

## Biological control: disputing the indisputable

We dispute the implication made in the recent *TREE* article by Jervis<sup>1</sup> that, among other advantages, the safety of classical biological control is 'indisputable'. Rather than being unassailable, the safety of introducing non-indigenous biocontrol agents has not, in general, been supported by genuine post-release studies. Biological control is not viewed universally as desirable<sup>2</sup>.

Since the first paper a century ago<sup>3</sup> documenting the harmful environmental impacts of Koebele's introduction of generalist predatory coccinellids and other biocontrol agents into the Hawaiian Islands, evidence has been accumulating worldwide on the detrimental effects of non-indigenous biocontrol agents. Introduced agents have enhanced pest populations, failed to control pests, affected human welfare, and caused catastrophic population declines, indirect ecosystem effects, and extinctions among native species<sup>4–8</sup>. In fact, some of the best-documented cases of extinction have incriminated biocontrol agents. Since the definitive cause of extinction is unknown in most cases, the evidence implicating biocontrol introductions as the cause of some extinctions is not a comforting statistic for a technology claimed to be indisputably safe<sup>9</sup>.

Compared to the number of putative biocontrol agents released, the number of success stories in terms of actually achieving control, especially safe control, is extremely small<sup>2</sup>. In concept, biological control should be selective; that is, only the target organism should be affected. In practice, the 'judicious selection and screening of agents with respect to their host or prey ranges'<sup>1</sup> is rarely adequate. In fact, the biology and taxonomy of the putative biocontrol agent, the target pest, and other organisms in the potential new range of the agent, as well as the complex ecosystem interactions in which they all participate, are seldom if ever thoroughly understood.

Unsubstantiated claims of safety are unjustified and misleading. There will always be a risk associated with biological control. Minimizing this risk demands much greater caution in selecting biocontrol agents, and more thorough post-release studies on efficacy and nontarget effects, thereby determining the true fate of biocontrol releases.

**Robert H. Cowie**  
**Francis G. Howarth**

Hawaii Biological Survey,  
Dept of Natural Sciences,  
Bishop Museum, 1525 Bernice Street,  
Honolulu, HI 96817-0916, USA  
(fhowarth@bishop.bishop.hawaii.org)  
(rhcowie@bishop.bishop.hawaii.org)

### References

- Jervis, M.A. (1997) *Trends Ecol. Evol.* 12, 378–379
- Williamson, M.H. (1996) *Biological Invasions*, Chapman & Hall
- Perkins, R.C.L. (1897) *Nature* 55, 499–500
- Cowie, R.H. (1992) *Philos. Trans. R. Soc. London Ser. B* 335, 167–191

- Howarth, F.G. (1991) *Annu. Rev. Entomol.* 36, 485–509
- Louda, S.M. *et al.* (1997) *Science* 277, 1088–1090
- Samways, M.J. (1995) *Insect Conservation Biology*, Chapman & Hall
- Simberloff, D. and Stiling, P. (1996) *Ecology* 77, 1965–1974
- Civeyrel, L. and Simberloff, D. (1996) *Biodiv. Conserv.* 5, 1231–1252

## Reply from M.A. Jervis

I did not address explicitly the environmental 'safety' of biological control. However, Cowie and Howarth are justified in taking me to task over phraseology that portrays the issue of selectivity (i.e. target specificity) in biological control to be devoid of controversy. Biological control tends, by and large, to be far more target-specific than chemical control, but there is, as they mention, unequivocal evidence that some ('classical' biological control) introductions of exotic natural enemies have had adverse effects on non-target species. These form a very small proportion of the total<sup>1,2</sup>, and many relate to old practices including the introduction of vertebrates<sup>1</sup>, but give cause for concern nevertheless.

In principle, rigorous screening protocols ought to be applied to all introductions of exotic natural enemies even where an introduction would be confined to glasshouses<sup>3</sup>. When practised (not frequently enough in some cases, for example natural enemies of arthropod pests<sup>1</sup>), such screening is aimed at ensuring that, as far as possible, non-target species are not attacked. Biological control workers are now being made aware of the Food and Agriculture Organization of the United Nations' (see Ref. 4) code of conduct regarding the importation and release of biological control agents. The responsibility of the importer prior to importation is stated to be: 'An analysis of the host specificity of the biological control agent and any potential hazards posed to non-target hosts' (presumably the terms 'host' and 'hosts' are being used loosely here, and includes also prey of introduced predators). The code also encourages post-release monitoring for the assessment of effects not only on target organisms but also on non-target species.

Any risk of adverse environmental effects has to be weighed against those of: (1) doing nothing<sup>1,2</sup> and (2) alternative control methods, in particular pesticidal control (which could involve much more worrisome environmental and human health risks). Ideally, a rigorous cost-benefit analysis needs to be carried out with every introduction contemplated<sup>2,5</sup>, a demanding but essential task.

While Cowie and Howarth make a valid point about one aspect of biological control, I hope that our correspondence does not distract readers of *TREE* from the main subject of my article – the very exciting conceptual advance provided by Holt and Hochberg's paper<sup>6</sup> in relation to population genetics and dynamics in biological control.

**Mark Jervis**

School of Pure and Applied Biology,  
University of Wales, Cardiff,  
UK CF1 3TL (jervis@cf.ac.uk)

### References

- van Driesche, R.G. and Bellows, T.S. (1996) *Biological Control*, Chapman & Hall
- Simberloff, D. and Stiling, P. (1996) *Ecology* 77, 1965–1974
- van Lenteren, J.C. (1986) in *Insect Parasitoids* (Waage, J. and Greathead, D., eds), pp. 341–374, Academic Press
- FAO (1996) *International Standards for Phytosanitary Measures (ISPM) Publication No. 3*, FAO
- van Emden, H.F. and Peakall, D.B. (1996) *Beyond Silent Spring*, Chapman & Hall
- Holt, R.D. and Hochberg, M.E. (1997) *Ecology* 78, 1673–1683

## Animal foraging: more than met the eye

In a recent *TREE* article, Perry and Pianka<sup>1</sup> (PP, hereafter) review research on animal foraging and suggest future directions within the foraging research tradition. All reviews are biased, but we find that in this case too much was left. We broadly agree with PP's vision for the future, but find that some of the omissions in their review give a misleading image of past and present achievements in the field. In fact, proposals PP make for the future have already been developed but are missing from their article.

PP seem to base most of their views on old reviews, which range from 11 to 26 years old, even though more recent ones exist, such as Refs 2–5 below, and the chapters by Giraldeau, and by Cuthill and Houston in Ref. 6. As a consequence, fundamental areas of animal foraging research are missed. It is particularly striking that the whole areas of risk sensitivity and stochastic dynamic modelling are so lightly represented, and that a call is made for theoretical and empirical work to be integrated without mentioning the extensive history of cooperation between theory and experiment throughout the history of foraging research. As an example, remember that Charnov published the marginal value theorem after the first experimental test was attempted in collaboration with Krebs<sup>7</sup>, and that people such as Real and Caraco have been both theoretical and empirical developers of risk-sensitive foraging theory<sup>8</sup>. Even by the end of the 1970s, when the limitations of the first generation rate-maximizing models were already clear, there were papers which linked new theoretical perspectives such as optimal information-gathering and new techniques such as stochastic dynamic programming to empirical research<sup>9</sup>.

We find it surprising that PP write in 1997 that 'we define a behaviour as optimal when it maximizes net gain (i.e. long-term difference between profits and costs associated with obtaining these profits)', even though they go on to suggest that future workers should define optimal foraging behaviour as one that maximizes lifetime fitness. That issue has received so much attention, and the definition of long-term rate maximization has been questioned so many times on both theoretical and empirical grounds, that we wonder why this definition of optimal behaviour is put forward at this stage. In the case of risk

sensitivity, namely the area of research dealing with decision-making under uncertainty, PP not only devote little attention to the topic, but when they do mention it, they confound it with predation risk, by naming a recent issue of the *American Zoologist* [Vol. 36 (4) 1996] devoted to the former topic, and not to predation risk as they stated. Another journal, *Annales Zoologici Fennici* [Vol. 29 (4) 1992], dedicated an entire issue to predation risk but this is not cited. Risk sensitivity is currently a very active field and is probably the most inter-disciplinary area of foraging theory, resulting from interactions between experimental psychology, psychophysics, behavioural ecology and economics.

PP made only a passing comment on dynamic programming, a technique from engineering and economics that has constituted an important breakthrough in behavioural ecology in the past decade<sup>10,11</sup> precisely because its proponents emphasize the point that fitness maximization, rather than simply long-term net gain, should be the focus of attention of optimality theory, a point now recommended by PP. Also omitted is the influence of optimal foraging ideas on traditional ecological problems such as predator distributions, population dynamics and conservation, often reviewed and much evolved since the beginnings of ideal free distribution theory (see Goss-Custard and Sutherland in Ref. 6 for one recent review).

No short article can cope with the diversity of topics that have sprung from early foraging research. We are just puzzled that PP's narrow focus was not made explicit in the picture presented, because a moderately informed non-specialist might conclude from this article that not much has really happened in this area for decades. This would not really reflect the past and present of animal foraging, and hence would not be useful to shape the future.

### Rodrigo A. Vásquez

Depto de Ciencias Ecologicas,  
Universidad de Chile, Casilla 653,  
Santiago, Chile  
(rvasquez@abello.dic.uchile.cl)

### Alex Kacelnik

Dept of Zoology, University of Oxford,  
Oxford, UK OX1 3PS  
(alex.kacelnik@zoology.oxford.ac.uk)

### References

- 1 Perry, G. and Pianka, E.R. (1997) *Trends Ecol. Evol.* 12, 360–364
- 2 Hughes, R.N., ed. (1990) *Behavioural Mechanisms of Food Selection*, NATO ASI series, Springer-Verlag
- 3 Hughes, R.N. (1993) *Diet Selection: an Interdisciplinary Approach to Foraging Behaviour*, Blackwell Science
- 4 McNamara, J.M. and Houston, A.I. (1992) *Bull. Math. Biol.* 54, 355–378
- 5 Kacelnik, A. and Bateson, M. (1996) *Am. Zool.* 36, 402–434
- 6 Krebs, J.R. and Davies, N.B., eds (1997) *Behavioural Ecology: an Evolutionary Approach* (4th edn), Blackwell Science
- 7 Krebs, J.R. et al. (1974) *Anim. Behav.* 22, 953–964
- 8 Real, L.A. and Caraco, T. (1986) *Annu. Rev. Ecol. Syst.* 17, 371–390

- 9 Krebs, J.R. et al. (1978) *Nature* 275, 27–31
- 10 Mangel, M. and Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*, Princeton University Press
- 11 Houston, A.I. et al. (1988) *Nature* 332, 29–34

## Pests of non-indigenous organisms: hidden costs of introduction

We read with interest Daehler and Gordon's recent *TREE* article<sup>1</sup> and wish to introduce another factor into the debate on introductions of non-indigenous organisms: pests and microbes. These often unseen companions of introduced species deserve close scrutiny, as they have major economic importance and they may spread beyond their initial host in their new environment.

A good example is the history of perennial ryegrass (*Lolium perenne*) in Australasia. A series of introductions of this pasture species (probably both legal and illegal) into Australia and New Zealand over the past century has inadvertently introduced at least two species of endophytic fungi, endophytic yeast and bacteria, two eriophyid mites, ryegrass mosaic and ryegrass cryptic viruses and possibly barley yellow dwarf viruses and some of their aphid vectors<sup>2–8</sup>.

Economically, the most important introduction has been the perennial ryegrass endophyte (*Acremonium lolii*). This asymptomatic fungus has a major impact on the performance of ryegrass pastures. The association between plant and fungus is mutualistic with the host grass benefiting from endophyte presence through reduced herbivore feeding, increased resistance to insects, improved plant growth and possibly disease resistance<sup>2</sup>. However, ingestion of endophyte-infected grasses by livestock has been associated with a number of animal toxicoses<sup>2</sup>. Clearly, with the benefit of hindsight, it would have been prudent to debate the introduction of this endophyte as much as the introduction of perennial ryegrass.

Ryegrass mosaic virus (RgMV) was first reported from Australia in 1985 (Ref. 3) and New Zealand in 1992 (Ref. 4). Since these reports the mite vector *Abacarus hystrix* and a companion species *Aculodes mckenziei* have been recorded in both countries<sup>5</sup>. Studies of Australian herbarium specimens show that the mite vector (and probably RgMV) has been present since the 1960s (Ref. 6). Similarly, RgMV and the mites have been detected throughout New Zealand. Neither RgMV nor the mites are seed-transmitted, which implies that vegetative material was illegally imported. Worse than this, studies of restriction fragment length polymorphisms (RFLP) of New Zealand isolates suggest that vegetative material may have been introduced twice. RFLP studies of the coat protein gene indicate that two strains of the virus are present. One strain is common on the lower South Island while the other occurs on the upper South Island and the North Island. Both strains appear to be spreading into each other's territory<sup>7</sup>.

The endophytes and RgMV are restricted to ryegrass but other companions of introduced species are not. Barley yellow dwarf viruses (BYDVs) and their aphid vectors were introduced into Australasia on live Poaceae during the past 200 years<sup>8</sup>. We know this because BYDVs are only

transmitted by aphids, they are not seed transmitted, and there are no native aphids on Australasian Poaceae<sup>8</sup>. Since their introduction, the viruses and aphids have had a major and well-documented impact on the productivity and persistence of cereals and pastures in the region similar to that reported from other parts of the temperate world<sup>8</sup>. But more than this – they have spread into native grasses where they may be having an impact on productivity and biodiversity of the region's ever shrinking native floras. BYDVs infect native *Agrostis*, *Danthonia*, *Festuca*, *Poa* and *Themeda* species at both highly disturbed and wilderness sites<sup>9,10</sup>.

If all this were not enough, there is also the possibility that species introduced without their complement of microscopic companions may become hosts for pathogens in their new environment and thereby add to the complexity of disease ecology.

**P.L. Guy  
D.E. Webster  
L. Davis**

Dept of Botany, University of Otago,  
PO Box 56, Dunedin, New Zealand

**R.L.S. Forster**

Hort+Research, Private Bag 92169,  
Auckland, New Zealand

### References

- 1 Daehler, C.C. and Gordon, D.R. (1997) *Trends Ecol. Evol.* 12, 424–425
- 2 van Heeswijck, R. and McDonald, G. (1992) *Aust. J. Agric. Res.* 43, 1683–1709
- 3 Guy, P.L. and Sward, R.J. (1991) *Acta Phytopath. et Entomol. Hungarica* 26, 199–202
- 4 Guy, P.L. (1993) *N.Z. J. Agric. Res.* 36, 377–379
- 5 Guy, P.L. and Forster, R.L.S. (1996) in *Pasture and Forage Crop Pathology* (Chakraborty, S. et al., eds), pp. 289–302, Am. Soc. Agronomy and the Crop Science Society of America
- 6 Frost, W.E. (1993) *J. Aust. Ent. Soc.* 32, 389–390
- 7 Webster, D.E. et al. (1996) *N.Z. J. Agric. Res.* 39, 405–412
- 8 Johnstone, G.R. et al. (1990) in *World Perspectives on Barley Yellow Dwarf* (Burnett, P.A., ed.), pp. 228–239, CIMMYT Mexico
- 9 Guy, P.L., Johnstone, G.R. and Morris, D.I. (1987) *Aust. J. Agric. Res.* 38, 139–152
- 10 Jones, R.A.C., McKirdy, S.J. and Shivas, R.G. (1990) *Aust. Plant Pathol.* 19, 90–96

### Letters to *TREE*

Correspondence in *TREE* may address topics raised in very recent issues of *TREE*, or (occasionally) other matters of general current interest to ecologists and evolutionary biologists. Letters should be **no more than 500 words long with a maximum of 12 references and one small figure**; original results, new data or new models are not allowed. Letters should be sent by e-mail to [TREE@elsevier.co.uk](mailto:TREE@elsevier.co.uk). The decision to publish rests with the Editor, and the author(s) of any *TREE* article criticized in a Letter will normally be invited to reply. Full-length manuscripts in response to previous *TREE* articles will not be considered.