$  (the initial densities were randomized in each area). We then ran the simulation until equilibration, defined as the point when the average postmigration density of the population (averaging over areas  $1, 2, \dots, \Omega$ ) was changing by less than 0.01% over the course of 100 generations.

To introduce the first asexual mutant into the equilibrium population, our programme used a procedure that, mathematically speaking, is exactly equivalent to the following sequence of events. First, a sexually produced adult is chosen at random, and its location and phenotype are noted. We assume that this adult is asexual. Then previously published methods<sup>25</sup> are used to calculate the probability ( $P$ ) that a clone derived from this adult will become established (that is, it will not be lost from the population as a result of stochastic processes). If the clone is established (which happens with

probability  $P$ ) then it grows in number until a new equilibrium is reached. If the clone is not established, a new sexually produced adult is selected to begin the procedure again. This continues until a clone becomes established.

It can be shown that, after a clone becomes established, the proportion of members of the clone that reside in each area will eventually approach a particular distribution (an eigenvector), and this invasion distribution will remain for as long as members of the clone are very rare in all areas. The invasion distribution depends on the phenotype of members of the clone, but is independent of the area in which the initial asexual mutant appeared. The eigenvector in question is calculated from an  $\Omega \times \Omega$  matrix, in which the entry in the  $i$ th row and the  $j$ th column is given by  $\Theta M(i, j) K(i) W(i, z^*) \bar{N}(i)$ , where  $z^*$  gives the phenotype of the new clone and  $\bar{N}(i)$  is the equilibrium density (before the introduction of the new clone) of all individuals (regardless of whether sexual or asexual) on site  $i$  after viability selection and migration.

To calculate the postinvasion equilibrium distribution for asexuals and sexuals, we added asexual juveniles having the phenotype of the newly established clone to the juveniles living in each of the areas, immediately after viability selection and migration. The relative numbers of members of the new clone in each area is determined by the invasion distribution above. We normalized the densities of the new clone to ensure that, initially, the ratio of clone density to total density could not exceed  $10^{-3}$  in any area. In general, we allowed the population to evolve until the average postmigration density of both species (averaging over areas) was changing by less than 0.01% over the course of 100 generations. Results from numerical experiments strongly suggested that this criterion was usually sufficiently stringent to ensure accurate calculation of the equilibrium. However, for some trials in which evolution appeared to proceed very slowly, we applied an even more stringent criterion for determining when to stop the simulation.

After the first clone to invade successfully has reached equilibrium, we initiate a series of new mutants as follows. For each new mutant, the probability that the mother of the mutant will have a particular phenotype is equal to the frequency of that phenotype among all the asexuals. The phenotype of the new mutant is chosen using a discretized normal distribution. The probability that the mutant will have phenotype  $i$  is given by  $C \exp(- (i - j)^2 / 2)$ , where  $j$  is the phenotype of the parent of the mutant, and  $C$  is chosen to ensure that the distribution sums to unity when the sum is over all  $i$  such that  $-\infty \leq i \leq \infty$ . After each new mutant is produced, it either becomes established, leading to a new equilibrium, or it goes extinct. This continues with successive mutants until an equilibrium is achieved for which there is no possible phenotype that is not present among the asexuals living in the habitat, and that could possibly become established (that is, for which  $P > 0$ ).

Before each trial, we choose  $\Theta, \beta_r, \beta_v$  and  $\beta_m$  from rectangular distributions. The intervals for these distributions were as follows: for  $\Theta$ , [0.7, 1.1]; for  $\beta_r$ , [0.01, 0.5]; for  $\beta_v$ , [1, 10]; and for  $\beta_m$ , [1, 3].

living individuals who are part of a clone will either become large (in which case we say that the clone is established), or it will fall to zero (which means extinction of the clone). If the clone becomes extinct, we choose another sexual adult and begin again. If the number becomes large, we allow a new equilibrium to develop. Once an asexual clone is established and a new equilibrium has developed, we initiate a new clone by assuming that an adult asexual undergoes a mutation that alters its phenotype, and then we allow evolution to proceed until this new clone becomes extinct or becomes established and a new equilibrium develops. We continue with this process of introducing new asexual mutants until there is no longer any chance that a new asexual clone can become established. Analytic methods are used to determine when this final distribution has been achieved.

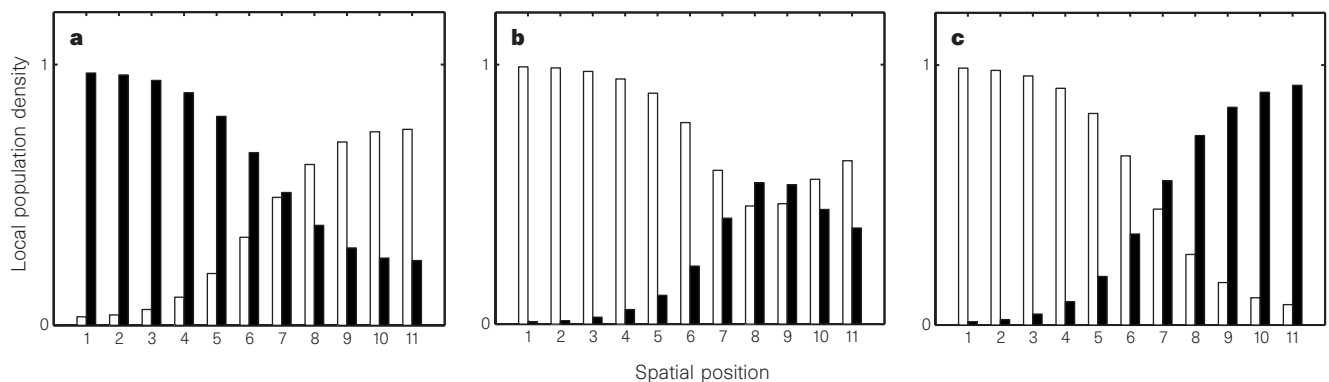
We ran 2,500 computer trials using these procedures. In 25.5% of these trials, we found that only asexuals were present by the time the trial ended. This happened whenever  $\Theta > 1$  (so that asexuals had a fertility advantage), and sometimes when  $\Theta < 1$  (in 0.5% of the cases where sexuals were absent at the end of the trial,  $\Theta < 1$ ). In 0.1% of the 2,500 trials, only sexuals were present at the final equilibrium. Finally, in 74.4% of the trials, both sexuals and asexuals were present at the final equilibrium; we call these the polymorphic trials.

In 96% of the polymorphic trials, we found that, once the final

equilibrium had been reached, the average position of sexual adults was further to the south than the average position of asexual adults. This outcome corresponds to the usual finding in nature<sup>1,2,4-8</sup>. We also found that, in 94% of the polymorphic trials, the density of sexual adults decreased from south to north, and the density of the asexual adults increased from south to north. An example of this sort of outcome is shown in Fig. 1a. In 4% of the polymorphic trials the final average position of the sexuals was further to the north than that of the asexuals (Fig. 1b, c).

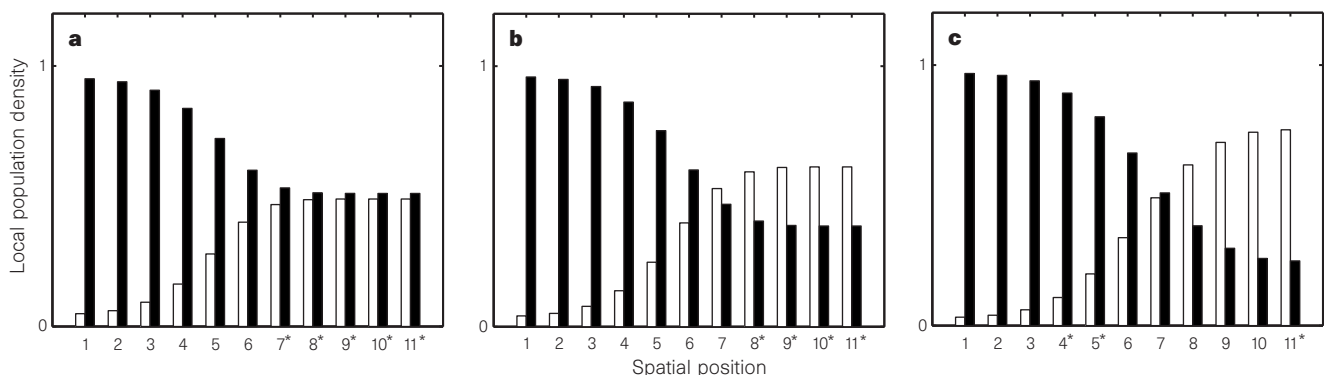
Why are patterns similar to those found in nature so common among the polymorphic trials? To answer this question, let us consider, in more detail, the trial for which the final distribution is given in Fig. 1a. In this trial (as in all the trials) the population density of sexual adults was the same everywhere before the first successful invasion of an asexual clone. However, data from the simulations show that, at this initial equilibrium, juveniles were least viable in the north. This is a consequence of the relatively high levels of fertility in the southern populations. As a result of the fertility differences, migrants and their recent descendants are more common (in terms of proportions) in northern populations than in southern ones. As migrants tend to have phenotypes that are not well adapted for local conditions, this depresses viability in northern populations.

Because of blending inheritance, the deleterious effects for sexuals



**Figure 1** Final equilibrium density distributions for three simulation runs. The abscissas give spatial position, with the southern-most position being farthest to the left. The ordinates are proportional to local population density. Black bars give data for sexual individuals, and white bars for asexuals. In 96% of the polymorphic trials, the average position for the sexuals was further to the south than for the

asexuals, once the final equilibrium had been reached. An example is shown in **a**. In 4% of the polymorphic trials, the average position of the asexuals was further south at the final equilibrium, as shown in **b** and **c**. In **a**, the values of  $\Theta$ ,  $\beta_s$ ,  $\beta_V$  and  $\beta_m$  were 0.743, 0.140, 2.27 and 2.67, respectively. In **b**, these same values were 0.961, 0.028, 2.99 and 1.63. In **c**, the values were 0.935, 0.461, 1.28 and 1.17.



**Figure 2** The intermediate equilibria leading to the final equilibrium shown in Fig. 1a. The abscissas give spatial position, and the ordinates are proportional to local population density. Black bars give data for sexual individuals, and white bars for asexuals. The asterisks indicate that an asexual clone with the optimal phenotype for the area marked had a non-zero probability of invading successfully. **a**, The equilibrium established after one successful invasion (with

an asexual clone optimal for area 6). **b**, The equilibrium after the second successful invasion (with an asexual clone optimal for area 7). **c**, The equilibrium after three more successful invasions (with clones optimal for areas 9, 8 and 10, in that order). An additional three successful invasions (by clones optimal for areas 5, 11 and 4) occurred before establishment of the equilibrium shown in Fig. 1a.

of migration into a particular region can be eliminated, in part, if similar numbers of immigrants come from the north and the south. However, if more immigrants come from the south, the mean phenotype in a given region will tend to be pushed to a value that is optimal for a more southerly region. It can be shown that the fertility of a local population, in comparison with the fertility of the population immediately to its south, becomes smaller (in proportional terms) as one moves further north. Thus we have another reason why the loss of fitness resulting from migration tends to be largest in the far north.

In the trial shown in Fig. 1a,  $\Theta < 1$ , so asexuals have an intrinsic fertility disadvantage. Analysis shows that this disadvantage precludes a successful invasion by asexuals with a phenotype that is optimal for region number 5, or by asexuals with phenotypes optimal for any of the regions south of region 5. However, a successful invasion is possible by an asexual phenotype that is optimal for any of the regions north of region 5. This pattern of asexuals being able to invade the initial equilibrium successfully only if they are adapted to northern regions was often found among the polymorphic trials (about 25% of the time). However, we also found that, in about 75% of the polymorphic trials, asexuals optimal for any region could invade the initial equilibrium successfully. Nevertheless, even among these trials, the probability of establishment of a clone after its introduction was generally higher if the clone was adapted to the north and was introduced in the north than if the clone was adapted to the south and introduced in the south.

What accounts for the difference in the likely fate of north- and south-adapted asexual clones? Roughly speaking, members of these clones do not mate, and so individuals with the optimal phenotype for a given region produce offspring with this same optimal phenotype. In contrast, a sexual adult with the locally optimal phenotype may have a non-optimal mate (possibly a migrant), and so many of the offspring may also be non-optimal. Immigrants and their recent descendants are most common in the north, so the initial invasion of asexuals is more likely in northern areas (where their mode of reproduction confers the largest advantage) than in the south. A similar explanation has been proposed to account for the presence of self-fertilizing plants in areas with unusual local environments<sup>21</sup>. Note that a loss of fitness due to maladapted migrants is a well-known phenomenon in natural populations<sup>21,22</sup>, and has recently been implicated in speciation and the establishment of the limits of species ranges<sup>23,24</sup>.

Throughout the series of invasions that led to the equilibrium shown in Fig. 1a, asexual clones adapted to the far south were at a disadvantage compared with some north-adapted clones (see Fig. 2). The reasons for this are similar to those state above with regard to the initial all-sexual equilibrium.

But what accounts for the 77 polymorphic trials (4%) in which the average position for asexuals was further south than that for sexuals at the final equilibrium? The answer appears to have something to do with the occurrence of unlikely events in the series of invasions leading to the final equilibrium. Strong support for this idea comes from tests in which we re-ran each of the exceptional trials 10 times. In all but 14 of the 77 cases, the average position of sexuals was further south than that of asexuals at the final equilibrium for most of the 10 trials run.

In addition to the simulation study just described, we have also carried out a set of simulations using a model in which the phenotype of the clone that makes the first successful invasion is as described above, but all the subsequent clones are produced as mutations to randomly chosen sexual individuals (just like the first clone), not as mutations to asexual individuals. The results were similar to those described above.

As we have seen, the tendency of the model to produce patterns similar to those found in nature depends on the presence of relatively short growing seasons in the north, and this leads to

high frequencies of migrants in northern areas. However, short growing seasons also occur at high altitudes. Thus the processes described here may also explain the tendency of asexuals to occur at high altitudes. Migrants should also be common on the margins of populations because the population density in these areas is often very low compared with nearby (but more central) regions. It has often been asserted that asexuals tend to occur on the margins of populations<sup>2-8</sup>, and given our results it seems likely that this is a result of a process similar to the one described above. We have now carried out a simulation study that supports this view (results not shown). □

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## Activity-dependent scaling of quantal amplitude in neocortical neurons

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Information is stored in neural circuits through long-lasting changes in synaptic strengths<sup>1,2</sup>. Most studies of information storage have focused on mechanisms such as long-term potentiation and depression (LTP and LTD), in which synaptic strengths change in a synapse-specific manner<sup>3,4</sup>. In contrast, little attention has been paid to mechanisms that regulate the total synaptic