THE ORIGIN OF THE SPECIES: USING GENETICS IN PEST MANAGEMENT

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ABSTRACT: Key questions in pest management include the number of individuals that have invaded an area, their origin, whether invasive populations are expanding or declining, whether they are transient or resident and which individuals disperse. New methods from human forensics may illuminate the dynamics of invasive populations better than traditional approaches. These genetic analyses have recently become more accurate and feasible as a result of improved technology and statistical methods, and in combination with ecological data offer a new perspective into the dynamics of populations and the movement of individuals. Although rarely used for this purpose, such an approach may prove vital for pest and disease management. To demonstrate the application of genetics to pest management, we are using the westward expansion of the European starling (Sturnus vulgaris) as a test case to study an invasion in progress. We aim to provide a clearer picture of starling movements in Australia by using population genetics, and provide information to relevant agencies to improve pest management strategies.

INTRODUCTION

The use of genetics to infer information about wild populations is not a new concept but has traditionally been hindered by technical and computational constraints. Since the quality of results is often linked to the amount of genetic variation found, there is increasing demand for larger datasets. Fortunately, advances in laboratory techniques continue to increase speed and lower the cost of genetic analyses, allowing for greater numbers of individuals and genes within them to be screened. Of equal importance is the revolution in population genetic statistics resulting from increased computational power. Generally, these novel statistical methods are more useful for management than those traditionally used in genetics because they are less dependent on assumptions that are rarely met in real populations (Pearse and Crandall 2004).

Examples of applied genetics are more commonly found in the field of conservation, and are generally focused on protection of endangered populations. However, many of these techniques can be applied to pest management because they provide information that can be used to limit pest populations and to understand underlying dynamics leading to successful invasions. This paper explores some of the genetic tools available to assist population managers in answering questions about the number of individuals that have invaded an area, their origin, the number of invasion events and the dynamics of invasive populations. The invasion of the European starling (Sturnus vulgaris) into Western Australia (WA) is used to illustrate how these methods may be beneficial to population managers.
USES OF GENETIC DATA

Defining Management Units
Management and control policies may differ depending on the degree of connectivity between populations. For example, eradication may be possible in a series of small, discrete populations whereas in geographically large, genetically mixed populations, management may be the best possible outcome. In situations when population subdivision is unclear, the incorrect assessment of the number of populations may bias results (Taylor 1997). Recently described methods that cluster similar genotypes can be used to determine the number of populations sampled and define boundaries, removing the necessity to pre-define populations (e.g. Pritchard et al. 2000). Robertson and Gemmell (2004) used this approach to define boundaries in rat (Rattus norvegicus) populations on South Georgia Island. They concluded that isolated populations could be sequentially eradicated without a high risk of reintroduction. The effectiveness of eradication efforts can be checked by distinguishing survivors from new immigrants using genetic methods (see Abdelkrim et al. in press).

Population Demographics
It is challenging to determine appropriate levels of control effort if population size is unknown. Assessment of population size may be hampered by habitat structure, geographic extent, mobility, size of the individual, and magnitude of the population. In situations where direct census is not possible, genetic estimations of population size may be useful. Genetic data can be used to calculate effective population size (Ne), which is an estimate of the expected rate of certain genetic changes. Ne is a function of many factors including historical population size, sex ratio, breeding structure and family size (Halliburton 2004). Assuming other factors remain constant, changes of Ne imply changes of N, the total population size (Frankham 1995). Indeed, if the goal of the management agency is to model population expansion, Ne may be more meaningful than total size as it accounts for reproductive success.

Genetic tools have the ability to identify important demographic characteristics for pest animal management. For an expanding population, these tools can identify populations close to the “front” of expansion (Pearse and Crandall 2004). Genetic tools can also be used to provide feedback on the effectiveness of control programs by identifying sudden population contractions or “bottlenecks” (e.g. Hampton et al. 2004). Many of the methods developed to detect such events are reviewed in Emerson et al. (2001) and Pearse and Crandall (2004). The choice of the most appropriate method will depend on the timescale of interest (Abdelkrim et al. in press). Current developments attempt to model demographics of introductions over very recent history and have been used to estimate numbers of colonizing birds (Zosterops lateralis) (Estoup and Clegg 2003).

Population of Origin
Effective control of invasive populations may largely depend on the ability to pinpoint the source. In many situations, place of origin is unclear, or there may be multiple sources of an invasive population. A variety of methods have been developed to assign an individual to a population of origin, based on the level of genetic similarity between that individual and the individuals in the source population. The type of genetic data available, the resolution of those data and the question under investigation should be considered when choosing one of these methods. Recently, sophisticated tools such as STRUCTURE (Pritchard et al. 2000) and GENECLASS2 (Piry et al. 2004) have been used to calculate the number of populations sampled, assign individuals to populations, exclude them from populations, and identify migrants or descendants of migrants. Moreover, this method can incorporate prior information such as geographic data. These tools have the ability to be cross-validated, in
order to compare the accuracy of the data output. Such approaches have also been validated using conventional mark-recapture data (e.g. Berry et al. 2004) re-enforcing the power of these new tools.

By virtue of their ability to assign individuals to populations, assignment programs can be used to determine the minimum number of introductions that have occurred in a particular area. Davies et al. (1999) used an assignment test to determine that multiple medfly (Ceratitis capitata) introductions had occurred in California. Single introductions might be identifiable by examining the amount of genetic variability in an introduced population as compared to potential source populations. If no variation is found in an introduced population in a gene that is variable in source populations, it may be reasonable to assume a single introduction has occurred (Hänfling et al. 2002), although multiple introductions of the same genotype could also result in this pattern. Conversely, invasive populations containing greater genetic diversity than is found in any source population may indicate multiple introductions from different sources (see Kolbe et al. 2004).

Characteristics of Dispersal
In order to effectively implement population control, an understanding of dispersal is vital. Dispersal can be difficult to measure but gene flow may be used as a proxy. Measures of population structure such as F-statistics (F_{ST}) or Analysis of Molecular Variance (AMOVA) (Excoffier et al. 1992) are frequently used to infer the relative presence or absence of gene flow between populations. F_{ST} can be transformed into the number of dispersers per generation and has been used extensively to calculate levels of dispersal. However, this model depends on a long list of assumptions that are highly improbable in real populations (Whitlock and McCauley 1999). Since invasive populations are typically small and thus are extremely likely to violate these assumptions, F_{ST} transformations are unsuitable as a literal indicator of dispersal. Despite this, there are myriad programs available that calculate dispersal rates based on transformations of F_{ST} which should be avoided unless the required assumptions are met. Additionally, these methods estimate historical rather than current rates of exchange. In contrast, BAYESASS (Wilson and Rannala 2003) departs from the traditional use of F_{ST} by using Bayesian methodology similar to the assignment methods discussed above. This program is likely to be of greater use in pest management as it addresses contemporary dispersal rates, does not require populations to be at equilibrium and can handle most types of genetic data. It should be noted that the F_{ST} methods described here measure dispersal of only those individuals who have reproduced, whereas assignment methods measure dispersal of all individuals sampled (Favre et al. 1997)

Patterns of dispersal may also provide useful information for management as they can illuminate the mechanism of introduction as well as identify particular demographic groups more likely to disperse. Using genetic analyses, it is possible to determine the sequence of a group of introductions and to distinguish primary from secondary introductions (see Sved et al. 2003, Kolbe et al. 2004). Spatial Analysis of Molecular Variance (SAMOVA) (Dupanloup et al. 2002) groups populations on the basis of genetic similarity and can be used to identify geographic barriers to dispersal, thus assisting in the strategic placement of control operations. Sex-biased dispersal can be detected by comparing the level of population structure between maternally inherited mitochondrial genes to bi-parentally inherited nuclear genes. Alternatively, sex-specific assignment tests (Favre et al. 1997) and other methods (Goudet 2002) can be used to identify sex-biased dispersal using data from bi-parentally inherited genes.
STARLINGS AS A TEST CASE

The starling (*Sturnus vulgaris*) is an ideal model for the study of invasive species as it has been introduced successfully on multiple continents including Australia. In Australia, acclimatization societies introduced starlings to Victoria, South Australia and New South Wales between 1856 and 1881 (Long 1981). Following a rapid spread, starlings became resident in most of eastern Australia but due to geographical features and control efforts, are yet to become established in WA. This provides an excellent opportunity to study mechanisms of invasion as they occur. Since starlings are highly mobile, small, and tend to inhabit areas difficult to survey, it is especially challenging to use traditional ecological methods to quantify population dynamics, identify source populations and understand population demographics. Therefore, genetic techniques discussed above will be used to address these issues. If source populations or particular groups of individuals prone to dispersal can be identified, more effective and targeted control may be possible.

Methods

Thirty to fifty individuals will be sampled from eight potential source populations in eastern Australia, from areas on the leading edge of the starling invasion in WA and along the Nullarbor (western South Australia), and a museum collection from WA. Fine scale sampling will be conducted in one area for which tracking data exists (Munglinup located west of Esperance in WA, see Woolnough *et al.* this volume). For each individual, over 20 genes will be sampled through DNA sequencing, microsatellite analysis and allozyme analysis. Additional data will also be gathered for each sample including condition, age and sex, which will be determined by dissection or genetic analysis.

Eastern Australian starling populations, which are resident and therefore expected to be stable, will be used to produce baseline population genetic data. Allozymes used in previous studies of introduced starling populations in New Zealand and the US will also be selected for this study so that changes in diversity can be compared across different sites of introduction. To ensure that microsatellite data conform to assumptions, we will use GENEPOP (Raymond & Rousset 1995) to check for evidence of null alleles and genotypic disequilibrium. STRUCTURE will be used to determine the number of genetically distinct populations and to assign individuals sampled in WA and the Nullarbor to populations of origin. Museum samples from past WA incursions will be included in this dataset to determine whether those samples form a distinct genetic group. If they do, then they will be included as a potential source population for the recent invasions. If not, we will assess whether historical and contemporary movements are consistent. We will look for evidence of multiple invasions or sequential invasion. GENECASS2 will be used to corroborate assignments, to exclude populations that do not fit criteria, and to determine whether Western Australian populations are transient. BAYESASS will be used to calculate migration rates. SAMOVA will be used to check for discontinuities in dispersal. Sex biased dispersal will be evaluated by comparing maternally and bi-parentally inherited genes. Additionally, adults from WA identified as dispersers will be used to compare population structure between sexes. Genetic data will be investigated for evidence of population expansion or decline, because we would expect to see evidence of a bottleneck in the Australian population in general, and in any WA resident populations. We will look for genetic evidence of contemporary population expansion.

Possible Management Outcomes

If it is determined that Western Australian starling populations are from the nearest source populations across the Nullarbor, then it may be best to focus additional eradication effort on
these source populations. However, the current management policy of controlling incursions in WA should be continued if Western Australian individuals or their immediate ancestors appear to be from many populations in eastern Australia. Alternatively, if Western Australian individuals appear to form a distinct population, then it may indicate that cryptic resident populations exist. If this scenario seems most likely, management may choose to increase control efforts in WA to locate and eliminate any resident populations. Additionally, if dispersal appears to be skewed toward any particular demographic group, then control efforts aimed at that group may be more effective.

CONCLUSIONS

Much of the challenge of managing wild populations stems from a lack of information regarding their dynamics. The novel statistical methods outlined in this review offer hope for improved understanding and, ultimately, more successful control of invasive species. As with all methods, independent data should be used to validate results and assumptions should be carefully checked. There exist many other examples of the application of genetic data to evaluate and control invasive populations including the comparison of historical and current levels of invasion (Hebert and Cristescu 2002), the identification of invasive species that are morphologically similar to natives (Vazquez-Dominguez et al. 2001) and the identification of hybridization between invasive and native species (Bond 2002). Screening communities for invading species that cannot be morphologically distinguished from natives has been suggested as a future use of these techniques (Hebert and Cristescu 2002). The application of genetic methods to pest management, although currently in its infancy, offers an important new dimension to strategic control and decision making processes.

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REFERENCES


