collections of specimens; data associated with collections (such as labels and indexes); and comprehensive libraries. If an important part of 'the real work of systematics' lies in describing, inventorying and mapping critical taxa[7], the role of collections-based institutions is fundamental. A consequence is a move towards greater centralization of taxonomic resources: a problem is that such a trend could lead to fewer taxonomic institutes world-wide and a further uneven loss of taxonomic positions, and thus capacity, in a profession noted already for the unbalanced distribution of specialists in terms of taxon size[8].

The wider value of systematics and taxonomic resources has been discussed for several years, but the subset of papers in Oxford concerned with this outreach provided a focus for what feels like a transformation. Quite possibly, the momentum for increased outreach by systematists has at last become unstoppable given the collective and individual enthusiasm that evidently is developing globally. In his abstract, Vernon Heywood (University of Reading, UK) suggested that a revolution is beginning to take place in the way in which taxonomic information is being packaged and presented to various groups of consumers. It is hard to refute this view given the steady rise in the number of large taxonomic datasets and, less well appreciated, efforts to organize and make available taxonomic data on a global basis. But now that at least a significant section of the systematics community has shaken off much of its somewhat downbeat image, it is essential that the momentum is maintained. Should it be impeded, the reasons will probably be shortage of funds or, just as likely, their misdirection, and the threat of the human predisposition towards protectiveness, inward-lookingness and competition. Let us hope that the externalizers and enthusiasts prevail.

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The rise and fall of new mutations

The life of a new mutation is not an easy one. Even when a mutation confers a selective advantage on the individual possessing it, the first few generations of its existence are dominated more by the whims of fate than by the determinism of natural selection. The individual carrying the mutation might die prematurely or its offspring might not find a mate. Any run of bad luck spells doom for a mutant when it exists at such low copy numbers.

Much the same problem faced the British aristocracy about a century ago, when concern was raised that many of the great family names were in danger of dying out. A few early deaths, sterility, or too many female children could mean the end of a lineage that had existed for centuries. The solution to the problem of the longevity of names, first worked out by Francis Galton in 1889 (Ref. 1), turns out to be the same for figuring out the chance that a mutant will have its day in the sun. Seventy years ago, J.B.S. Haldane[2] used this approach (known as a branching process) to calculate the probability that a new advantageous mutation will eventually become fixed in a population. He found this to be approximately $2s$, where s is the relative fitness advantage that those possessing the new mutation have relative to those who lack the mutation. Since selection is thought to be fairly weak on most amino acid variants ($s \approx 10^{-3}$ to 10^{-5}) (Ref. 3), this probability could be quite low.

Haldane's result has stood over the decades, with some minor modifications[4], as a reminder that even the best mutants are usually lost from populations. Now, a recent paper by Otto and Whitlock[5] in *Genetics* provides several elegant extensions to this result with some potentially profound evolutionary implications.

The branching process

The predicament in which a new beneficial mutation finds itself is caused by the underlying stochastic nature of selection. Individuals under natural selection differ in the probability of survival and/or the average number of offspring. Population geneticists tend to treat these probabilities and averages as deterministic descriptions of large populations; when there are enough individuals, random fluctuations tend to balance each other out. No matter how large the population, however, a new mutation most likely arises in a single individual (although this assumption has been challenged[6]). It is the limited population composed of this individual and its descendants that determines the initial fate of the mutation. Even an increase in the probability of survival from, say, 50% to 80% (a substantial gain) will not help the new mutant if the individual possessing it happens to be in the unlucky 20% that die that generation.

Haldane[2] (and Fisher[7]) approached this problem by imagining that the new mutation sits at the root of a tree of descendants. Once the tree branches a few times, random pruning is unlikely to kill off all of the branches at once. The crucial phase for the new mutation is therefore the first few generations of existence when the number of branches is small (that is, when its allele frequency is less than about $1/Ns$)[8]. Here the central question is the probability that the mutation will persist through the initial branching process to become prevalent enough for the deterministic effects of selection on a large population to take over and drive the mutation to fixation. Solving this problem yields the $2s$ result.

Fluctuating population size

Haldane's result assumes that the size of the population in which the mutation arises remains constant through time. Otto and Whitlock have generalized this approach to include cases in which population size rises and falls through time, as every natural population is certain to do. Building on the branching-process approach, they show that the probability of fixation of a new mutant in an exponentially growing or shrinking population is approximately $2(s + r)$, where r is the rate of population increase (a negative r denotes a decreasing population). Thus, a

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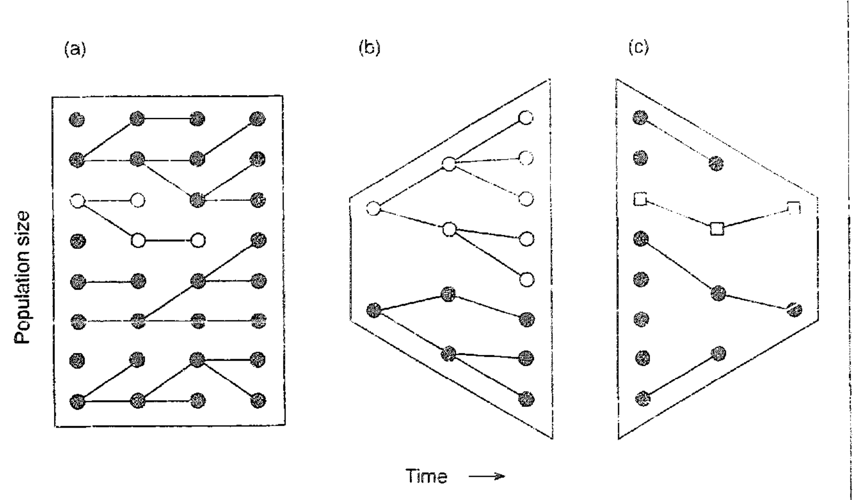

Fig. 1. Evolution as a branching process. A new mutant usually begins its life as a single copy, no matter how large the population. In a stable population (a), each individual replaces itself on average, and the mutant (open circles) can be lost because of random termination of its branching pattern during the early part of its spread. In growing populations (b), advantageous mutations rapidly escape the risky period in which they are at low copy number because the total number of branches is growing, independent of the mutation's selective advantage. The mutation is therefore more likely to persist long enough for selection to drive it to fixation. In shrinking populations (c), all branches are being pruned, so it is less difficult for a deleterious mutation (squares) to become fixed by chance.

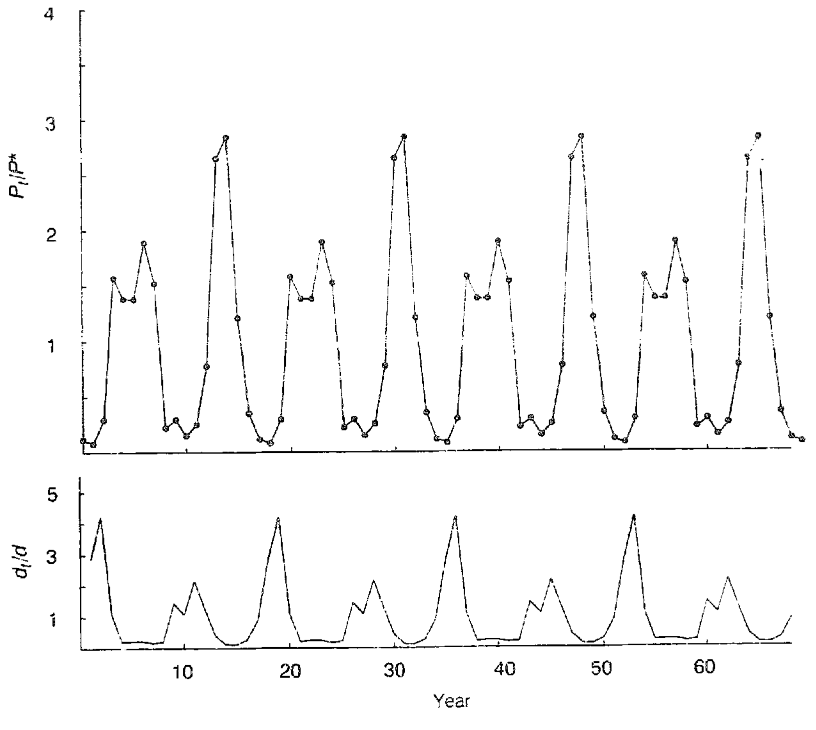

Fig. 2. Change in the probability of fixation of a beneficial mutation in snowshoe hare populations. The upper graph shows how the probability of fixation (P_t) varies relative to expected probability of fixation in an unvarying population of equivalent average size (P^*) as the population size of the hares varies from year to year (lower graph). Population size is depicted in terms of the density through time (d_t) divided by the mean density. *Reproduced with permission from Ref. 5.*

mutant that finds itself in a rapidly growing population is much more likely to be fixed than one that is in a shrinking population. This is because it is less likely that a particular branch in the mutant's family tree will die out by chance when there is an increasing number of twigs that branch every generation (Fig. 1).

Interestingly, the opposite result is found for deleterious mutations. Deleterious mutations have virtually no chance of fixing in growing populations, but are much more likely to be established in shrinking populations (Fig. 1). Otto and Whitlock also look at cases in which population size asymptotically approaches a fixed value or cycles between several values, and find that approaching a fixed population size leads to a fixation probability that converges upon Haldane's result for stable populations, whereas a cycle in population size drives a similar cycle in fixation probabilities. For instance, using the classic example of population size fluctuations in snowshoe hares[9], Otto and Whitlock calculate that, depending on whether the population is growing or shrinking at any given moment, the probability of fixation of new mutants could be as much as three times greater or ten times smaller than a prediction based on the average population size (Fig. 2).

The ecological context of new mutations

Incorporating population dynamics into the evolutionary process has interesting implications for many areas of evolutionary ecology. For example, the explosive diversification of many groups of organisms within a short period (adaptive radiation) has traditionally been thought to accompany a shift to a previously unoccupied habitat. The classical example of this is, of course, Darwin's finches on the Galápagos[10]. Otto and Whitlock's result suggests that rapid population growth following such an invasion could feed back on itself to accelerate the rate of evolutionary change during the radiation. As natural selection adapts the new visitors to local conditions, the new mutations necessary for that adaptation are more likely to successfully make their way into the growing population. In addition, as the population becomes larger, we expect more mutations to enter the population in the first place.

Unfortunately, if populations are instead driven towards extinction, like so many current endangered species, this windfall turns into tragedy. Because of the increased probability that deleterious mutations will become fixed in populations in decline, the mean fitness of the population will be driven down even further as populations become small, yielding a process that has been called 'mutational meltdown'[11].

How rare are beneficial mutations?

The ecological dynamics of a population can have a profound effect on the persistence of new mutations, and may play as large a role in effecting evolutionary change as the deterministic effects of natural selection that dominate the latter half of a mutation's life. Much of this importance, however, depends on exactly how rare advantageous mutations are. If advantageous mutations are common, then the fate of any individual mutation is not important, eventually one of the mutants will make it to fixation. However, if advantageous mutations are rare or even unique, such as some gene duplications or rearrangements might be, then population-size fluctuations may be very important indeed. At present we know too little about how to spot an advantageous mutation to estimate its mutation rate, although looking at the rate of accumulation of new mutations under continued selection provides a good place to start[12].

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Secondarily solitary: the evolutionary loss of social behavior

William T. Wcislo and Bryan N. Danforth

Studies of social behavior frequently assume that evolution proceeds from a solitary state to a social one, and that social lineages give rise to lineages that are also social, excluding parasitic taxa. Recent phylogenetic studies of some bees contradict this assumption, and more examples are known or hypothesized in other animals. Social behavior can be lost to give rise to species that are secondarily solitary. Studies of the conditions that lead to the suppression or loss of social behavior can help to illuminate those factors that lead to its origins and maintenance.

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An understanding of the evolution of social behavior has been critical in formulating general evolutionary principles (e.g. kin selection[1]). Often these studies are dominated by an *a priori* assumption that eusociality – social behavior involving a sterile caste of workers (Box 1) – is an evolutionary endpoint[4]. That is, eusocial ancestors give rise to descendant species that are also eusocial, unless they evolve social parasitism[5]. As applied to insect sociality, 'Dollo's law' of irreversible evolution[6,7] holds true for termites (Isoptera), ants (Formicidae), paper wasps (Vespidae), honeybees (Apini), stingless bees (Meliponini) and bumblebees (Bombini) – we know of no reversals to solitary nesting within these exclusively eusocial clades[8–11]. Wilson[12] hypothesized that these taxa irreversibly crossed a threshold of social integration. Among insects, the benefits of sociality (e.g. more-efficient work, improved defense) are enhanced by strict division of labor, but the resulting co-dependency may make it difficult to regain the full behavioral repertoire of solitary individuals[12,13]. As a general rule, however, there are no *a priori* reasons to suggest that the evolution of eusociality must be irreversible. Eusociality, like any phenotypic trait, is not inherently 'advanced' relative to alternatives such as solitary behavior or communal nesting, and different environmental circumstances may favor one lifestyle over the other[12–16].

The possibility that eusociality can revert to solitary behavior has been hypothesized previously[12–14], especially by biologists studying halictine bees[15–20], yet reversals have been shown empirically only in recent years. Phylogenetic studies of taxa that contain both solitary and social species reveal evidence of apparent evolutionary transitions from eusocial to solitary behavior, contradicting the assumption of unidirectional social evolution. Here, we highlight recent studies and discuss their implications for our understanding of the evolution of social behavior (see also Refs 13, 14 and 20).

Phylogenetic methods and character mapping

Widespread use of cladistic methodology is generating a growing data base that facilitates hypothesis-testing of historical patterns and allows the inference of ancestral states[21–23]. We will not discuss the strengths and weaknesses of different methodologies, except to note that reconstructing ancestral character states is dependent on the veracity of the phylogenies[24]. Hypotheses that require the fewest number of *ad hoc* assumptions about evolutionary changes in character states are preferred over

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