Harvey[3] laments that of 29 papers that analyzed comparative data and that were published in journals of the British Ecological Society during the first nine months of 1995, 25 failed to use phylogenetically based methods. Nevertheless, phylogenetically informed analyses are appearing more frequently, as user-friendly software becomes more available and published phylogenetic hypotheses proliferate. More to the point, many authors have felt pressure from reviewers and editors to adopt phylogenetically based methods of comparison; principally, the method of independent contrasts (that is, PIC). This is easy enough to do, as long as one is not too fussy about the quality of the underlying phylogeny. It does not seem to matter much anyway, as the results of comparative analyses are relatively insensitive to the actual topology or branch lengths of a phylogenetic hypothesis[12].

Contributors to the debate on 'phylogenetic correction' in J. Ecol. are unanimous about the value of phylogenetic information to understanding evolution and contemporary ecological significance of trait variation and covariation. In response to Fitter's[13] question about how one can distinguish independent evolutionary origins of a trait from common inheritance when a phylogeny is not available, Harvey et al.[11] pointedly respond, 'The answer is that it is not possible.' But beyond this kernel of general agreement, disagreement continues to swirl around methods for phylogenetically based comparative analysis, how to interpret results of these analyses, and even whether or not these methods are really necessary. One cannot address the last issue without comparing phylogenetically based methods with phylogeny-free methods. Where such comparisons have been made, phylogeny seems to make a difference in some cases[14,15] but not in others[16]. With respect to the relative merits of different approaches, proponents of one or another method have not been completely forthright about limitations of various techniques. For example, in the case of independent comparisons, calculation of contrasts requires estimation of ancestral character states based on some model of evolutionary change through lineages, subtractions of trait values between pairs of taxa or nodes associated with each contrast, and, in some applications, standardization by branch lengths. The first estimation adds uncertainty to calculated contrasts, while the second increases the error variance of contrasts, and the third may actually bias the magnitudes of contrasts.

In addition, it is difficult to use contrasts to assess changes in patterns of evolutionary response within a lineage over time, because branches of a phylogeny are highly variable in length. When basal and terminal contrasts in a phylogenetic tree are mixed, changes over time in relationships between trait values are blurred. To approach this question at present, one must use hierarchical (nested) analysis of variance and covariance[17,18] to separate basal and distal evolution within a lineage. Despite Ackerly and Donoghue's[6] disdain for using taxonomy for this purpose, taxonomy does bear a correspondence to phylogeny, and it is hierarchically organized. Eschewing its potential to reveal patterns of variation bearing on the nature of historical processes seems nearly as shortsighted as ignoring phylogeny altogether.

The Forum series on comparative methods in J. Ecol. has provided a healthy assessment of new ways of thinking about, and analyzing data pertaining to, evolutionary diversification. The issues raised in these pages are by no means settled, nor should they be at this point. In the end, comparative methods will be judged by how well they serve to increase our understanding of evolutionary processes and the ecological contexts of evolutionary change. On this, the jury is still out. No one should doubt, however, that comparative analysis is merely one step, possibly the easiest step, to this sought-after understanding. Pattern will certainly suggest possibilities for underlying process but, in the end, understanding process will depend on studying process directly.

Robert E. Ricklefs

Dept of Biology, University of Missouri-St Louis, 8001 Natural Bridge Road, St Louis, MO 63121-4499, USA (ricklefs@ecology.umsl.edu)

References
1 Harvey, P.H. and Pagel, M.D. (1991) *The Comparative Method in Evolutionary Biology*, Oxford University Press
2 Harvey, P.H., Read, A.F. and Nee, S. (1995) *J. Ecol.* 83, 535–536
3 Harvey, P.H. (1996) *J. Anim. Ecol.* 65, 255–263
4 Westoby, M., Leishman, M.R. and Lord, J.M. (1995) *J. Ecol.* 83, 531–534
5 Rees, M. (1995) *J. Ecol.* 83, 891–892
6 Ackerly, D.D. and Donoghue, M.J. (1995) *J. Ecol.* 83, 730–733
7 Cheverud, J.M., Dow, M.M. and Leutenegger, W. (1985) *Evolution* 39, 1335–1351
8 Armstrong, D.P. and Westoby, M. (1993) *Ecology* 74, 1092–1100
9 Stearns, S.C. (1983) *Oikos* 41, 173–187
10 Westoby, M., Leishman, M. and Lord, J. (1995) *J. Ecol.* 83, 727–729
11 Harvey, P.H., Read, A.F. and Nee, S. (1995) *J. Ecol.* 83, 733–734
12 Garland, T., Jr and Adolph, S.C. (1994) *Physiol. Zool.* 67, 797–828
13 Fitter, A.H. (1995) *J. Ecol.* 83, 730
14 Garnier, E. (1992) *J. Ecol.* 80, 665–675
15 Kelly, C.K. and Purvis, A. (1993) *Oecologia* 94, 356–360
16 Ricklefs, R.E. and Starck, J.M. *Oikos* (in press)
17 Derrickson, E.M. and Ricklefs, R.E. (1988) *Funct. Ecol.* 2, 417–423
18 Bell, G. (1989) *Am. Nat.* 133, 553–579

Evolution in fluctuating environments: a game with kin

A dry summer or a hurricane exemplify the many unpredictable environmental fluctuations that affect all members of a population. Such fluctuations are known to have some counter-intuitive consequences for what strategies survive in the long term, and now McNamara[1,2] has formalized the idea that relatives should behave as if playing a cooperative game. This and other recent work[3–5] will enable evolutionary biologists to understand quantitatively how organisms are adapted to cope with occasional fires, famines, frosts or floods.

Seed dormancy in annual plants is the classic example[6]. Suppose that a plant can produce seeds that germinate in their first spring and also special seeds that remain dormant for several years. In some years, frost kills all germinating plants, so genotypes that produce some dormant seeds will clearly be the only survivors in the long term. On the other hand, dormant seeds reproduce more slowly and have more chance of being eaten, so some ordinary seeds should also be produced to increase reproductive rate in frost-free years. It is because the environmental fluctuations affect the whole population that optimal strategies involve a mixture of actions. Biologists who are used to thinking in terms of maximization of individual fitness are often perturbed that a seed should 'agree' not to germinate immediately when its own chances of reproducing are lower if it spends a year in dormancy. In fact, there is no parent–offspring conflict[6] because what counts is how many copies of a gene survive, not numbers of direct descendants. If nearly all seeds from a plant have been programmed to germinate immediately, on average it favours the long-term success of the genes shared by all the seeds and the parent if a few seeds lie dormant (and vice versa). Thus the optimal proportion of dormant seeds will be the same as if the seeds were playing a cooperative game.

'Game' is a technical term describing the situation where each player's best strategy depends on the strategies used by the others. What is remarkable about game theory being applicable to fluctuating environments is that the players (relatives) need never physically interact, compete or even communicate; nor need there be any frequency-dependent selection, such as is needed to maintain some genetic polymorphisms. Normally in biological games, the evolutionarily stable mixture of actions can be realized by several genotypes, each coding for one action, but in fluctuating environments this is not stable to invasion by a single mixed strategy, where each individual 'flips a coin' to decide which action to perform[7].

To explain the recent formalization and developments of these intuitive ideas, let us suppose that various actions are available (each signified by a_i). A single action corresponds to, for example, reproducing in May rather than June, or laying five eggs rather than four. The optimal mixture of actions P^* specifies the probability that each action is performed. Sasaki and Ellner[3] wrote down a condition for this mixture to be optimal, which is also used by Haccou and Iwasa[4], and which McNamara[1] has generalized. For all actions included in the optimal strategy:

$$\int_0^\infty \frac{D(a_i,s)}{r_{P^*}(s)} f(s)\mathrm{d}s = 1 \qquad (1)$$

and, for all other actions, this quantity will be less than or equal to 1. $D(a_i,s)$ is the number of descendants produced when following action a_i and when the environmental conditions that year are s. $f(s)$ is the probability of the conditions being s. $r_{P^*}(s)$ is the number of descendants produced when the conditions are s, if the mixture of actions followed is optimal. The left-hand side of eqn (1) is thus just a weighted sum of descendants under all possible environmental conditions if one single action is followed, where the weighting emphasizes conditions that are harsh [$r_{P^*}(s)$ low] and common [$f(s)$ high].

Eqn (1) says that whether or not an action should be performed depends not only on the number of descendants present when following that action [$D(a_i,s)$], but also on the success of other actions performed by other members of the genotype [$r_{P^*}(s)$]. McNamara[1] has shown that there is a precise quantitative analogy with a playing-the-field game in a non-fluctuating environment. Thus, in game theory, the pay-off associated with one action depends on the actions of other individuals: to find the best strategy for any one player we need to know the pay-off of each strategy, but the eventual pay-off depends on what is the best strategy for the other

players. Similarly, the difficulty with using eqn (1) to find the optimal mixture of actions is that we do not know $r_{P^*}(s)$ until the optimal mixture is already known.

Nevertheless, eqn (1) is a powerful tool, because techniques exist to find evolutionarily stable strategies (ESSs) in biological games. The simplest application uses eqn (1) to check whether or not a particular mixture of actions is optimal[1,4]. McNamara[1] also gives a procedure guaranteed to find the optimal mixture. Try out one mixture P_0 by first calculating $r_{P_0}(s)$ and then find any action for which:

$$\int_0^\infty \frac{D(a_i,s)}{r_{P_0}(s)} f(s)\mathrm{d}s > 1 \qquad (2)$$

Increasing the probability that this action is performed will improve the mixture of actions; using this improved mixture P_1, the procedure is repeated, and by this method of successive improvement, the mixture converges to the global optimum. Without such a method, finding an optimum would often be very difficult since all combinations of probabilities of all possible actions should be evaluated and any optimum found may just be a local optimum.

McNamara (unpublished) uses his method to calculate a bird's optimal clutch size. The results confirm one verbal explanation for why field workers usually find that an egg added to a nest does not reduce the number of offspring fledged[8] [in a non-fluctuating environment any such manipulation should reduce success; but in a fluctuating environment birds should have smaller clutch sizes that budget more for the rare, poor year, when $r_{P^*}(s)$ is low]. A more startling insight is that the optimal clutch size appropriate for a particular quality of territory cannot be predicted without knowing the likely qualities of other territories that relatives may occupy. Another paper[2] tackles a more complex scenario, where each action is a sequence of decisions. This problem in a fluctuating environment is equivalent to a dynamic game in a non-fluctuating environment, which is solvable using dynamic programming and, again, an iterative technique of successive improvements.

Others have taken a complementary approach, avoiding these iterative numerical techniques and finding analytic solutions to eqn (1) in simpler cases, where well-behaved functions specify fitness and the probability distribution of environmental conditions[3,4]. The main question addressed has been how many different actions should be used by the optimal strategy. With little environmental stochasticity a single action is still optimal, although this differs from the action appropriate in a constant environment. As stochasticity increases the optimal strat-

egy will select randomly from two or more actions, but not necessarily from a continuous range of actions. Nevertheless, continuous ranges of actions are optimal in certain situations and perform well in others[4], so it is still controversial how often they should occur in nature. What is important is that the range of actions shows sufficient variance. Paradoxically, in uncertain environments some individuals can take much greater risks than in constant environments, since the success of their genotype is 'insured' by the extra-safe actions now taken by relatives.

Nobody has yet applied this game-theoretic approach to model real populations subject to measured environmental fluctuations; to do so, various further complications will often need to be incorporated. It usually should be possible to deal with sexual reproduction by discounting the number of descendants by their relatedness[2]. A more elaborate, state-dependent dynamic model would be required when organisms gradually acquire knowledge of the forthcoming conditions[2], for instance, because conditions between years are autocorrelated (a drought will be worse if no rain fell the previous year). Being able to estimate conditions has some consequences similar to a reduction in environmental stochasticity[4]. A technically much more difficult complication is a state-structured population[5], for example, where the choice of action should depend on how many years old the animal is or how large the tree has grown. The optimal policy is then conditional on the distribution of states in the whole population (which will depend on past as well as current conditions), but it may be unrealistic to model the organism as being able to assess this very accurately.

However, I see a more fundamental problem being that, in real life, strategies are not immutable[4]. What genetic and developmental mechanisms exist to stop the strategy evolving away from the long-term optimum between the occasional catastrophes? Long-term field studies, such as that on Darwin's Finches evolving in response to occasional El Niño events[9], are required to test how well the theory applies in practice.

John M.C. Hutchinson

*School of Biological Sciences,
University of Bristol, Woodland Road,
Bristol, UK BS8 1UG*

References
1 McNamara, J.M. (1995) **Implicit frequency dependence and kin selection in fluctuating environments,** *Evol. Ecol.* 9, 185–203

NEWS & COMMENT

2 McNamara, J.M., Webb, J.N. and Collins, E.J. (1995) Dynamic optimization in fluctuating environments, *Proc. R. Soc. London Ser. B* 261, 279–284

3 Sasaki, A. and Ellner, S. (1995) The evolutionarily stable phenotype distribution in a random environment, *Evolution* 49, 337–350

4 Haccou, P. and Iwasa, Y. (1995) Optimal mixed strategies in stochastic environments,

Theor. Popul. Biol. 47, 212–243

5 McNamara, J.M. Optimal life histories for structured populations in fluctuating environments, *Theor. Popul. Biol.* (in press)

6 Ellner, S. (1986) Germination dimorphisms and parent–offspring conflict in seed germination, *J. Theor. Biol.* 123, 173–185

7 Cooper, W.S. and Kaplan, R.H. (1982) Adaptive 'coin-flipping': a decision-theoretic

examination of natural selection for random individual variation, *J. Theor. Biol.* 94, 135–151

8 Boyce, M.S. and Perrins, C.M. (1987) Optimizing Great Tit clutch size in a fluctuating environment, *Ecology* 68, 142–153

9 Grant, B.R. and Grant, P.R. (1993) Evolution of Darwin's finches caused by a rare climatic event, *Proc. R. Soc. London Ser. B* 251, 111–117

Whorled, wiled webs

'Oh what a tangled web we weave, When first we practise to deceive!' These much-parodied lines of Sir Walter Scott probably sprang from his familiarity with textile manufacturing rather than from knowledge of spiders. At least, that is what I would have assumed, having presumed that spider webs are just passive filters whose deceptive nature is limited to imperceptibility. In a series of papers, however, Catherine Craig and her colleagues have proposed that some spiders practise more active forms of visual deception, exploiting insect visuomotor responses to wile prey into their webs.

Craig, Bernard and Coddington[1] documented that nocturnal foraging activity and production of silks with peak reflection in the ultraviolet (UV) region of the spectrum are primitive characters for spiders (see Fig. 1 in Craig's 1992 *TREE* article[2]). Radiation of the lineage produced some groups that foraged in dim habitats (diurnal forest) and others that foraged in bright zones (diurnal nonforest). The spectral qualities of spider silks also diversified, so that some showed 'flat' spectra (high reflectance from short to long wavelengths), while others had peaks in the yellow–red part of the spectrum with low reflectance in UV. The latter spectral property of silks is found only in members of the superfamily Araneoidea, a diverse group of aerial web spinners that forage diurnally, some in forests and some in open habitats. The viscid silk of araneoids is produced by unique glands and is unusually elastic.

Whether the UV-reflecting properties of primitive spider silks arose as a specific adaptation or as some accidental side-effect of its production is not clear. Nevertheless, Craig and Bernard[3] demonstrated a potential benefit of UV reflection. They showed that fruitflies (*Drosophila* spp.) are more attracted to such webs when the webs are illuminated by white light containing a UV component than when they are illuminated by white light without UV. Other experiments showed that the webs could be seen when UV light was not present, but that they were then avoided; this suggested that the fruitflies would prefer

to avoid the webs, but that they were attracted to them when they reflect UV light. Craig and Bernard proposed that the insects' motor responses to UV perception could not be modified significantly by learning or selection because of their importance in insect foraging. UV insect attraction could be advantageous both to spiders whose prey are caught primarily at night and to those spiders who are active in the diurnal forest understory[4]. Craig[5] also noted that the attractive effect of UV-reflecting webs could make insects locally abundant even when they are scarce overall and thereby make possible the communal social organizations seen in some spiders.

Why should the derived aerial web spinners produce catching silks that are spectrally flat or with reduced reflectance in the UV? Possibly, the molecular structure and mechanical properties needed to capture large or fast-flying prey in aerial webs are somehow inconsistent with a high UV reflectance peak for the catching silk. In any case, silks with flat spectra will still have a reflectance component in the UV, and species with catching silks that do not reflect UV may nevertheless use UV lures. Craig and Bernard[3] showed that *Argiope argentata* – an araneoid whose catching silks have low UV reflectance – adds to its webs silk 'decorations' that do reflect UV. Experimental manipulations indicated that the webs of this species capture more prey with the UV decorations than without them. The dorsal body surfaces of *A. argentata* also reflect UV, and Craig and Ebert[6] found that more pollinating insects were attracted to webs when this surface was experimentally enhanced than when it was concealed. Craig[5] showed further that more prey were attracted to webs when *A. argentata* occurred in clusters than when they were isolated. The spiders' ability to vary their decorative patterns and locations of UV reflection may also help to impede avoidance learning by insects[7].

Unlike *A. argentata*, some advanced araneoids apparently produce little or no UV reflection on either their bodies or their webs. Have they given up attractive deception? In at least one case, the an-

swer is 'not necessarily'. Craig[8], and Craig, Weber and Bernard[9] studied the golden orb weaver (*Nephila clavipes*) in Panama. They showed that individual *Nephila* could produce webs of varying appearance, depending on the spiders' light environment, under both free-living and laboratory conditions. In forested habitats, and in laboratory trials using blue–green light that is characteristic of such habitats[10], the spiders produced webs of whitish silk, like the non-decorative parts of *A. argentata* webs. In open habitats, light gaps, and laboratory trials conducted under light that was rich in yellow and orange wavelengths, these viscid silks appeared golden yellow. This yellow cut-off filter effect is caused by masking pigments added to the silk proteins and viscid droplets that coat the silk[9].

Why make the webs golden yellow in brightly illuminated sites? Craig and her colleagues found that capture probability of *Trigona fluviventris*, a stingless bee that is an important prey of *N. clavipes*, was not affected by web pigmentation in shaded habitats; but, in brightly illuminated sites, the bees seemed positively attracted to yellow-pigmented webs and showed difficulty learning to avoid them. Although the bees more often avoided yellow webs than unpigmented webs on first encounter under these light conditions, their tendency to return to the yellow webs made them more vulnerable to capture in the long run. It was suggested that this may be another case of spiders exploiting a prey species' taxic responses to flower coloration, in this case yellow. Because the yellow silk pigments provide little if any benefit in dim habitats, the tendency of the spiders to reduce or eliminate silk coloration in such sites may indicate that the pigments are somehow costly.

A number of questions spring from this work. Do the behavior patterns of *Drosophila* and *Trigona* represent those of most orb-weavers' prey? Why do primitive spiders produce webs with only a UV reflectance peak, rather than with flat spectra or several peaks (some flowers, after all, have several reflectance peaks)? Was the evolutionary loss of UV reflectance in silks of advanced orb-weavers a trade-off allowing the development of some other advantageous silk property, or was this loss itself adaptive? What is the nature and magnitude of the cost of pigment production for