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SPECIAL PROFILE: IMMUNOCONTRACEPTION

The ecological challenge of immunocontraception: editor's introduction

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Summary

1. The problems of vertebrate pests are greater now than ever before, with vertebrate control constrained by problems of humaneness, scale and environmental impact. However, immunocontraception involves a conceptually ideal solution. Although not intrinsically novel, its delivery in baits or by a self-spreading vector and its effectiveness in pest control, are now the focus of growing international interest.

2. Major ecological questions correspond to the two forms of delivery: baits and vectors. First, given an effective immunocontraceptive, inserted into a bait and eaten by a pest, would the resulting level of sterilization in the population effectively suppress densities? Secondly, given that the immunocontraceptive agent can be inserted into a microparasitic or macroparasitic infective vector, would the modified vector persist at sufficient prevalence in the host population, and hence suppress densities to the required extent?

3. The papers published in this Special Profile focus on behaviour following sterilization or they model the likely impact of viral-vectored immunocontraception. They highlight advantages and disadvantages of immunocontraception and some general, novel and specific issues. These include the possibility of behaviourally mediated population responses to fertility control; the possible advantages of a mixed baiting and vector strategy; the competitiveness of a modified vector; the appropriateness of immunocontraception for controlling invasive vertebrates on islands; and the need for a 'pay-off' methodology for assessing genetic modifications against alternatives.

4. The findings offer significant benefits for management and policy: they will inform decisions on whether to pursue immunocontraception as a control option; and they provide evidence about efficacy and risk in applications to release genetically modified vectors.

5. Although many of the problems in developing immunocontraception technology are biotechnological, questions about the effectiveness of immunocontraceptive pest control are ultimately in the domain of ecologists.

Key-words: behaviour, fertility control, models, pest control, possums.

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Introduction

The following three papers in this Special Profile focus on immunocontraception which, in its present incarnation, is a new technology for vertebrate pest control. It poses challenges in virtually every area of animal biology, not least applied ecology. The technology involves using one or more proteins from the reproductive system of the target pest, typically the *zona pellucida* of the egg or the sperm coat, to induce an immune response which attacks the target's reproductive system as well as the invading protein. The delivery mechanisms would typically be a bait or a self-spreading vector such as a virus, and the ecological dimension involves the issue of

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whether the delivery of a successful immunocontraceptive would suppress the populations to the extent required for control. There is growing international interest in the technology and the ecological challenges associated with its successful application, largely because of increasing problems with conventional vertebrate pest control.

The problems of vertebrate pest control

While many of the principles of pest management apply equally to invertebrates and vertebrates, the history and literature is considerably more extensive in the first case than in the second, and vertebrate pest management poses problems which invertebrate pest management does not. These are primarily associated with humaneness, real and perceived, environmental contamination and scale. For example, culling by trapping, shooting and poisoning raises the humaneness issue. Poisoning using baits may impact on non-target species, and all three methods may have to be applied over such large, and often inaccessible, areas as to render the control uneconomic and the environmental impact unacceptably large. The alternative is biological control. Although well established for the control of invertebrate pest control, when applied to vertebrates it immediately raises problems. First, there is no equivalent to species-specific insect parasitoids. Secondly, there tend to be few candidate pathogens that suppress populations, kill humanely and are species-specific. Both the problems of vertebrate pests and the difficulties associated with their control appear to be growing: about 10% of the papers published in recent issues of the *Journal of Applied Ecology* relate to vertebrate pests classified as nuisance species on some criteria (Table 1). Although the Table includes both native and introduced wildlife from a range of taxa, the most likely candidates for control using immunocontraception will probably be those outside their normal range. Against this background, it is hardly surprising that immunocontraception has become 'the holy grail of vertebrate pest control in Australia' (McCallum 1996), or that it is being pursued with equal vigour elsewhere.

The characteristics of immunocontraception

Immunocontraception relies on generating an antigenic response in the target and so the antigen must somehow be introduced into the target's bloodstream. The delivery systems fall into two general classes: baits and self-spreading micro- or macroparasites. This distinction between two types of immunocontraception also represents stages in the technology's evolution, namely non-disseminating and disseminating or vectored. Vectored immunocontraception is true biological control, and presents

Table 1. Recent papers in the *Journal of Applied Ecology* involving vertebrate species definable as nuisance species by virtue of perceived damage to economic resources, interference with features of conservation importance or involvement in issues of human health

Division by taxa	References
Exotic or invasive species	
Red fox *Vulpes vulpes* L.	Pech & Hood 1998; Hone 1999; Banks 1999
European rabbit *Oryctolagus cuniculus* L.	Pech & Hood 1998, Hone 1999, Twigg *et al*. 2000
House mouse *Mus domesticus* Rutty	Brown & Singleton 1999, Hone 1999
American mink *Mustella vison* Schreb.	Ferreras & Macdonald 1999; Rushton *et al*. 2000
Native species	
Striped skunk *Mephitis mephitis* Schreb.	Lariviere & Messier 1998
Redtail monkey *Cercopithicus ascanius schmidtii* Matschie	Naughton-Treves *et al*. 1998
Olive baboon *Papio cynocephalus anubis* Lesson	Naughton-Treves *et al*. 1998
Chimpanzee *Pan troglodytes schweinfurthii* Giglioli	Naughton-Treves *et al*. 1998
Wild boar *Sus scrofa* L.	Spitz & Lek 1999
European mole *Talpa europaea* L.	Edwards, Crawley & Heard 1999
Red fox *Vulpes vulpes* L.	Green & Etheridge 1999
Badger *Meles meles* L.	Woodroffe, Frost & Clifton-Hadley 1999; Moore *et al*. 1999; Tuyttens *et al*. 1999
African elephant *Cervus elephans* L.	Hoare 1999
Wolverine *Gulo gulo* L.	Landa *et al*. 1999
Red colobus *Procolobus kirkii* Gray	Siex & Struhsaker 1999
Fat sand rat *Psammomys obesus* Cretz	Fichet-Calvet *et al*. 2000
Cormorant *Phalacrocorax carbo* (L.)	Staub *et al*. 1998; Suter 1998; Bearhop *et al*. 1999
Great skua *Catharacta skua* Br.	Phillips, Thompson & Hamer 1999
Wood pigeon *Columba palumbas* L.	McKay *et al*. 1999
Yellow-legged gull *Larus cachinnans* Pal.	Bosch *et al*. 2000

Journal of Applied Ecology, **37**, 897–902

significantly greater problems than does non-disseminating immunocontraception. A disseminating system may still require periodic re-releases of the modified vector. However, each release may offer a more prolonged impact than a single application of baits because of the possibility of multiple cycles of infection by the immunocontraceptive vector before its disappearence from the population. This would represent inundative biological control, as opposed to classical biological control in which the vector persists without the need for reintroduction.

Immunocontraception *per se* is not new; it has been studied for many years in the context of human contraception, and has been used on a limited scale for wildlife control (e.g. Kirkpatrick *et al.* 1997). More novel is the idea of disseminating immunocontraception, which became the basis for a new Co-operative Research Centre in Australia in the mid-nineties (Tyndale-Biscoe 1994, 1995), and the development of antigenic baits targeting a variety of different species (for example, foxes *Vulpes vulpes*, house mice *Mus domesticus*, rabbits *Oryctolagus cuniculus*, and brushtail possums *Trichosurus vulpecula*). Even non-disseminating immunocontraception using baits is still in its infancy as a technology and no such system has been applied in the field. However, considerable progress is being made, particularly in relation to possum control. For example, carrots *Daucus carota* which are a proven substrate for the delivery of 1080 poison (sodium monofluoroacetate) against possums, have been genetically engineered to express possum zona pellucida protein and it appears that the plant material somehow protects the protein from digestion (P. Cowan, personal communication). The protein can reduce fertility by up to 75% when injected. Other delivery systems being trialled include 'bacterial ghosts' and virus-like particles. 'Bacterial ghosts' are bacterial shells which could carry possum proteins on the outer coat, while virus-like particles are virus coat proteins which spontaneously reassemble, minus the viral DNA content. Both have the added advantage of being immunogenic, thereby enhancing the immune response to an introduced possum protein (P. Cowan, personal communication).

Advantages and disadvantages

As emphasized in conferences (McCallum 1996; Tyndale-Biscoe 1997), and some recent reviews (Cowan 2000; Robinson *et al.* 2000), practical aspects of the delivery of immunocontraception still pose substantial challenges. They span a wide zoological spectrum from genetics, cell biology and immunology, through reproductive physiology to behaviour. Even botany is involved in the design of suitable baits. However some of the largest gaps are ecological, and hence the three papers in this Special Profile represent important contributions individually and collectively. They add particularly to the areas of behaviour (Ji, Clout & Sarre 2000) and population modelling (Courchamp & Cornell 2000; Hood, Chesson & Pech 2000).

The specific benefits of both vectored and non-vectored immunocontraception are emphasized by all three papers (see also Tyndale-Biscoe 1994, 1995; Chambers, Singleton & Hood 1997). For example, Ji, Clout & Sarre (2000) highlight the problems of conventional control in the particular case of brushtail possums in New Zealand. These Australian natives are by far New Zealand's most significant pest, with a population of around 70 million and a major impact on native forest structure and the country's bovine TB status. Under conventional control using 1080 baits, depleted populations recover through recolonization of controlled areas and enhanced breeding, maintenance of low densities is expensive, poison-shyness is an increasing problem, and there is growing public unease about trapping and poisoning (Ji, Clout & Sarre 2000). All these problems would be obviated through effective vectored immunocontraception, and the last two would probably be overcome through non-disseminating immunocontraception.

Courchamp & Cornell (2000), focusing on the control of invasive feral cats *Felis catus* on islands, cite the benefits of vectored immunocontraception as humaneness, environmental safety, low cost, wide coverage of inaccessible areas, and probable species-specificity. Hood, Chesson & Pech (2000) add the further advantage of a probable enhanced immunogenic response in the host from infection by a vector. The disadvantages (Courchamp & Cornell 2000) are irreversibility and difficulty in controlling the vectors once released, the need for engineering of a genetically modified vector and possible public resistance to this, together with a slow population response (Barlow 1994; McCallum 1996), possible development of resistance, and the risk of genetic alteration of the target population through selection. All these problems are shared by non-disseminating immunocontraception, with the exception of the irreversibility. Certainly, genetic engineering is likely to be involved in developing a bait that expresses an immunocontraceptive protein.

The ecological issues

Non-disseminating and disseminating immunocontraception pose different ecological questions. The first is the efficacy of fertility control and is a matter of population dynamics (see for example Bomford 1990; Hone 1992; Seagle & Close 1996; Barlow, Kean & Briggs 1997; Pech *et al.* 1997): given that an effective immunocontraceptive agent can be produced, inserted into a bait and eaten by the pest, would the resulting level of sterilization in the population be sufficient to suppress densities to the extent required? Disseminating immunocontraception adds a second ecological question, which is to do with epidemiology and disease/host interactions (Barlow 1994, 1997; Courchamp & Cornell 2000; Hood, Chesson & Pech 2000): given that the immunocontraceptive agent can be inserted into a microparasitic or macroparasitic infective vector, would the modified vector persist and reach a high prevalence in the host, and if so, would it provide a high enough level of sterilization to achieve the efficacy criterion above?

While the efficacy of fertility control is determined by population dynamics, behaviour and physiology are involved since they affect death rate, birth rate and density dependence. For example, mating and social systems affect the effectiveness of fertility control (Caughley, Pech & Grice 1992; Newsome 1995; Cowan & Tyndale-Biscoe 1997), because they impose an additional change on the birth rate, over and above that occasioned by the sterilization itself. For most mating systems, the result is that the percentage reduction in per capita birth rate is less than the percentage of females sterilized (Caughley, Pech & Grice 1992). Ji, Clout & Sarre (2000) focus on other physiological and behavioural consequences of sterilization in female New Zealand possums. The authors showed three effects: a longer period of oestrus and mating by sterilized females; reduced body condition of males; and an increased local density of males, possibly because they were attracted to the females in oestrus. It is clearly possible that the reduced body condition of males may lead to increased mortality (Ji, Clout & Sarre 2000), albeit sex-specific. It is also possible that the extended oestrus of sterilized females would impair the probability of mating for the remaining fertile females with shorter oestrus periods.

In many ways, Ji, Clout & Sarre (2000) reveal more about disseminating than about non-disseminating immunocontraception in possums. As they suggest, there are several implications. First, if there is additional mortality of males, its effect may equate to that of 'vector-induced mortality'. Although in this case indirect and sex-specific, such mortality has a major impact on pest suppression in models (e.g. Barlow 1994). Secondly, if the enhanced local density of males arose through an aggregative response to sterilized females with extended oestrus periods, then this could enhance transmission of a vector by increasing the number of males contacting sterilized, therefore infected, females.

Courchamp & Cornell (2000) use a theoretical modelling approach to consider the ecological feasibility of both non-disseminating and disseminating immunocontraception of invasive cats on islands. Interestingly, the authors also examine an integrated control strategy involving a mixture of both methods: effectively augmentative biological control. The vector was assumed to be horizontally transmitted, to allow no recovery, and to provide 100% permanent sterilization upon infection. This follows a similar approach adopted to evaluate vectored immunocontraception in possums (Barlow 1994, 1997), except that the latter models assumed the degree of sterilization achieved to be variable. Unlike previous models, which determined the level of successful immunocontraception necessary to provide acceptable control (e.g. Barlow 1994, 1997), Courchamp & Cornell (2000) assumed this to be fixed and instead compared the efficiency of the three types of control and the sensitivity of the results to issues like the mode of transmission (proportional mixing or mass action) and whether density dependence acted on mortality or recruitment. Results involving vector transmission were presented for a range of assumed transmission rates, since this parameter was unknown. The outcome was that eradication of cats was possible using all methods except disseminating immunocontraception alone with mass-action transmission. Baiting alone appeared to be the least efficient method, and the most efficient was a combination of both.

The theoretical analysis is lent credibility by the suggestion of possible candidate vectors such as feline retroviruses. Courchamp & Cornell (2000) also put a persuasive case for invasive species on islands as particularly appropriate targets for disseminating immunocontraception. Among other things, competition is less likely to limit the immunocontraceptive vector since there is a chance that the wild type vectors are absent from the islands. Interestingly, the authors argue that the characteristically slow response to immunocontraception (Barlow 1997) may even be advantageous because it would obviate possible 'mesopredator release'. This involves rapid reduction in one predator which allows another to increase, with a resulting impact on endemic prey that exceeds that of the original predator.

Hood, Chesson & Pech (2000) present a rather different theoretical analysis, in this case of a disseminating immunocontraceptive virus in rabbits and mice. In contrast to other models of this kind, Hood, Chesson & Pech (2000) considered a vector with a short infectious period and hosts recovering but remaining sterile for life. However, similar Anderson/May models were used in their analysis, with the explicit aim of translating efficacy in laboratory trials on individuals, which are currently underway, into efficiency at the small population level. Further work will consider larger spatial scales using explicit spatial models. A particular feature of this paper, which also distinguishes it from other models for disseminating immunocontraception, is that the vector is assumed necessarily to be pathogenic. Thus, the authors expressed efficacy of immunocontraception over and above that achieved by the vector alone, defining a 'pay-off' from introdu-

Journal of Applied Ecology, **37**, 897–902

cing an immunocontraceptive vector ($=1 - N_s/N_n$ where N_s is the host density realized in the presence of a sterilizing virus and N_n that when the non-sterilizing virus is present). Results showed that benign but highly transmissible parasites gave the highest pay-offs, and that hosts with low birth rates and moderate mortality rates formed the best targets. A second feature of the paper is the focus on competition between a genetically modified vector and the wild type, with a different approach to that of Barlow (1997). The authors show that sterilization of the host does not impair the virus' competitive ability against the wild type.

Synthesis

Immunocontraception through baits or vectors is in its infancy as a technology, let alone in its ecological application, so that one of the greatest needs now is for information. It is unsurprising therefore that two of the papers in this Special Profile are theoretical. But in preceding practice, these workers provide some important pointers for future empirical assessment. They also provide at least a theoretical view of whether immunocontraception could be effective in population control. This will be crucial evidence for any future application to release a potential immunocontraceptive vector. In this respect, one of the most generally relevant issues in all three papers is that of 'pay-off', introduced by Hood, Chesson & Pech (2000) to consider the benefits of a genetically modified sterilizing virus. As Hails (1999) emphasized in the opposite context of GMO risk, the impact of a genetic modification, whether positive or negative, should be assessed relative to that of the non-modified alternative(s). More specifically, and as Hood, Chesson & Pech (2000) advocate, 'appropriate pay-off functions should be developed as a basis for research and development on genetically modified organisms'.

In the final analysis, the future constraints on the use of immunocontraception in controlling vertebrate pests may turn out to be social more than biological. On the one hand, the potential benefits of immunocontraception are in providing a broad-scale, cheap, humane and potentially species-specific way of controlling vertebrates that represent major economic and conservation problems. On the other, immunocontraception is genetic engineering, and hence in some quarters will be treated with suspicion. As in many other areas of our subject (Ormerod, Pienkowski & Watkinson 1999; Ormerod & Watkinson 2000), there is a major need for ecologists to enter these wider debates from an informed perspective. No matter how inspired the genetics, immunology, cell biology and reproductive physiology, nor how heated the social debates, questions about whether immunocontraceptive pest control can ever be effective are ultimately in the domain of ecologists.

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