

- 27 Schluter, D. (1995) **Adaptive radiation in sticklebacks: Trade-offs in feeding performance and growth**, *Ecology* 76, 82–90
- 28 Smith, T.B. and Skulason, S. (1996) **Evolutionary significance of resource polymorphisms in fish, amphibians and birds**, *Annu. Rev. Ecol. Syst.* 27, 111–133
- 29 McPhail, J.D. (1984) **Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): Morphological and genetic evidence for a species pair in Enos Lake, British Columbia**, *Can. J. Zool.* 62, 1402–1408
- 30 Schluter, D. (1994) **Experimental evidence that competition promotes divergence in adaptive radiation**, *Science* 266, 798–801
- 31 Schluter, D. and Nagel, L.M. (1995) **Parallel speciation by natural selection**, *Am. Nat.* 146, 292–301
- 32 Rice, R.R. and Hostert, E.E. (1993) **Laboratory experiments on speciation: what have we learned in 40 years?** *Evolution* 47, 1637–1653
- 33 Orr, M.R. (1996) **Life-history adaptation and reproductive isolation in a grasshopper hybrid zone**, *Evolution* 50, 704–716
- 34 Feder, J.L. *et al.* (1997) **Selective maintenance of allozyme differences among sympatric host races of the apple maggot fly**, *Proc. Natl. Acad. Sci. U. S. A.* 94, 11417–11421
- 35 Feder, J.L. *et al.* (1994) **Host fidelity is an effective premating barrier between sympatric races of the apple maggot fly**, *Proc. Natl. Acad. Sci. U. S. A.* 91, 7990–7994
- 36 Endler, J.A. and Basolo, A.L. (1998) **Neuroecology, perceptual biases, and sexual selection**, *Trends Ecol. Evol.* 13, 415–420
- 37 Endler, J.A. and Théry, M. (1996) **Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds**, *Am. Nat.* 148, 421–452
- 38 Ryan, M.J. and Wilczynski, W. (1991) **Evolution of intraspecific variation in the advertisement call of a cricket frog (*Acris crepitans*, Hylidae)**, *Biol. J. Linn. Soc.* 44, 249–271
- 39 Seehausen, O., van Alpen, J.M. and Witte, F. (1997) **Cichlid fish diversity threatened by eutrophication that curbs sexual selection**, *Science* 277, 1808–1811
- 40 Brower, A.V.Z. (1994) **Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution**, *Proc. Natl. Acad. Sci. U. S. A.* 91, 6491–6495
- 41 Zink, R.M. and Dittmann, D.L. (1993) **Gene flow, refugia, and evolution of geographic variation in the song sparrow (*Melospiza melodia*)**, *Evolution* 47, 717–729
- 42 Mayr, E. (1963) *Animal Species and Evolution*, Harvard University Press
- 43 Felsenstein, J. (1981) **Skepticism towards Santa Rosalia, or why are there so few kinds of animals?** *Evolution* 35, 124–138

Mast seeding and Lyme disease

We wish to comment on two issues relating to a prediction raised in the article by Randolph¹ about our work². Randolph argues that because 'low acorn production and moderate mouse densities are the norm [our] data do not explain the cause of the severe acorn failures and contingent crash in mouse populations that might initiate [gypsy] moth outbreaks'. We made no attempt to explain masting periodicity, but autumnal mast production does predict white-footed mouse (*Peromyscus leucopus*) density the following summer^{3–5}. Moderate mouse densities are indeed the norm. In most summers, densities are at or above c. 10 mice ha⁻¹, which is sufficient to keep gypsy moth (*Lymantria dispar*) populations low via pupal predation^{4–6}. However, mouse populations do periodically collapse to below 10 ha⁻¹ for one to two summers^{3,4}. Evidence indicates that this is when moth populations, with their high fecundity, can rise to levels mice cannot suppress^{2,4,5}. Mouse population collapses tend to occur if major masting events, which result in very high mouse densities, are followed by mast failure and food limitation. These events occur with a frequency similar to moth outbreaks^{3,4}.

Randolph challenges our conclusion that white-footed mice play the major role in infecting *Ixodes scapularis* ticks with *Borrelia burgdorferi*. However, in the eastern United States, *P. leucopus* is both the most abundant host for ticks and by far the most competent reservoir for *B. burgdorferi*⁷. Furthermore, Mather and Ginsberg⁸ demonstrated that the prevalence of spirochete infection in nymphal *I. scapularis* ticks strongly correlates with white-footed mouse density in the previous year. In our forests, acorns markedly affect mouse density, the density of host-seeking larval ticks and the number of ticks attached to mice². Therefore, we conclude that acorn production should allow epidemiologists to predict Lyme disease risk well in advance, here in the USA⁹.

The European situation, in which several tick hosts are competent reservoirs, will probably make predicting Lyme disease risk more difficult. Nevertheless, we hope that epidemiologists will test the power of acorn production as a predictor of Lyme disease risk in European oak forests.

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References

- 1 Randolph, S.E. (1998) *Trends Ecol. Evol.* 13, 301–303
- 2 Jones, C.G. *et al.* (1998) *Science* 279, 1023–1026
- 3 Wolff, J.O. (1996) *J. Mammol.* 77, 850–856
- 4 Ostfeld, R.S., Jones C.G. and Wolff, J.O. (1996) *Bioscience* 46, 323–330
- 5 Elkinton, J.S. *et al.* (1996) *Ecology* 77, 2332–2342
- 6 Elkinton, J.S. and Liebhold, A.M. (1990) *Annu. Rev. Entomol.* 35, 571–596
- 7 Mather, T.N. (1993) in *Ecology and Environmental Management of Lyme Disease* (Ginsberg, H.S., ed.), pp. 43–62, Rutgers University Press
- 8 Mather, T.N. and Ginsberg, H.S. (1994) in *Ecological Dynamics of Tick-borne Zoonoses* (Sonenshine, D.E. and Mather, T.N., eds), pp. 68–90, Oxford University Press
- 9 Ostfeld, R.S. (1997) *Am. Sci.* 85, 338–346

In her cogent review of the factors controlling levels of Lyme disease, Randolph¹ makes one small error. She shows that 'mast years' (high acorn crops) are associated with outbreaks of mice, with variable effects on densities of the ticks that carry Lyme disease. In years of very low or no acorn production, reduced mouse predation allows higher survival of gypsy moths, which may trigger an outbreak of the moths. She then says that 'these data [on mast years], therefore, do not explain the cause of the severe acorn failures and contingent crash in mouse populations that might initiate ... moth outbreaks'.

This apparently reasonable but erroneous conclusion stems from confusion about the nature of mast seeding. Mast seeding does not describe occasional high years, while remaining silent about patterns of seed production in moderate or low years. Plants actually have a log-normal distribution of seed crops, with low and high years often being equally predictable from previous climatic conditions². For example in *Chionochloa* in New Zealand, crop failures occur when mean temperatures the previous January and February are less than 10°C (Ref. 3).

Therefore, any competent analysis of the acorn production pattern is likely to predict years of crop failure (and moth outbreaks) as well as 'mast years'. Combined with what Randolph describes about host specificity and interactions, the result is likely to be greater predictive power about disease dynamics.

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References

- 1 Randolph, S.E. (1998) *Trends Ecol. Evol.* 13, 301–303
- 2 Kelly, D. (1994) *Trends Ecol. Evol.* 9, 465–470
- 3 McKone, M.J., Kelly, D. and Lee, W.G. (1998) *Glob. Change Biol.* 4, 591–597