

out the globally rare and threatened – birds in the Everglades and Mauritius, antelope in Kazakhstan, mammal predators in Madagascar, exploited top-predatory fish across the oceans, monkeys, Caribbean corals and cloud forests. Nonetheless, many papers involved common species from Europe, despite the fact that most of its countries could disappear and, from a biodiversity point of view, none of them would be missed.

Obvious problems emerge when trying to understand war far from the front-line. At best, missing the experience of (say) trying to sleep in hot, saturated air under a mosquito net fails to build required character. At worst, one answers the wrong questions. The rapidly growing industry of computer-intensive conservation priority setting was the subject of several talks. Cutting edge exercises have massive data requirements on species' ranges that will probably be filled only from well-studied European countries where the answers cannot possibly matter. In many species-rich countries, the answers matter desperately; however, the habitats will go before we even glimpse what taxa they contain, let alone map them. The areas we save will be because we make choices that recognize what is economically practical, politically feasible, locally acceptable in a culture so different from our own, and, if we are really lucky, because we guess correctly that they hold the important species.

Likewise, detailed studies of the population dynamics of common temperate species might simply be impossible on tropical species that are far too rare to afford the necessary sample sizes. Nonetheless, learning basic skills on common species can be a good place to start.

Students certainly sense the lure of exotic places and rare species. Envy greeted the talks by Maggy Nugues and Christiane Shelton (University of York, UK). This was not because of undeniable management importance of understanding how agricultural runoff harms their species, but rather because – poor things – their species were corals accessible only by SCUBA off the coast of St Lucia. The conference surely broadened students' horizons as to what and where they can study.

The conference also demonstrated that well crafted studies can provide crucial management advice from first-rate science. Such was the theme of the conference's overall best paper by Mar Cabeza (University of Helsinki, Finland), who answered an explicit conservation problem with conceptually rich solutions. An endangered butterfly has declined to 10% of its original range within a decade. There is a critical need to know which habitat patches should be protected to prevent this species from going extinct in Finland. The problem is that patches differ in how long their local populations last depending on how large and how isolated they are. Patches also differ in how much they

cost to purchase. Persistent, cheap solutions differ from those that simply minimize costs or maximize current numbers. Although the cheapest solution might pick a few good sites, a slightly more expensive one might pick a much larger cluster of not so good individual sites but with excellent long-term prospects.

Students learn most from each other. Good talks motivate ever better presentations and the appreciation of what constitutes excellent science. Students needed no encouragement to mix socially. In doing so, long past the exhaustion of their seniors, they juxtaposed good science with globally important environmental problems. They probably absorbed the need to do both good science and yet sometimes chose different problems from those advisors who have trodden less relevant, if academically safer, paths. Both science and global problems will be aided as a consequence of this and by the future conservation conferences that Cambridge University is planning.

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## Biological control as a learning process

Since the old lady swallowed a spider to deal with the fly, leading to a runaway trophic cascade of successively more desperate attempts to cope with previous mistakes, the limits of classic biological control programmes have long been apparent. The propensity for some agents to swarm out of control is well documented. The so called 'indirect' effects that follow some releases of biocontrol agents have received considerable attention<sup>1</sup>. Well known examples include the *Cactoblastis* moths released to control prickly pears, but which subsequently spread to several other naturally occurring nonweed hosts<sup>1</sup>. These releases are spectacular failures, in the sense that the agent runs out of control, thus becoming a problem itself and a threat to biodiversity. Although addressing such problems will always be a major task in a biocontrol programme, recent theoretical work<sup>2</sup> has begun to look at the opposite of this

problem, namely the failure of agents to establish at all and how this might affect the design of releases.

How should research programmes be designed to cope with such failures? The answer to this question requires an understanding of the ecology of small populations, as well as the use of modelling techniques that allow the process of introducing agents to be considered as a series of decisions set within an ongoing research programme.

#### Failure of biological control agents to establish

The fate of a large proportion of attempted releases is abject failure: 65% and 41% of agents released to control insect and weed pests, respectively, have never got off the ground, with the agent failing to establish a viable population immediately following release<sup>3,4</sup>. It could be that there are good biological reasons for such failures: the

weather might have been poor, the release site might have been poorly chosen or the agent could have been released at the wrong stage. However, there might be another reason: quite simply, too few agents were released. The basis for this can be simply a numbers issue; if there are too few individuals then, just by chance, all might die or fail to reproduce. So called compensatory dynamics, resulting from demographic stochasticity<sup>5,6</sup>, result in a net positive relationship between population establishment probability and the size of release. Alternatively, the existence of 'Allee effects'<sup>7,8</sup>, resulting from positive effects of social interactions on population growth at low densities, might destabilize low-density populations and result in ultimate population extinction.

Whatever the reason, a tendency for population extinction to be larger for small populations is a highly pertinent phenomenon from the point of view of the biological control practitioner. Practical constraints mean that often few agents can be bred for release, and thus introductions are necessarily likely to be performed using small numbers of agents.

There are two consequences of such failures. The obvious proximate consequence is that no control is achieved. A less apparent, indirect consequence of the failure of an agent to establish is that misleading conclusions and recommendations might be generated from the unsuccessful trials. The failure of the agent to establish could easily be attributed to an inability of the species to maintain a viable population or to other external conditions, such as climate; however, the release might have been successful if more agents had been released.

Few studies on the success and failure of classic biological control agents have examined the role of such effects. This is because releases are either performed singly, or because all releases employ the same number of agents. However, a recent study has implicated the number of agents released in the success or failure of an attempt<sup>9</sup>. The success of establishment of individual releases of gorse thrips (*Sericothrips staphylimus*) was positively related to the size of the release, thus suggesting a role for compensatory dynamics or Allee effects<sup>9</sup>. Prompted by this kind of observation, for the first time Shea and Possingham<sup>2</sup> have now asked how biological control programmes should be designed, given that such effects might well be commonplace?

### Coping with failure – a dynamic programming approach

Shea and Possingham<sup>2</sup> used stochastic dynamic programming (SDP) to address this question. Stochastic dynamic programming has been used for a number of years to explore a range of problems in behavioural ecology<sup>10</sup>. In the context of animal behaviour, SDP is used to generate solutions to problems of predicting optimal decision making, such as predicting how animals should best allocate time or energy to different activities. The technique has received increasing attention in a range of disciplines, but the application of SDP to the design of bio-control release programmes is novel.

In general terms, SDP works as follows<sup>10</sup>: a state space is defined within which a single state is adopted at a given time. However, the state of the system is a dynamic variable and might change. Several constraints are imposed on the system, thus changes in state are limited. A strategy set represents the alternative decisions available through which the state of the system can be changed. Finally, the optimization criterion is the term for the outcome that is to be optimized. Typically, it is necessary to solve such models numerically, because they are often analytically intractable, particularly when the dimensions of the state space are large.

In the model by Shea and Possingham<sup>2</sup>, the state of the system is summarized by the number of successful releases, the number of potential sites that contain no agents and the number of sites at which the agent is present but has not yet established a persistent population. The constraints are the number of agents to be released, the number of sites available for releases and the probability of establishment of the agent as a function of release size. The strategy set is simply whether to make many small releases, a smaller number of intermediate sized releases or just a few large releases. The optimization criterion might then be set as finding the strategy that maximizes the ultimate number of successful releases.

### Optimal strategies and learning from failure

The main result of this analysis is simple – there is not a single best strategy for all situations. In simply stating this, the model analysis makes an important salutary contribution. The release size is an important determinant of the overall success or failure of a programme as a whole and needs to be considered at the design stage. More specifically, depending on the biology of the species involved, as well as the nature of the system, the strategy adopted by the practitioner has to vary. When only a few sites are available for releases, a small number of large releases are best; by contrast, for fast-reproducing species with only weakly compensatory dynamics, many small releases might be better. However, for a wide range of parameter values a single release size is not an optimal strategy. Mixed optimal strategies, in which a few large and a few small releases are made simultaneously, are better. The smaller releases might have a reasonable chance of establishment, but the likelihood of failure in these cases is nevertheless high enough that the larger releases are made to act as an 'insurance' against chance extinction of the smaller populations.

These mixed strategies have further advantages. For one thing, a release strategy that maximizes the number of successful releases will generate more agents for future releases. Furthermore, individual releases are not single isolated trials, but form part of an ongoing research project. Perhaps more importantly, therefore, not only do mixed strategies generate the best chance of establishing the agent across several sites, but they also give valuable data on the factors determining success or failure. A small number of successful releases might not generate a great deal of information to guide later releases because the sample size on which statistical analyses are based is necessarily small. A large number of small,

unsuccessful releases will generate little useful data, and indeed the failure of these could easily be misattributed to a factor other than release size. Furthermore, when a range of sizes of release have been made, one can statistically test for the existence of compensatory dynamics and hence be able to control for this in future attempts. Of course, this would not be possible if all releases were of the same size.

The lesson is that learning from ones' failures is as important a component of biological control programmes as generating successful releases. Whether the old lady would have been able to infer the failure of her release programme using a full SDP model is unlikely; however, the broad conclusions from the SDP model would have helped. The flexible, responsive approach that SDP suggests is essential. In broad terms, this new research suggests that rational biological control programmes should be designed with a view to incorporating the lessons learned from failures into future introductions.

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