Correlates of invasion success : evidence from New Zealand

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Abstract : Understanding the biology of alien invasive species (AIS) is a problem for pure , as well as applied biology. However , it is obviously not possible to conduct designed experiments to further our understanding. We can , however , study actual invasions ; the next best thing. We used historical data from New Zealand to explore the correlates of successful establishment of species in a new environment. Surprisingly , biological differences between species explained little of the variation in establishment success. Instead , what matters is how often , and in what numbers , a species is introduced into the new environment.

Key words : alien invasive species , biological invasions , New Zealand , introductions.

Introduction

We are now so aware of the dangers posed by AIS that it is often easy to forget that attitudes towards the introduction of species into new environments used to be very different. For example , a man called Eugene Scheffland wanted all the species of birds mentioned in Shakespeare to be in Central Park , New York , and introduced 100 pairs of starlings (*Sturnus vulgaris*) in 1890. Fifteen pairs survived , and obviously did not realise that they and their progeny were supposed to confine themselves to the park and have subsequently spread over all of the U. S. A.

In Britain , the aristocracy has been very important in the intentional introduction of species. A Duke of Bedford in the 19th century built up a large deer collection at Woburn Abbey , the family home , including Chinese muntjac deer (*Muntiacus reevesi*) , which escaped and are now very successful , having the largest range of any deer species in Britain. Interestingly , the Duke also established a population of Pere David's deer (*Elaphurus davidianus*) , imported from China. This species subsequently went extinct in China and , in the 1980s , the Duke of Bedford (whose second title is the Marquis of Tavistock) agreed to a Chinese request to return some deer as part of an effort to re-establish the population in China. Fortunately , this effort has been successful so far , with the total Chinese population reaching 671 in 1997 (Jiang *et al.* , 2000).

Perhaps the most systematic and sustained introduction efforts were carried out in the 19th and early

20th centuries in New Zealand by the Acclimatisation Societies (McDowall , 1994). These were set up for the sole purpose of introducing European species. These introductions had two reasons : a) hunting ; hence the red deer (*Cervus elaphus*) , rabbits (*Oryctolagus cuniculus*) , game birds and so on : b) to make New Zealand look more like home in Britain.

As a result of the Societies' efforts , there have been introduced into New Zealand : about 36 species of birds , 33 species of mammals , 40 species of earthworms , 60 species of spiders and mites , 12 slug and snail species , 1100 species of insects and 1700 species of flowering plants. The program of introduction was only stopped when one of the introduced species , the red deer , began to cause devastating damage to the forests : it had become a serious AIS (King , 1984).

What is interesting is that many of these historical introduction efforts were not successful. For example , the starling was released many times unsuccessfully in USA , but it failed to establish a population in Cincinnati between 1872 and 1873. Although about 36 species of birds established in New Zealand , over 130 species were liberated overall. So bird introductions in New Zealand conform to the emerging generalisation that most introduction attempts fail. Nearly as twice as many mammal species were released as ultimately established , giving a success rate of about 50% .

In principle , we can exploit this variation in establishment success to address a fundamental question about the biology of AIS : what determines whether or

not a species establishes a population in a new place ? This question is of importance not only in the specific context of AIS , but conservation biology more generally. In conservation biology , we often intentionally introduce species either for the purpose of re-establishing populations of a species that used to live in a place but is currently extinct (e. g Pere David’s deer in China) , or because we want to establish a species in a new area because it is no longer viable in its previous area. We would like to know what produces success.

There are two broad categories of possible explanations for the successful establishment of a species : a) biological features of the species—perhaps some species are intrinsically easy or hard to establish because of their biology or life history : b) aspects of management are important i. e. how much effort was put into establishing the species. In the case of AIS , the latter possibility is interpreted in terms of how many times , and in what quantities , the AIS was introduced into the new environment.

The Acclimatisation Societies of New Zealand kept records of their efforts to introduce species and these provide what is perhaps a unique set of data from which we can learn about what determines the success or failure of an introduction attempt.

Methods

We analysed data for 79 bird species involved in 496 introduction events. The data set and full statistical analysis can be found in Veltman *et al.* (1996). This data was compiled from the records of the Acclimatisation Societies by Thomson (1922).

We used multiple logistic regression models to predict the success or failure of the introductions. The biological predictor variables were as follows : taxon (order) , body mass , body length , geographic range size , clutch size , brood frequency , diet , migratory status and habitat at use. The management (introduction effort) predictor variables were : number of release events and number of individuals introduced.

The present-day status of each species in New Zealand , present or absent , was used as the response variable in fitting a multiple logistic regression model using generalised linear models. We began the analysis with all the predictor variables included in the model and then deleted those variables with no significant effects. We ended up with a ‘minimal model’ which only included those factors whose deletion significantly

reduced goodness of fit (chi-square) in the model.

Results

We found two minimal models , each with two predictor variables. One model included the number of releases and migratory status and the other included number of individuals and migratory status , so they differ only in the way introduction effort was quantified.

A considerable amount of variation in introduction success was explained by introduction effort and migratory status of the bird. For example , number of releases and migratory status explains nearly 60% of the variation in introduction success. The migratory status variable was not further investigated as its influence seemed obvious : birds with programmed migration behaviour will just fly off into the ocean if transplanted to New Zealand.

We conducted further statistical analysis of the influence the number of releases was having on establishment success. It seemed obvious that if a species was released more times then it would have a better chance of establishment. We analysed a null model to see if this was a sufficient explanation : to our surprise , it was not. It turns out those species which were released more times have a higher probability per release of successful establishment. So there is something else going on.

We believe it may have to do with the fact that reproductive potential is confounded with the number of releases. Reproductive potential is the ratio—natality/mortality : ‘ natality ’ is the product of the clutch size and number of broods. So species that live a long time and have numerous large clutches have high reproductive potential. In our data set , there is a significant correlation between reproductive potential and number of releases : so those species that were released more often had higher reproductive potentials.

Another possible explanation is : Acclimatisation Societies were distributed all over New Zealand. It is likely then that the birds that were introduced frequently had been released at many different locations , rather than just being released at one location again and again. This might mean better chance of being released in the ‘ right ’ place for establishment. Indeed , there was a significant relationship between number of releases and how many different places the species was released.

We also identified some species that were striking

outlyers from the model. Cirl buntings (*Emberiza cir-lus*), mute swans (*Cygnus olor*) and kookaburras (*Dacelo novaguineae*) became established in spite of low number of introductions and propagules. At the other extreme , the European partridge (*Perdix perdix*) failed to colonise in spite of nearly 700 individuals being released in 24 introduction attempts.

Discussion

There have been numerous other studies of the unique New Zealand introduction data. For example , Sorci *et al.* (1998) postulated that species subject to more intense sexual selection may be less likely to establish because they are more burdened with characteristics that are sub-optimal from the point of view of natural selection. As an indicator of the intensity of sexual selection they used dichromatism – a species is dichromatic if the two sexes have different coloration. This variable has been often used as an indicator of sexual selection (e. g. Barraclough and Nee 1995). Whatever the merits of this idea , they did indeed find a significant negative correlation between dichromatism and the probability of establishment.

Sol & Lefebvre (2000) postulated that bird species with greater behavioural flexibility may be more likely to successfully establish. Using the relative size of the fore-brain as a proxy variable for flexibility , the anticipated relationship was found to be highly significant.

Forsyth & Duncan (2001) analysed a data set for New Zealand birds and ungulates that included the number of individuals released as well as the number of release events : they found that both of these variables were significantly correlated with establishment. In an overview of the literature on bird and plant introductions , Kolar and Lodge (2001) again conclude with the generalisation that these two variables are important.

It is a curious irony that , from a modern perspective , a sustained campaign of environmental vandalism should provide a valuable data base for ecological researchers. It is unfortunate that contemporary campaigns of ecological destruction – such as the stocking of Australian lakes with sports fishing species – is not being as meticulously recorded.

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References

Barraclough T and S Nee, 1995. Sexual selection as a cause of diversity in passerine birds. *Proceedings of the Royal Society of London Series B*, **259**: 211 ~ 215

Forsyth D M and R P Duncan, 2001. Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *American Naturalist*, **157**: 583 ~ 595

Jiang Z, C Yu, Z Feng, L Zhang, J Xia, Y Ding and N Lindsay, 2000. Reintroduction and recovery of Pere David’s deer in China. *Wildlife Society Bulletin*, **28**: 681 ~ 687

King C, 1984. Immigrant Killers. Oxford University Press, Auckland

Kolar C S and D M Lodge, 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, **16**: 199 ~ 204

McDowell R M, 1994. Gamekeepers for the Nation: the Story of New Zealand’s Acclimatisation Societies. Canterbury University Press, Christchurch

Sol D and L Lefebvre, 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos*, **90**: 599 ~ 605

Sorci G, A P Moller and J Clobert, 1998. Plumage dichromatism of birds predicts introduction success in New Zealand. *Journal of Animal Ecology*, **67**: 263 ~ 269

Thomson G M, 1922. The Naturalization of Plants and Animals in New Zealand. Cambridge University Press, Cambridge

Veltman C J, S Nee and M J Crawley 1996. Correlates of introduction success in exotic New Zealand birds. *American Naturalist*, **147**: 542 ~ 557

Wolf C M, T Garland and B Griffith, 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation*, **86**: 243 ~ 255

新西兰鸟类入侵成功的有关因素

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摘要：了解外来入侵物种(alien invasive species ,AIS)的生物学涉及纯生物学及应用生物学的问题。但是靠预先设计的实验来加深人们的了解显然是不可能的。然而我们可以研究现有的入侵 ,这也是一个很好的途径。本文利用新西兰历史上的一些记录 ,探讨了物种在新环境中成功定居的因素。令人惊奇的是 ,物种间的生物学差异对成功的定居几乎没有什么作用 ,相反 ,真正起作用的是一个物种被引入新环境的频率及数量。

关键词：外来入侵种 ,生物入侵 ,新西兰 ,引入

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