

appropriate to that level, laws that are not conveniently reducible to laws at lower levels'. A football player may play brilliantly in one team and perish after transfer to another. The qualities of a good player not only include his dribbles, passes and headers, but foremost his interactions with other players in the field.

Peter H. Van Tienderen

Netherlands Institute of Ecology,
PO Box 40, 6666 ZG Heteren,
The Netherlands

References

- 1 Rollo, C.D. (1994) *Phenotypes: Their Epigenetics, Ecology and Evolution*, Chapman & Hall
- 2 Van Tienderen, P.H. (1995) *Trends Ecol. Evol.* 10, 509–510
- 3 Dawkins, R. (1982) *The Extended Phenotype*, Oxford University Press

Chaos and evolution

In their recent *TREE* review on the significance of chaos for evolutionary processes, Ferrière and Fox¹ argued convincingly that nonlinear and complex dynamics should be taken into consideration when studying the general problem of evolution. One of the topics of the article was the evolution of chaos itself as a possible form of population dynamics.

To support the claim that complex population dynamics should evolve, the authors cited their own work showing that chaos is favoured by natural selection in one particular model. However, they did not mention that another study showed opposite results in a more general setting².

We considered models for populations with discrete generations of the form $N(t+1) = N(t) f[N(t)]$, where $N(t)$ is the population density at time t , and $f(N)$ is the fitness function, that is, the reproductive output per individual at a given density N . This fitness function is determined by demographic parameters such as the intrinsic growth rate and the carrying capacity of the population, and these parameters in turn determine the type of dynamics exhibited by the population. Such models were used by May³ to introduce the paradigm of chaos to ecology. We showed² that for three general fitness functions describing competitive interactions, the demographic parameters typically evolve to regions in parameter space that code for stable equilibria. Thus, in these models there is a clear tendency for natural selection to favour simple dynamics.

These results are more general than those obtained from the model referred to in the review, and more precise than the verbal arguments given there for the evolution of chaos. Thus, Ferrière and Fox did not deal objectively and even-handedly with the literature. The same can be said with respect to the effects of segregation and recombination on dynamic stability. Here, several studies^{4–7} show the field to be less void of results than claimed by these authors and these studies reveal that

complex dynamics are less likely in ecological models that incorporate population genetics.

Michael Doebeli

Zoology Institute, University of Basel,
Rheinsprung 9, CH-4051 Basel,
Switzerland (doebeli@ubaclu.unibas.ch)

Jacob Koella

Dept of Zoology, University of Aarhus,
Universitetsparken B135, DK-8000
Aarhus C, Denmark (koella@aau.dk)

References

- 1 Ferrière, R. and Fox, G.A. (1995) *Trends Ecol. Evol.* 10, 480–485
- 2 Doebeli, M. and Koella, J.C. (1995) *Proc. R. Soc. London Ser. B* 260, 119–125
- 3 May, R.M. (1976) *Nature* 261, 459–467
- 4 Doebeli, M. and Koella, J.C. (1994) *Proc. R. Soc. London Ser. B* 257, 17–23
- 5 Doebeli, M. (1995) *J. Evol. Biol.* 8, 173–194
- 6 Ruxton, G.D. (1995) *J. Theor. Biol.* 175, 595–601
- 7 Doebeli, M. *Evolution* (in press)

Age and breeding performance in monogamous birds: the influence of mate experience

In a comment referring to our *TREE* article¹, Cézilly and Nager² suggest that individuals may improve their reproductive performance through repeated breeding attempts with the same partner, and they refer to studies that show mate experience to be associated with an increase of reproductive performance. Furthermore, they propose that testing the significance of breeding experience on reproductive performance should systematically control for the amount of mate experience, especially in species with a high rate of mate fidelity. Cézilly and Nager have drawn attention to an important issue that clearly requires further discussion.

The possibility that mate experience may improve reproductive success was only briefly mentioned by us¹. However, contrary to Cézilly and Nager, we argue that: (1) the mechanisms leading to possible benefits of mate experience are largely unknown; (2) empirical evidence of a causal relationship between mate experience and reproductive performance is lacking; and (3) testing the effects of breeding experience when holding mate experience constant (or vice versa) needs experimental rather than statistical control.

Increased reproductive performance through increased mate experience is usually believed to be caused by fine-tuning the coordination of breeding activities, such as changeover in shared incubation, nest protection against predators, and other parental duties^{2,3}. However, no study has demonstrated mate coordination to increase the efficiency in any of these activities³. Clearly, the lack of data indicates the need to specifically investigate the potential mechanisms of mate coordination.

Several studies have shown mate experience to be associated with increased reproductive performance, especially in the beginning of a long-term pair-bond^{2,3}. However, many have not

controlled for the confounding effects of age and breeding experience², and none has controlled for differences in individual quality³. Thus, present empirical evidence for reproductive benefits accruing as a result of mate experience suffer from the same problems of confounding factors as most studies investigating effects of breeding experience^{1,4}. For example, individuals with long-lasting pair-bonds may be of better quality than those with shorter pair-bonds, either because high-quality individuals are more likely to stay together⁵ or owing to selective death of poor quality individuals³. As a result, pairs with much mate experience may be better performers than pairs with less mate experience because of differences in individual quality and not because of mate experience *per se*.

Cézilly and Nager suggest that when testing for effects of breeding experience one should systematically control for the duration of the pair-bond (i.e. mate experience)². We agree with this opinion, but disagree with their recommendation of using statistics to obtain the 'control'. This is because statistics cannot control for factors that are not measured, such as individual differences in quality. Instead, making an experiment is a reliable method for separating the different causes of increased reproductive performance with age and for avoiding the confounding effects of individual quality differences^{1,4}. Obviously, there are a number of difficulties of performing such an experiment in the field, since the effects of age, breeding experience and individual quality of both partners must be controlled for. An alternative therefore may be to investigate the mechanisms of mate coordination. For example, one could compare the sex roles in nest protection, incubation and the exploitation of food resources in time and space when feeding young, before and after an experimentally induced divorce. Although age, breeding experience and individual quality are not controlled for in such an experiment, at least it allows the testing of whether parental behaviours are affected by mate experience.

To conclude, and as we emphasized in our *TREE* paper¹, we believe that only carefully designed experiments can disentangle the relative importance of mate experience, and other factors, on reproductive performance.

Tomas Pärt

Dept of Wildlife Ecology, SLU, Box 7002,
S-750 07 Uppsala, Sweden

Pär Forslund

Dept of Wildlife Ecology, SLU,
Grimsö Wildlife Research Station,
S-730 91 Riddarhyttan, Sweden

References

- 1 Forslund, P. and Pärt, T. (1995) *Trends Ecol. Evol.* 10, 374–378
- 2 Cézilly, F. and Nager, R.G. (1996) *Trends Ecol. Evol.* 11, 27
- 3 Ens, B.J., Choudhury, S. and Black, J.M. (1996) in *Partnership in Birds: The Study of Monogamy* (Black, J.M., ed.), pp. 344–400, Oxford University Press
- 4 Pärt, T. (1995) *Proc. R. Soc. London Ser. B* 360, 113–117
- 5 Perrins, C.M. and McCleery, R.H. (1985) *Ibis* 127, 306–315