amphibian population declines [10]. More research, preferably experimental and at the population level, is badly needed.

Acknowledgements
I thank Josh Van Buskirk for helpful comments and the Forschungskredit of the University of Zürich for support.

References
1 Sih, A. *et al.* (2004) Two stressors are far deadlier than one. *Trends Ecol. Evol.* 19, 274–276
2 Relyea, R.A. (2002) Predator cues and pesticides: a double dose of danger for amphibians. *Ecol. Appl.* 13, 1515–1521
3 Boone, M.D. and Semlitsch, R.D. (2001) Interactions of an insecticide with larval density and predation in experimental amphibian communities. *Conserv. Biol.* 15, 228–238
4 Forbes, V.E. and Calow, P. (2002) Population growth rate as a basis for ecological risk assessment of toxic chemicals. *Philos. Trans. R. Soc. Lond. Ser. B* 357, 1299–1306
5 Boone, M.D. and C.M. Bridges (2003) Effects of pesticides on amphibian populations. In *Amphibian Conservation* (Semlitsch, R.D., ed.), pp. 152–167, Smithsonian Institution Press
6 Forbes, V.E. *et al.* (2003) Joint effects of population density and toxicant exposure on population dynamics of *Capitella* sp. I. *Ecol. Appl.* 13, 1094–1103
7 Vonesh, J.R. and De la Cruz, O. (2002) Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia* 133, 325–333
8 Biek, R. *et al.* (2002) What is missing in amphibian decline research: insights from ecological sensitivity analysis. *Conserv. Biol.* 16, 728–734
9 Davidson, C. *et al.* (2002) Spatial tests of the pesticide drift, habitat destruction, UV-B, and climate-change hypotheses for California amphibian declines. *Conserv. Biol.* 16, 1588–1601
10 Houlahan, J.E. *et al.* (2000) Quantitative evidence for global amphibian population declines. *Nature* 404, 752–755

doi:10.1016/j.tree.2004.06.006

Letters Response

Response to Schmidt. Pesticides, mortality and population growth rate

Andrew Sih[1], Jake Kerby[1], Alison Bell[2] and Rick Relyea[3]

[1]Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA
[2]Environmental and Evolutionary Biology, University of Glasgow, UK, G12 8QQ
[3]Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, USA

In his comment on our recent *TREE* report [1] about new work showing very strong synergistic effects of pesticides and predation risk on tadpole mortality [2], Schmidt makes two important points [3]: (i) individual effects (e.g. behavior or mortality) do not necessarily translate into population effects; and (ii) if there is strong density dependence in the larval stage, enhanced tadpole mortality might not be very important. We agree with his basic points, but come to a different conclusion. Schmidt concludes that the work described in our report 'might help us to understand only a little about the processes leading to local and global amphibian population declines' [3]. By contrast, we suggest that studies on individual responses are a crucial part of an integrative approach to understanding multiple stressor impacts on natural populations. Our view is based on both conceptual and practical grounds.

From a conceptual perspective, we believe that an ideal approach should blend individual and population-level studies to gain a multi-level integrative mechanistic understanding of factors governing population performance [4]. Whereas Schmidt [3], following Forbes and Calow [5], emphasizes that it is difficult to predict population performance from individual effects, we emphasize the flipside – that it is difficult to understand population and community dynamics without studying individual responses [6]. In particular, understanding how individuals cope (or do not cope) with conflicting demands is likely to be crucial for understanding multiple stressor impacts on populations.

From a practical perspective, although it is easy to suggest that we should study impacts of toxicants (and, ideally, synergistic effects of toxicants and natural biotic stressors) on populations, this is a 'challenging task', as Schmidt [3] notes. In his article [3], Schmidt also emphasizes that work by Forbes and colleagues [7] shows that it can be done; however, this study was carried out on a small, relatively immobile, short-lived (with a generation time of a few weeks) invertebrate. Comparable studies on amphibians would take years, probably decades, and should be done on a metapopulation landscape scale. Doing this for one species is challenging; doing it for hundreds of amphibian species and tens of thousands of registered chemicals is infeasible. A practical alternative is to make inroads by studying individual-level responses to multiple stressors in multiple life-history stages.

Schmidt's other main point (drawn from [8]), that strong density dependence can make the larval stage relatively unimportant to population ecology, is intriguing. The implication is that exposure to pesticides and predation risk (predator cues), which caused up to 90% larval mortality in just a few days, might be unimportant. This criticism potentially applies not only to ecotoxicology, but also to larval amphibian ecology in general. Have

Corresponding author: Andrew Sih (asih@ucdavis.edu).
Available online 24 June 2004

hundreds of amphibian ecologists been wasting their time? Probably not. In fact, changes in amphibian larval habitat quality that alter larval mortality rates often have major impacts at the population level [9,10]. Larval mortality does matter. Even with density dependence, insights on how interacting factors influence larval mortality should contribute to our understanding of amphibian decline.

References

1 Sih, A. *et al.* (2004) Two stressors are far deadlier than one. *Trends Ecol. Evol.* 19, 274–276
2 Relyea, R.A. (2002) Predator cues and pesticides: a double dose of danger for amphibians. *Ecol. Appl.* 13, 1515–1521
3 Schmidt, B.R. (2004) Pesticides, mortality and population growth rate. *Trends Ecol. Evol.* Doi.: 10.1016/j.tree.2004.06.06
4 Sih, A. and Gleeson, S.K. (1995) A limits-oriented approach to evolutionary ecology. *Trends Ecol. Evol.* 10, 378–382
5 Forbes, V.E. and Calow, P. (2002) Population growth rate as a basis for ecological risk assessment of toxic chemicals. *Philos. Trans. R. Soc. Lond. Ser. B* 357, 1299–1306
6 Sutherland, W.J. and Norris, K. (2002) Behavioural models of population growth rates: implications for conservation and prediction. *Philos. Trans. R. Soc. Lond. Ser. B* 357, 1273–1284
7 Forbes, V.E. *et al.* (2003) Joint effects of population density and toxicant exposure on population dynamics of *Capitella* sp. I. *Ecol. Appl.* 13, 1094–1103
8 Vonesh, J.R. and De la Cruz, O. (2002) Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. *Oecologia* 133, 325–333
9 Gamradt, S.C. and Kats, L.B. (1996) Effect of introduced crayfish and mosquitofish on California newts. *Conserv. Biol.* 10, 1155–1162
10 Vredenburg, V.T. (2004) Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. *Proc. Natl. Acad. Sci. U. S. A.* 101, 7646–7650

doi:10.1016/j.tree.2004.06.011

Book Reviews

Gone to the dogs

Biology and Conservation of Wild Canids edited by David W. Macdonald and Claudio Sillero-Zubiri. Oxford University Press, 2004. £80.00/US$135.75 hbk, £37.50, US$63.75 pbk (432 pages) ISBN 0 19 851555 3/0 19 851556 1

Joshua Ginsberg

Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA

David Macdonald's lab at the University of Oxford has produced an impressive amount of information about the biology and conservation of wild canids and, not surprisingly, many of the authors of chapters in *The Biology and Conservation of Wild Canids* have passed through his lab. The volume is divided into two sections and has many splendid chapters that describe our current knowledge of the 36 extant wild species in the Family Canidae.

In the 'Reviews' section, four chapters stand out. Wang *et al.* ('Ancestry') deftly blend morphological, paleontological, and genetic data into a well woven story about the evolution of the Family. Flowing seamlessly on after 'Ancestry' is a tour-de-force chapter 'Population Genetics' by Wayne *et al.* Wayne, his students and associates have dominated the study of canid genetics for 20 years and summarize what we know about the genetics of the Family, with 12 insightful case studies. After reading this chapter, no one will ever ask again about the relevance of genetics to setting conservation priorities, the understanding patterns of species differentiation, or the relationship between the two.

'Society' (by Macdonald *et al.*) reviews the remarkable variety of canid sociality. Most canids live in pairs but sociality in canids shows remarkable variation, from almost solitary behavior of some foxes to species such as the African wild dog, in which sociality has been taken to its extreme in cooperative breeding, and hunting. The chapter is at its best when it focuses on aspects of communal living, although discussions of dispersal and explanations for sociality round out the chapter nicely. In 'Infectious Disease', Woodroffe and co-authors show that, although wild canids are vectors, they are more often victims of disease. Their relatedness to domestic dogs, their position in food chains, and their wide-ranging behavior all make canids particularly susceptible to disease.

In 'Management', Sillero-Zuberi *et al.* cover the complex issues surrounding canid–human conflict: a change of title to better reflect the focus on conflict, expansion of scope, and the addition of tables (well used in the disease chapter) would make the chapter more useful. The 'Tools' chapter provides a gloss on too many issues, many covered in greater detail in other chapters. In the first chapter in the Reviews section, '*Dramatis personae*' Macdonald and Sillero-Zubiri give a good overview of the book, and its themes, but the chapter is encumbered with a 23-page species-by-species account of canids that is often redundant with the 'Case Studies' chapters and might have been better presented in a few tables, or perhaps as an addendum for those species not covered.

The 'Case Studies' section covers nearly half of the described canid species and the chapters divide into straightforward reviews and comparative ecology analyses (although are not grouped as such, alas). Several chapters represent some of the best discussion and synthesis of what we know about individual species and

Corresponding author: Joshua Ginsberg (jginsberg@wcs.org).
Available online 12 May 2004