To the Graduate Council:

I am submitting herwith a dissertation written by Gregory Joseph Witteman entitled "Characterization and Conservation of Populations". I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of doctor of Philosophy, with a major in Ecology.

Stuart L. Pimm, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

CHARACTERIZATION AND CONSERVATION OF SMALL POPULATIONS

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Gregory Joseph Witteman
May 1992

DEDICATION

If the phone doesn't ring... it's me; here's a quarter, call someone who cares; and I've got friends in Low places. ...

Once again it's time for Greg to rant and rave. Many of us are now aware and concerned about the future of our planet. Acid rain is scary and the thought of having to wear spf 400 sunblock scares the hershey-kisses out of me. The questions are these: 1) Does our current knowledge of our environment give us the control we need to preserve it in perpetuate? and 2) If not, why do ecologists, and conservation biologists in particular, have to boot-leg money to continue their research?

Unless your LASL, or you work on an organism that is "warm and fuzzy" or a "charismatic megaverterbrate", your experimental materials are more likely to come from Home Depot than the work-group machine shop. As ecologists, what do we do? I don't know, but the first thing we must do is complain.

The adults of this future won't experience "fear and loathing...", but rather beer and bloating while playing Nintendo on the couch in front of the TV. Yuppies are now Grumpies, and Dinks are the only people who can afford kids. The crazy people are gone and business majors are breeding like flies - (emphasis here on the *maggot* portion of the life-cycle). Not a pretty picture. When do we learn that treating environmental issues as topics that are "politically correct", or not, will doom us all? So, this is dedicated to all conservation biologists.

"... Oh bother..."

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Abstract

The following dissertation contains a body of work that addresses both theoretical and applied issues for small and variable populations. The first section is an overview. The second part explores the extent to which non-cyclic, non-equilabrating, yet deterministic trends are found in populations. Part three defines, tests, and explores the applied implications of a model that relates a population's probability of becoming extinct when faced with a combination of demographic accidents, environmental events, and Alee effects. The fourth section explores the effect that habitat fragmentation has on Hawaiian forest bird communities over a variety of scales. It proposes both a theoretical foundation for, and explores the applied implications of scale dependant fragmentation effects. The final section reflects work completed in the first year of an on-going effort to create a self-sustaining wild population of a species that is currently only found in captivity.

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Vitae!

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PART 1
General introduction

Introduction

We can identify a variety of abiotic or physical factors, such as elevation, latitude or precipitation, that strongly influence large scale patterns in species' distributions. The patchiness of species distributions, and their often tight relationship to environmental variation, led early ecologists to focus on the role abiotic forces play in regulating community composition. At the same time, some biologists realized that the role of abiotic limitation was often usurped by interactions between species (Forbes 1880; Camerano 1880). Although unappreciated until recent times, these pioneering works set the stage for contemporary ecology.

Early theoretical works in characterizing single species growth and two-species interactions lead to field studies of biotic population interactions (Voltera 1927, Preston 1948). Biotic interactions can can take many forms ranging from mutualism to competition. However, competition and predation have played a dominant role in the development of ecological theory. For example, competition between and within species has been shown to strongly influence population sizes for multiple species systems (Park 1948, Connel 1961). In a similar fashion, predation can initiate cascading effects which interact with competitive interactions to either promote the coexistence of competitors or add additional instabilities (Paine 1966). In fact, the effect of predation can even masquerade as competition between two species which share a common predator (Holt 1977).

In addition to environmental gradients and interspecific interactions natural populations may experience a mixture of both deterministic and stochastic environmental events. Often environmental events reduce species

abundance to a level where occurences become critical. These stochastic processes are particularly critical during the invasion process where a few founder individuals colonize a new habitat. Here I present four studies that explore dynamic characteristics that are important to small populations.

First, I explore the temporal variability of populations for which there are long-term data sets. The extent to which a population varies can determine its relative probability of extinction from year to year. A highly variable population might experience low densities from which it is unlikely to recover. On the other hand, populations with little variability and relatively high abundance should not suffer the consequences of such chance extinctions. Clearly, both the magnitude and frequency of population density changes are important in evlauating a population's risk of extinction or probability of persistence. The range of these fluctuations in natural populations has only recently been examined.

A single species population can usually be characterized as either being at or approachin some equilibrium, or fluctuating through time. Models of single species population growth exibit dynamics that range from classic equilibrium behavior through deterministic chaos (May 1987). Generally, as population growth rate is increased a critical point is reached where population dynamics shift from equilibrium to chaos. Hassell, Lawton and May (1976) concluded that population dynamics more complex than equilibreum should be rare. They based this conclusion on the actual growth rates of natural populations. In the first chapter I explore the potential dynamics of populations through the analysis of seventy-two single population data sets that were collected for periods of more than fifty years. The result of my analysis suggests that the extent to which

non-cyclic, non-equilabrium, yet deterministic trends are found in populations has been underestimated.

In the next chapter, I explore the relationship between population size and the probability of extinction. I propose that there are three distinct processes relevant to extinction: 1) *allee effects*, 2) *demographic accidents*, and 3) *environmental effects.* Allee effects are experienced by a population at extremely low numbers. At these numbers, the populations growth rate aproaches zero because individuals are unlikely to encounter mates. Demographic effects, such as all individuals of one generation being the same sex, are also experienced at low numbers but become very unlikely at larger population sizes. Stochastic environmental effects, such as a tornado or typhoon, might drive a local population to extinction or sufficiently reduce abundance to a point where Allee effects and demographic accidents become important.

I propose that when faced with a combination of these three effects, the probability of a population surviving is a logistic function of its population size. This relationship has implications in both the design of desirable species introductions and in preventing invasive species from becomming established. Previous models, without any inflection (ie: not logistic) suggest strategies that are both counter-intuitive and biologically unrealistic. They suggest, for example, that a higher overall chance of persisting is always achieved by splitting a population into two smaller ones for even the smallest population sizes.

The next chapter explores the effect that habitat fragmentation has on Hawaiian forest bird communities over a variety of scales. I propose a theoretical foundation for the applied implications of scale dependant

fragmentation effects, and then explore the merits of various models that relate species distribution and abundance to habitat island (or patch) size. Habitat fragmentation and native versus non-native bird distribution were explored for three characteristic scales.

The final section reflects work completed in the first year of an on-going effort to create a self-sustaining wild population of a species that is currently only found in captivity. The results and conclusions of the previous chapters, in particular, native species and habitat edge effects, population size to persistance relationships, and population varability through time, were considered when designing and modifying reintroduction strategies for the Guam rail (*Rallus owstoni*).

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PART 2
The extent of complex population changes in nature

Summary

Many models of animal populations show complex yet predictable patterns of density changes under simple and plausible assumptions. Yet one previous attempt to determine the extent and importance of complex dynamics concluded that they were likely only in some laboratory populations, but not in field populations. Ecologists have treated changes more complex than a return to a simple equilibrium, such as the cyclical changes in populations of lynx and voles in the arctic, as special cases. Highly variable populations, such as insects, are usually thought to be driven by unpredictable changes in the weather. Here, I assemble 71 populations counted for over 50 years, and suggest that complex yet predictable population changes are more common than previously thought.

1. Introduction

Following disturbances, the densities of model populations may return to, or be "attracted" to a point equilibrium. A persistent, almost strident claim by ecological theoreticians is that changes in population densities ought to be more complex than this (May 1987). In reviewing the 'bestiary' of possible dynamical behaviors Schaffer and Kot (1986) have reported a wide variety of other possibilities (herein called *complex dynamics*) in models with very simple assumptions. For example, in a one predator - one prey model, in which prey growth rates are reduced at low *and* at high prey densities, trajectories of the predator and prey densities may approach a limit cycle. If the prey species has a seasonally varying birth rate, the pattern of density changes of the prey and predator and the prey's varying birth rate may flow on a torus. Or with very simple and plausible assumptions, densities of model populations may return to a complex object known as a strange attractor. Even simple Lotka-Volterra models with as few as three species can generate such dynamics (Gilpin 1979).

A major question in ecology is whether the fluctuations of natural populations represents the complex behavior of simple ecological systems or the results of the unpredictable environmental variables that also determined population changes. This is an issue that far transcends population ecology. The nature of population change is a central feature of all arguments in community ecology. And suppose we assume that the selective advantages of phenotypic traits are partly dependant on population density. Then the prevalence of cyclical (or more complex) changes in density suggest a broader set of scenarios in evolutionary ecology than those that implicitly assume that densities (and hence selection) have some simple central tendency plus

unpredictable variation. Thus if all populations changed cyclically, and all traits were density dependant, then selection would change cyclically too!

To address this issue, we need to separate the environmental noise from the predictable patterns. Ecologists have recognized that complex dynamics do occur in nature and the familiar examples are the many arctic vertebrate populations that change cyclically. Using a method we shall presently describe, Schaffer and Kot (1985, 1986) have found that the number of cases of childhood diseases such as measles and chicken-pox fluctuate widely but not randomly. Rather, population trajectories define an an attractor that bears a striking resemblance to the one found in simple disease models with seasonally changing infection rates (Schaffer 1985).

Important though these examples may be, they are still restricted enough for them to have often been viewed as special cases. Previous attempts to determine the generality of complex yet predictable dynamics in nature have taken indirect approaches. In particular, Hassell *et al.* (1976) analyzed a one-species discrete generation model to determine what parameter values would lead to a point equilibrium, a limit cycle, or deterministic chaos. They estimated the parameters for 24 field and 4 laboratory populations of insects and concluded "that the majority of populations show a monotonic return to a stable equilibrium." Interestingly, at least one population that the model predicted would return to a stable equilibrium was known to cycle. Though quick to point out their method's limitations, Hassell *et al.*'s conclusions were sufficiently emphatic that many ecologists discounted complex dynamics except as special cases.

A better approach to investigating dynamical complexity may be the direct study of long-term data, but there are obvious difficulties with this. There

are questions about what methods to use and we shall discuss these presently. Long-term data in ecology may still involve very few years relative to the requirements of these methods. Moreover, as the length of the study increases, the quality of the data decreases. A professional ecologist may study a population for a decade but a century of data will have been collected for other purposes than the ones we plan for them. None the less, we should still ask what long term data can tell us about population changes. We shall return to the limitations of the data in our discussion. Finally, our experience suggests that publishing catalogues of ecological studies challenges other ecologists to report similar studies that were overlooked. If the compilation of studies presented here is quickly shown to be incomplete and biased in its conclusions, then so much to the good.

2. Methods of data analysis

The analysis of long-term data can proceed in at least two ways. The first is to look for cycles directly using studies of autocorrelation (Chatfield 1984; Finerty 1980 discusses the methods in an ecological setting). Each density is correlated with the density one year in the past, two years in the past and so on. When there are cycles of x years in duration, the correlations will be significant and positive for x, $2x$, $3x$,... years and significant and negative for $x/2$, $3x/2$, $5x/2$,... years. Unfortunately, not all complex trends in population data are sufficiently periodic to be detected by autocorrelation methods. The classical example is the single-species, finite difference analogue of the logistic equation: with the appropriate parameters, the density changes are both predictable and aperiodic (May 1987). The fact that these changes are predictable can be readily seen by plotting the density at one period of time versus the population at the previous period of time. Unfortunately, complex

dynamics may be generated, for example, by the interaction between three or more species (such as Gilpin's 1979 "spiral chaos"). The underlying pattern of such changes may be visible if we plot successive densities of all three species but the difficulty is that such data are rarely, if ever, available for ecologists.

The second way of seeking complex dynamics is due to Takens (1981) who has suggested an alternative for detecting deterministic patterns when measurements of just one variable (the population density of one species, for example) are available. He showed that plots of a single successively lagged variable (densities x(t), x(t-T),... x(t-nT)) will display characteristics that are equivalent to those generated by plotting each of the state variables against one another. This is the method used to great effect by Schaffer and Kot (1986a) on particular species to suggest predictable changes in the density of apparently randomly-fluctuating species. We will use this procedure in simply a descriptive fashion and make no inferences about the patterns generated. But such a procedure does suggest likely candidates for more detailed analyses.

a. The data

To determine the extent of complex yet predictable dynamics in temperate and arctic populations we have assembled 71 populations counted for at least 50 years (Table 1). There were 27 bird populations of 7 species, 27 mammal populations of 10 species, and 17 insect species. Wherever possible, we excluded segments of data at the beginning or end of censuses if these segments contained many zeros. None of the population censuses included more than two consecutive zeros during the years that we selected for analysis. Of the bird and mammal populations, only one, the grey heron (population 1 in Table 1) was censused directly. Abundances for the remaining populations were estimated from historical records of annual harvests based either on game

bag records from various estates in Britain (populations 2-32), on the number of animals exported from Iceland (population 50), or on the number of fur returns, shipments or sales from Canada and Alaska (populations 51-71). Ten of the 17 insect populations are of migratory Lepidoptera recorded by amateur naturalists in Britain (populations 33-42). Four are of German forest pest Lepidoptera that were directly counted (populations 43-46). The remaining three insect populations (47-49) are exceptions in that they were censused for only a few years. They were included because they were counted more than once a year, and so more than 50 population estimates were available.

Twenty-six of the bird populations (7 species), 6 of the mammal populations (3 species), and all 17 insect populations (17 species) were censused in temperate regions. The remaining populations (23 mammal populations: 7 species, and one bird population) are from arctic regions. There are no tropical populations, and we are still compiling long term studies from aquatic and marine communities. We analyzed these studies using both autocorrelation and Takens' lag-plot methods.

b. The autocorrelation analysis

Before performing the autocorrelation analyses, we square-root transformed the data and removed linear trends lasting the entire census period. These procedures first make the data more symmetrical and so less sensitive to unusual extreme values and more normally distributed, the distribution required for the assumptions of the statistical inferences to be met. We took out the longest-term effects because these may reflect gradual changes in the species' environment. We could not use a logarithmic transformation on the data because there were a few zero values in the data. We classified our results into three categories: significant, likely significant, and

not significant. We considered an autocorrelation *significant* when a population density was both significantly negatively correlated with a population density at the half cycle period and positively correlated with the population density at the full cycle period. The significance level chosen was 5%. An autocorrelation was considered *likely to be significant* when the half or full cycle correlation was significant, *and* the full or half cycle (respectively) correlations were significant at the 10% level.

The reasons behind these choices are these. First, the densities often showed significant autocorrelations over very short time lags -- particularly those of one year. This is not surprising. For many of the species, the densities in one year would correlate with those of the previous year because the same individuals may be present in both years. Our choice excludes such significant autocorrelations for they say nothing about the presence of cycles.

Second, our significance levels were calculated to correct for the fact that many different correlations were being performed on each population. Obviously, if we did not correct for this, then we would typically find one "significant" correlation per population because we always looked at correlations out to lags of at least twenty years. However, even with this correction, we sometimes found significant autocorrelations that seemed meaningless in the context of cycles. For example, we might find a 20-year significant positive autocorrelation in an insect species, when the 10-year autocorrelation was neither negative nor significant. Our choices would reject such an autocorrelation as being either significant or likely significant.

Third, we feel that our choices are conservative. We rejected as even likely significant those populations where there were marginally significant positive and negative correlations at matching integer and half integer periods.

These were all in species for which other populations of the species did show significant autocorrelations and, moreover, at the same periods. These correspondences suggests that we ought to have included these as being significant.

In short, we have made choices designed to minimize the chance of finding apparent cycles when we were merely performing the same analysis on a large number of essentially randomly-fluctuating populations.

c. Phase portrait (Lag-plot) reconstruction

Next, we used Takens' approach. Before plotting the data, each of the original data sets was three-point moving averaged, logarithmically transformed, and splined. The moving average smooths the data and so removes any unusually high or low points. The logarithmic transformation makes these points more symmetrical. While the original data contain some zero values, the moving averages do not, and so the logarithmic transformation can be used. Splining is strictly an aid in visualizing the reconstruction; it does not alter the relationship between the actual points, but merely fills in values in between them.

Although Takens' method is relatively insensitive to the lag interval chosen (Schaffer and Kot 1986b) , some intervals produce portraits in which the underlying dynamics can be seen more easily. There is a technical literature on this subject (Fraser and Swinney 1986, Fraser 1989). A common option chooses lag intervals that are 0.2 - 0.5 of the period of the highest prominent cycle length in each data set's autocorrelation analysis (Schaffer and Kot 1986b). This is because if there were strong cycles, there would be a negative correlation at the half period, there is an inevitable perfect correlation at the zero lag (each density with itself), and half way in between there should be no

correlation at all. That is, one chooses a lag so that the plotted points are independant of each other. We started with a lag of 0.4 and, after some exploration, chose 0.2 for all the plots because that lag gave us results that were more visually appealing.

3. Results

The data and the results of our analyses are summarized in table 1. In the data from arctic regions, the one bird population showed a likely significant autocorrelation. Significant autocorrelations were found in 16 of the 21 mammal populations and a further 3 populations showed autocorrelations that were likely significant. Simply, in *every* species w
e found at least likely cycles.

In the data from temperate regions, 2 of the 26 bird populations (both of the same species) showed significant autocorrelations. Moreover, populations of two additional species of bird had a likely significant autocorrelation according to our definition. There were no significant autocorrelations in the 6 populations of the 3 species of mammals; however, one population had a likely significant autocorrelation. In the 14 insect species censused yearly, 2 showed likely autocorrelations.

For the populations with significant autocorrelations, Takens' method should reproduce a closed curve and indeed, this is what we find. For two additional populations that did not show even likely autocorrelations, we found patterns that *to us* suggest cycles for one temperate mammal (population 30, table 1) and one temperate bird population (population 9, table 2). These species were those in which autocorrelations had already been found and indeed the populations were both physically close to populations for which significant autocorrelations had been found.

More interestingly, in 4 insect populations (table 1, numbers 33, 36, 43, 46) we found patterns that suggest *to us* attractors; we show these in figure 1.

Of the three insect species censused monthly, we expected yearly cycles and this is what we found. However, for one of the insects counted monthly, an attractor has already noted by Schaffer and Kot. (1986a). We did not see the suggestions of an attractor in either of the other two species.

In short, cycles are common in the arctic, indeed, they appear to be the major pattern of population changes there. In temperate birds, 2 of 7 species, in temperate mammals 1 of 3 species, and in temperate insects, 7 or 14 species counted annually, and 1 of 3 counted monthly are at least suggestive of complex dynamics. Complex dynamics are clearly more prevalent than Hassell *et al.*'s (1976) previous analysis suggests.

4. Discussion

We recognize that our conclusions may be controversial at least in part because there are so many limitations to our analyses. Certainly, the data were collected haphazardly. The migratory Lepidoptera were counted by several generations of amateurs. The game bag records span two world wars when sportsmen and game keepers were occupied in other activities. Furthermore, these and other harvesting records may reflect changing management strategies as well as the intrinsic dynamics of the populations. However, such problems might be expected to obscure patterns in the data rather than to create them. The relatively few data points (114 years - the maximum) should make it difficult to detect anything other than the most pronounced of patterns. So, we may have underestimated the prevalence of complex dynamics.

Conversely, the British migratory and German pest Lepidoptera are expected to be unusually variable in density because migratory species in

general and species considered pests are generally more variable than species classified otherwise (Pimm 1990). Highly variable populations may be more likely to demonstrate complex density changes than a random selection of populations. In any case game birds and mammals and migratory insects are hardly a random selection of species. We will not know whether our species are special in some way unless we discover other long-term data. While we searched diligently for terrestrial long-term studies, we expect that we have overlooked many comparable studies. We have not yet compiled studies from aquatic and marine communities. We hope, indeed we expect, that our analyses will prompt others to report and analyze other long-term studies that we missed.

Four of our claims are based merely on the visual appeal of figure 1 where they are presented to show their most suggestive viewpoints. The eye may detect patterns too subtle to pick up with simple statistical techniques, but we realize that we can be easily fooled by random patterns. More detailed analyses of these populations are needed; our aim in presenting them is to stimulate such analyses. The complete 3-dimensional coordinates are available from us on disc. The relatively very short spans of data available mean that the most powerful way of detecting non-random population changes will be to have *a priori* models to test, rather than to seek general methods for identifying these changes.

For example, three of these four species (all but the clouded yellow butterfly) have patterns that are suggestive of cycles, but which did not satisfy our criteria of being likely significant in the autocorrelation analysis. One of these (the bordered white moth) showed marginally significant positive and marginally significant negative correlations at compatible times, and our

exclusion of it from the likely significant category may be a reflection of too strict a criterion. The clouded yellow shows a pattern that we find particularly intriguing, though we know of no model that might generate such a pattern. Clearly, such a model would have to be firmly based in the detailed natural history of this species. If such a model predicted the patterns *a priori*, then we would have more confidence that the patterns are not spurious.

Finally, even if densities changes do show, say, predictable cycles, then the mechanisms still need to be understood. There is no reason to think that these cycles will always driven by ecological interactions. The environment itself may be periodic, or the oscillations may be driven by interactions between the population and a fluctuating environment.

We feel, however, that these patterns are sufficiently compelling to refute the hypothesis that complex dynamics are special cases in geographically restricted habitats. Even the suggestion of complex dynamics in these long-term data poses an important challenge to traditional population and community ecology. Certainly, cycles are more prevalent in the arctic, but they also occur elsewhere. This prompts us to ask what situations conducive to complex dynamics are more common in the arctic than elsewhere, not what situations are restricted to the arctic. Studies of vole cycles have suggested that it is the relatively simplicity of arctic communities that lead to cycles (Hanson 1987, Hansson and Hentonnen 1985, Hentonnen *et al.* 1987). Yet it is not model simplicity that leads to cycles but model complexity. This raises the possibility that complex dynamics may be prevalent in temperate areas too, but only in the arctic are the dynamics routinely complex yet simple enough, (that is they are cyclical) for us to appreciate them.

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Table 1. Summary table of the data used and the results.

Common Name	Scientific Name	Auto-Correlation? (period in years)	Suggests Attractor?	Reference[b]	Dates of Census[c]	N[d]	Location	Pop. No.
Temperate								
Birds								
Grey heron	*Ardea cinerea*	likely(16)		Stafford 1971[6], Reynolds 1979[7]	1928-1977	50	England and Wales	1
Black grouse	*Tetrao tetrix*	no		MacKenzie 1952[8]	1866-1938	73	Central Scotland[e]	2
Black grouse	*Tetrao tetrix*	no		MacKenzie 1952	1850-1938	89	South Scotland	3
Capercailie	*Tetrao urogallus*	no		MacKenzie 1952	1866-1938	73	Central Scotland	4
Ptarmigan	*Lagopus mutus*	no		MacKenzie 1952	1876-1939	64	Central Scotland	5
Red grouse	*Lagopus scoticus*	likely(10)		MacKenzie 1952	1866-1938	73	Blair Atholl, Scotland (Moor 1)	6
Red grouse	*Lagopus scoticus*	likely(10)		MacKenzie 1952	1866-1938	73	Blair Atholl, Scotland (Moor 2)	7
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1866-1938	73	Blair Atholl, Scotland (Moor 3)	8
Red grouse	*Lagopus scoticus*	no	yes	MacKenzie 1952	1866-1983	73	Blair Atholl, Scotland (Moor 4)	9
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1859-1938	80	Central Scotland	10
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1854-1938	85	Wales	11
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1886-1938	53	Hebrides, Scotland	12
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1834-1938	105	South Scotland	13
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1870-1938	69	East & Central England	14
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1855-1938	84	Ireland	15
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1887-1938	52	North-west Scotland	16
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1879-1938	60	West Scotland	17
Red grouse	*Lagopus scoticus*	no		MacKenzie 1952	1869-1938	70	North-east Scotland	18
Red grouse	*Lagopus scoticus*	likely(5)		Middleton 1934[9]	1848-1904	57	Cumberland, England[f]	19
Red grouse	*Lagopus scoticus*	yes(6)		Middleton 1934	1849-1904	56	Aberdeenshire, Scotland	20
Red grouse	*Lagopus scoticus*	yes(6)		Middleton 1934	1858-1909	52	Lanarkshire, Scotland	21
Woodcock	*Scolopax rusticola*	no		Middleton 1934	1846-1932	87	Sussex, England	22
Partridge	*Perdix perdix*	no		Middleton 1934	1843-1933	91	Norfolk (Estate a), England	23
Partridge	*Perdix perdix*	likely(5)		Middleton 1934	1862-1932	71	Norfolk (Estate b), England	24
Partridge	*Perdix perdix*	no		Middleton 1934	1843-1933	91	Yorkshire (Estate b), England	25
Partridge	*Perdix perdix*	no		Middleton 1934	1879-1932	54	Hertfordshire, England	26
Mammals								
European hare	*Lepus europaeus*	no		Middleton 1934	1862-1932	71	Norfolk (Estate b), England	27
European hare	*Lepus europaeus*	no		Middleton 1934	1843-1932	90	Yorkshire (Estate a), England	28

Table 1 (continued)

European rabbit	*Oryctolagus cuniculus*	no		Middleton 1934	1867-1928	62	Yorkshire (Estate b), England	29
European rabbit	*Oryctolagus cuniculus*	likely(7)		Middleton 1934	1862-1932	71	Norfolk (Estate b), England	30
European rabbit	*Oryctolagus cuniculus*	no	yes	Middleton 1934	1869-1933	65	Norfolk (Estate a) England	31
Weasel	*Mustela vulgaris*	no		Middleton 1934	1879-1930	52	Perthshire, Scotland	32
Insects (yearly)								
Clouded yellow	*Colias croceus*	no	yes	Williams 1958[10]	1855-1955	101	Britain	33
Convolvulus hawk moth	*Herse convolvuli*	no		Williams 1958	1851-1955	105	Britain	34
Death's head moth	*Acherontia atropos*	no		Williams 1958	1856-1955	100	Britain	35
Humming-bird hawk moth	*Macroglossa stellatarum*	no	yes	Williams 1958	1881-1955	75	Britain	36
Camberwell beauty	*Nymphalis antiopa*	no		Williams 1958	1855-1955	101	Britain	37
Painted lady	*Vanessa cardui*	no		Williams 1958	1877-1955	79	Britain	38
Red admiral	*Vanessa atalanta*	no		Williams 1958	1875-1955	81	Britain	39
Silver Y	*Plusia gamma*	no		Williams 1958	1877-1955	79	Britain	40
Silverstriped hawk moth	*Hippotion celerio*	no		Williams 1958	1877-1926	50	Britain	41
Striped hawk moth	*Celerio lineata livornica*	likely(10)		Williams 1958	1856-1906	51	Britain	42
Bordered white moth	*Bupalus piniarius*	no	yes	Varley 1949[11]	1881-1940	60	Letzlingen, Germany	43
Pine spinner moth	*Dendrolimus pini*	no		Varley 1949	1881-1940	60	Letzlingen, Germany	44
Pine hawk moth	*Hyloicus pinastri*	likely(9)		Varley 1949	1881-1930	50	Letzlingen, Germany	45
Pine beauty moth	*Panolis griseovariegata*	no	yes	Varley 1949	1881-1940	60	Letzlingen, Germany	46
Insects (monthly)								
Apple thrips	*Thrips imaginis*	likely(1)	yes	Davidson & Andrewartha 1948[12]	1932-1938	81	Near Adelaide, Australia	47
Chaff scale	*Parlatoria pergandei*	yes(1)		Bodenheimer 1958[13]	1929-1936	88	Hedera	48
Florida wax scale	*Ceroplastes floridensis*	yes(1)		Bodenheimer 1958	1929-1936	96	Hedera	49
Arctic								
Birds								
Ptarmigan	*Lagopus mutus*	likely(12)		Williams 1954[14]	1864-1914	51	Iceland[g]	50
Mammals								
Arctic fox	*Alopex lagopus*	no		Elton 1942[15]	1834-1925	92	Hebron, MM,Canada[h]	51
Arctic fox	*Alopex lagopus*	yes(4)		Elton 1942	1834-1925	92	Hopedale, MM, Canada	52
Arctic fox	*Alopex lagopus*	yes(4)		Elton 1942	1834-1910	77	Nain, MM, Canada	53
Arctic fox	*Alopex lagopus*	yes(4)		Elton 1942	1834-1906	73	Okak, MM, Canada	54
Arctic fox	*Alopex lagopus*	yes(4)		Elton 1942	1868-1924	57	Ungava District, HBC, Canada	55
Coloured fox	*Vulpes fulva*	yes(4)		Elton 1942	1834-1918	85	Hopedale, MM, Canada	56
Coloured fox	*Vulpes fulva*	yes(4)		Elton 1942	1854-1918	65	Nain, MM, Canada	57
Coloured fox	*Vulpes fulva*	yes(4)		Elton 1942	1854-1918	65	Okak, MM, Canada	58

Table 1 (continued)

Coloured fox	*Vulpes fulva*	yes(4)	Elton 1942	1854-1918	65	Hebron, MM, Canada	59
Marten	*Martes americana*	no	Elton 1942	1846-1916	71	Hopedale, MM, Canada	60
Marten	*Martes americana*	no	Elton 1942	1853-1908	56	Nain, MM, Canada	61
Marten	*Martes americana*	likely(8)	Elton 1942	1853-1909	57	Okak, MM, Canada	62
Muskrat	*Ondatra zibethicus*	likely(10)	Elton & Nicholson 1942a[16]	1849-1927	79	MacKenzie River, HBC, Canada[i]	63
Lynx	*Lynx canadensis*	yes(10)	Elton & Nicholson 1942b[17]	1821-1891	71	Athabasca Basin, HBC, Canada	64
Lynx	*Lynx canadensis*	yes(10)	Elton & Nicholson 1942b	1821-1891	71	West Central,HBC, Canada	65
Lynx	*Lynx canadensis*	yes(10)	Elton & Nicholson 1942b	1821-1934	114	MacKenzie River HBC, Canada	66
Lynx	*Lynx canadensis*	yes(10)	Elton & Nicholson 1942b	1821-1891	71	Upper Saskatchewan, HBC, Canada	67
Lynx	*Lynx canadensis*	yes(10)	Elton & Nicholson 1942b	1821-1891	71	Winnipeg Basin, HBC, Canada	68
Lynx	*Lynx canadensis*	yes(10)	Elton & Nicholson 1942b	1821-1891	71	North Central, HBC, Canada	69
Snowshoe hare	*Lepus americanus*	yes(11)	MacLulich 1957[18]	1849-1904	56	HBC	70
Wolverine	*Gulo gulo*	likely(10)	Rausch & Pearson 1972[19]	1910-1964	55	Alaska	71

[a] Only populations that showed no significant autocorrelations (no multi-annual cycles) but that, from Takens' method, suggest an attractor are scored with a 'yes' here.

[b] We provide the reference from which we obtained the data. See these references for primary sources.

[c] Dates refer to the years of the census that we included in our analyses.

[d] N refers to the number of observations included in our analyses. All populations except 47-49 were censused annually, and so N equals the number of years. (Abundances for populations 47-49 were provided for each month.)

[e] Annual abundances for populations 2-5 and 10-18 were estimated as the total number of game bags from a variable number of moors within the region shown. For each population, we corrected data according to the number of moors included in the annual counts.

[f] Annual abundances of populations 19-32 are based on the number of animals killed on one individual estate in each of the locations shown.

[g] Ptarmigan abundances were estimated as the total number of birds exported from Iceland each year. We corrected these totals by the duration of the open season, which changed throughout the census period.

[h] MM, Moravian Missions.

[i] HBC, Hudson's Bay Company.

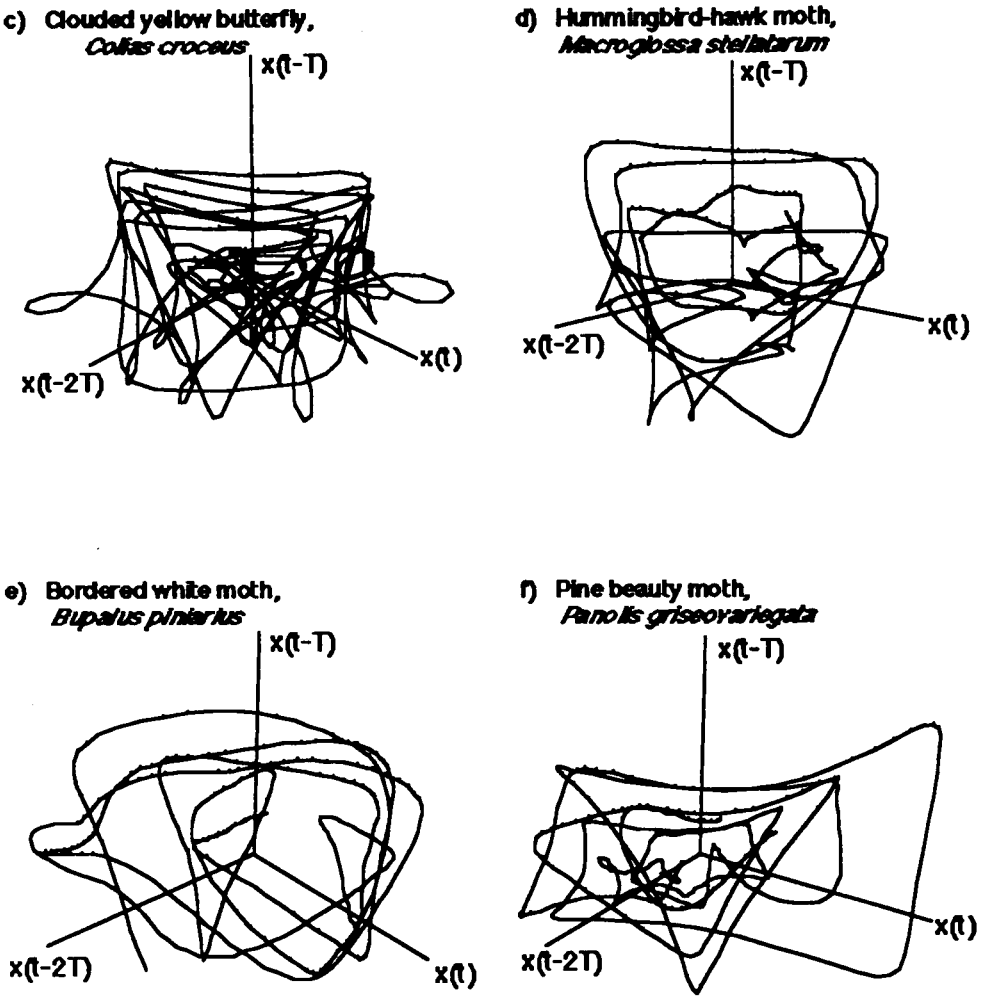


Figure 1. Phase portraits obtained by applying Takens' method to four populations. The lag intervals chosen are (a)1.6 (b)2.0 (c)2.5 and (d)1.5 years. The sources of the original data are given in Table 1.

PART 3
The Risk of extinction: Lessons from introduced species

Abstract

The chance that a population will persist from year to year, or an introduction succeed, is a function of its population size. Environmental events, demographic accidents, and Allee effects determine the shape of that function. Theory predicts that the relationship between size and chance of persisting should be sigmoidal in shape when Allee effects are important. When they are not, the relationship will not be inflected. The inflection point is the population size at which the per-individual contribution to the population's chance of success is highest. For deliberately introduced species, other factors, such as the source of the individuals (wild or captive-reared), the time of the release (winter or summer, for instance), and the method of the release, may also be important. I analyzed data on the fate of 790 introductions of 20 species of gamebirds released outside their native range. The success of these releases increased with the numbers of birds released, reaching an asymptotic success of about 15% at 200 released individuals. An inflected, sigmoidal function describes the data better than a function without an inflection. The inflection is at about 75 individuals and its existence suggests the importance of Allee effects. Releases made in the winter are more likely to succeed than ones made at other times of the year. Introduction of wild-caught individuals are much more likely to succeed than those of captive-raised individuals.

1. Introduction

Ecologists encounter extremely small populations when species are near extinction and shortly after species invade new locations. Knowing the minimal number of individuals necessary to sustain a population is important in both establishing populations of a desirable species, and preventing undesirable species from invading new locations. Here I examine factors that are important in determining the fate of small populations. First, I explore a variety of models that relate extinction to factors both internal and external to the population. I then test the predictive value of these models with data on the introductions of game birds.

Between 1960 and 1970, the United States Fish and Wildlife Service's Foreign Game Importation Program (FGIP) released over 130,000 game birds into 44 states and three territories (Bohl & Bump 1970). Following the end of this federal program, game bird introductions continued until 1978 in 23 of these states (Banks 1981). When combined, these two sources document the fate of 790 introductions of 20 species of birds. The smallest number of individuals released (henceforth, *propagule size*) was six and the largest was over ten thousand. Releases of these birds were made in every month of the year. Habitats ranged from temperate through tropical.

Whether a single introduction succeeds or fails clearly depends on the number of individuals introduced. However, the reasons why similar sized introductions fail in some places, yet succeed in others is less clear. We will explore these reasons both theoretically and through our analysis of gamebird introductions.

2. Theory 1: Effects of Propagule size.

I divide this section into two parts. First I present a short discussion of environmental and demographic causes of extinction. I then explore how the inability to find a mate (*Allee effects)* can also doom sparse populations. The second part introduces models that relate the chance of a population's extinction, from one year to the next, to its initial size. Finally, we examine factors other than propagule size which can influence an introduced population's chance of becoming established.

a. The process of extinction

Models of the dynamics of small populations recognize demographic accidents and environmental disturbances as two major causes of extinction (Leigh 1975; Goodman 1987). *Demographic accidents* arise when a population experiences chance and independant events among its individuals. When these events are combined the population may become extinct. Consider a population consisting of only a single pair that produces only two offspring. If those two offspring form the next generation, but are both the same sex, the population will certainly become extinct. The sex of the pair's offspring are independently determined, and the potential change in sex-ratio is intrinsic and unavoidable. For successively larger population sizes, ten pairs for example, the chance that all pairs will produce offspring of the same sex is negligible. Similarly, all the individuals in a small population may die for independent reasons in the same year. This is quite unlikely for a large population, but much more likely for a small one, and unavoidable for a population of just one individual.

Unlike demographic accidents, chance *environmental* effects kill many individuals of a population for the same reason. External factors are

responsible for individuals' deaths. For example, a large portion of a population may perish in a fire, a severe storm, or a drought. When faced with the most severe of disturbances, even the largest of populations may become extinct. How long a population lasts before it experiences an environmental effect large enough to cause its extinction depends on both the population's and the disturbance's distribution in time and space.

Allee effects act upon a population's ability to grow rather than the chance of its individuals dying. Consider a population of a single male and female on an island. If the individuals move very little or the island is large, the two individuals may never meet each other, and thus mating is impossible. With tens or hundreds of individuals on the same island, it is hard to imagine there would be too few matings to sustain the population. There must be enough successful matings for the population's births to be at least as frequent as its deaths. If not, the population's extinction is inevitable.

The time-to-extinction is related to a population's size in a characteristic way for each of the above effects. When faced with demographic effects alone, time to extinction increases very rapidly for incrementally larger population sizes. The time-to-extinction due to environmental effects also increases for successively larger populations. However, no population may be large enough for the most severe and widespread environmental disasters. For this reason, the time-to-extinction in the face of environmental effects approaches the time at which the most severe of disasters occur. For example, some Pacific islands experience typhoons once every five years and super-typhoons capable of completely scouring some atolls at about one-hundred year intervals. An island population of terrestrial animals might not be able to survive a storm if its

population has size **x**, but may survive at twice that population size. Even the largest population will become extinct in 100 years.

Like demographic effects, the time-to-extinction for a population experiencing Allee effects increases rapidly with increasing population size. There is a population size below which the time to extinction is effectively zero. When Allee effects are incorporated into population models including demographic and environmental effects there is a threshold below which populations cannot survive. Above this threshold, first demographic accidents, and then environmental effects are the primary causes of extinction.

One way of exploring these effects is to consider a population's time to extinction. There is both a theoretical literature (Leigh 1975,1981, MacArthur & Wilson 1967, Richter-Dyn & Goel 1972, Goodman, 1987) and empirical tests of these theories. For example, data in Pimm et al. (1988) support the models that predict the functional form of times to extinction when populations suffer demographic accidents and environmental effects. In contrast, data on species introductions tells us if a population survives from one year to the next. For this type of data, we require theories that relate a population's size to its yearly chance of extinction, rather than to the time it will likely become extinct.

b. The chance of surviving to next year

We now consider how demographic accidents, environmental and Allee effects determine the chance of extinction from one year to the next. The types of mechanisms responsible for each effect described above remains the same. Rather than consider each effect separately, we will successively incorporate effects into a single model. Our goal here is to present a theoretical framework that is conceptually simple, yet supported by previous work. (For a complete discussion see Dennis et al. 1989).

i: Demographic By definition, individuals dying for independent reasons are the cause of demographic accidents. If the chance of an individual dying is ϕ, then the chance that a population of size **n** will become extinct in the next year, is $p(n)=(\phi)^n$. Here, the chance that the entire population will become extinct in a single generation quickly approaches zero for larger initial populations. Conversely, the chance that the population will survive (P_{surv} = 1-p(n)) quickly approaches unity for large populations. Although intuitive, this approach to modeling the chance of extinction due to demographic accidents lacks population dynamics such as births and deaths.

Consider the birth-death process models of the form $dn/dt = \lambda(n) - \mu(n)$. (**n** is the population size, λ, the rate of births in the population, and μ is the rate of deaths in the population). This is probably the simplest form for a single species model of population growth . Having the birth rate a linear function of the population size, such as $\lambda(n) = \lambda n$, results in density independent or *simple linear* (SL) models. Ecologists have used this simple linear birth-death process as the basis for stochastic models of species colonization (MacArthur & Wilson 1967, Richter-Dyn & Goel 1972). The chance, p(n), that a population of size **n** will become extinct in this type of model is: $p(n) = (\mu/\lambda)^n$. This again quickly approaches zero for successively larger populations, and the probability that the population will persist approaches one.

ii. Environmental Environmental effects, by definition, kill a portion of the population for the same reason. When combined with the demographic accidents described above, some portion of the population dies for the same reasons, and individuals in the remaining population are still at risk of dying for independent reasons. For example if **1-q** of the population die for the same reason, then **qn** survive. The chance that a population of size **n** will become

extinct in this type of model is: $p(qn) = (\mu/\lambda)^{qn}$. As with models of demographic accidents alone, the relationship between population size and chance of extinction depends upon the specific forms used for birth and death functions. In this example these are linear functions of the population's size.

The chance that a population will become extinct due to environmental effects also will depend upon the specific functional forms used to model the severity and distribution of those effects. When there are no environmental effects (ie: $q = 0$), what remains is the original model that relates a population's size to its chance of extinction from demographic accidents alone. When environmental effects are present (ie: $q \neq 0$) the probability of survival at any given population size is lower than in the model that has only demographic effects.

iii. Allee The last addition we will make is to include density dependant mating encounters into the model of demographic accidents and environmental effects. As before, our population will have individuals die for both similar (environmental) and independent (demographic) reasons. However, rather than use simple linear forms in both the birth and death functions, mating encounters, and hence births, are assumed to be density dependant. Dennis (1989) shows that a simple way of modeling mating encounters between individuals is to assume that individuals' movements are analogous to gas molecules. When the density is high, collisions between two molecules are frequent. At the lowest of densities encounters between molecules are few or none.

For populations, if some portion encounters between individuals result in successful mating, then the birth rate will be of the form: $\lambda(n) = \lambda\alpha n^2$. (**n** and λ, are as described in the above simple linear models, and **a** is a constant). When

Dennis incorporates this type of density dependant mating into the stochastic birth-death models described above, the probability of extinction is: $p(n)=\gamma(n,\mu/(\lambda\alpha))\Gamma(n)$ (where $\gamma(.,.)$ is an incomplete gama function, and μ, λ, α are as in previous models). The chance that a population will survive a combination of Allee, environmental, and demographic effects is now a sigmoidal function of its size (for a complete derivation of this model see Dennis 1989). Furthermore, the sigmoidal relationship between population size and the probability that it will persist is consistent for a variety of mating-encounter functions, with different assumptions than the one described above. Alternatively, if Allee effects do not determine the fate of small populations, a population's probability of survival will be a monotonically increasing function of its size (Figure 1).

c. Species introductions

Combined, these theories suggest a sigmoidal shape for the relationship between propagule size and the probability that an introduction will succeed. At successively larger population sizes the probability of a successful introduction should accelerate if Allee effects affect the population. Above some population size, the risk of extinction due to Allee effects is negligible. For these larger populations, first demographic accidents, then environmental effects are the primary causes of extinction.

The risk of extinction due to Allee effects and demographic accidents are quickly overcome for incrementally larger populations. Conversely, successive increases in population size only slowly increase its probability of persisting when faced with environmental effects. Eventually, the chance that a population will persist reaches an upper bound at which increasing its size does not increase its chance of survival.

3. Theory 2: Factors other than population size

Although propagule size is important in determining whether an introduced population becomes established or persists, other factors may be equally important in determining its fate. The factors that we will consider are time of release, method of release, and the source and quality of the individuals. Although we do not present these in the same theoretical framework as above, they are important in suggesting factors that affect an introduced population's ability to survive.

What should be the optimal time of year in which to release a species? The amount of time allowed before the breeding season begins has two conflicting effects. The beneficial one is that individuals gain more experience in finding food and avoiding predators the longer they are there. The disadvantage is that natural mortality will take an inevitable toll, leading to a smaller breeding population and increased vulnerability to chance events. Introduce a species in the spring or summer and the abundance of food or other resources may enhance initial survivorship and lead to a crucial increase in population size. If the introduction is after the breeding season, then the population cannot breed for almost another year. In that time, it may have declined to a very low level. Alternatively, if one introduces a species in, or just prior to, the breeding season, the individuals' inexperience may lead to poor breeding success. Worse, the breeding attempts may expose individuals to very high levels of predation. In general, displaying males and nesting females are vulnerable; inexperience makes them even more so.

In short, we might expect that just prior to the breeding season is the best time to introduce species. This may be naive, however. Depending on the

relative importance of the conflicting effects of the previous paragraph, other times of year may be optimal.

Release methods can vary from transporting animals to new locations and immediately releasing them (*direct* releases), to holding them in large semi-natural enclosures with supplemental feeding and care until they are released by opening a gate or removing a fence (*gentle* releases). If the animals being introduced are sensitive to human disturbance or handling stress, we would want to minimize each of these effects. A direct release would increase the introduction's chance of success. Alternatively, individuals of an introduced population may experience more stress from being placed in a new environment. A species may not be able to immediately exploit resources it finds where it is released, for example. In this case, a gentle release with supplemental feeding or care would be more effective.

The source and quality of individuals is potentially critical in designing a successful introduction. We expect that wild birds may have experience that captive birds do not. Behaviors such as predator recognition and avoidance may be learned only in the wild. If they are important to the survival of an introduced population, we would expect populations of wild-caught individuals to be more successful than ones composed of captively-raised individuals.

Potential genetic differences between captive and wild sources of release individuals may be equally important. Although there is increasing concern about the genetic management of small captive populations, three problems still persist. First, there is the potential for the smallest of captive populations to experience severe and continuous genetic bottlenecks. Secondly, we may not have enough information to genetically manage both captive populations and the introduction propagules that they produce. For

example, we may not know if a release propagule consists of only closely related individuals. If it did, the resulting wild population may only represent a small portion of the original genetic diversity of the species. Thirdly, captive populations may undergo unintentional selection for those features that confer advantage in captivity, but not in the wild. For these reasons, released individuals from captive populations may have very different qualities than those of the original wild population.

4. The data and their analysis

The FGIP reports on game-bird releases in the United States listed the species of bird, the state or territory and county, the year and month, and the number of individuals introduced. Whether the birds came from a captive breeding facility or from the wild, the specific introduction methods, and whether the release was successful in establishing wild population were reported for the majority of introductions. Our analysis of these data is in two parts. In the first, we explore how specific release methods affect an introduction's success. Secondly, we explore the potential relationship between release propagule size and the chance that a population will became established.

From data in the original FGIP reports, we grouped the outcome of an introduction as either 'successful', 'persistent', or 'failure'. We considered an introduction 'successful' if the population became 'established' or developed a 'breeding population'. If there was some breeding and some surviving birds, but the population survived at progressively smaller numbers, then we assigned the introduction's outcome as 'persistent'. 'Failure' meant that the species became locally extinct. Because the eventual fate of the 'persistent' populations is unknown, we grouped 'persistent' populations with 'failures' and contrasted these with the releases that were *unquestionably* successful. In all of the

analysis discussed below, repeating the analyses with 'persistent' releases excluded rather than considering them failures does not change the result.

Of the total of 790 releases we were able to group only 544 into the three groups described in the previous paragraph. For the remaining 246 releases, the data were either missing or ambiguous. Of these 544 introductions, 68 were 'successful', 297 were 'failures', the rest were 'persistent'. Thirteen species (a total of 106 releases) were never successfully introduced, although some of these species' populations were 'persistent'. We feel that many of these species were unlikely candidates for introduction. For example, the thirteen failures included five species of tinamou (*Tinamidae*). These species may well always fail because they are neither adapted to feed or avoid predators where they were introduced. Excluding these species, leaves us with 438 releases of seven species, each of which at some time or place became successfully established (Table 1).

a. The effects of season, source of birds, and release method.

We first asked whether species differed in their success rate. The proportion of successful introductions was not different between species (c^2 test; df=6, p= 42). Two-thirds of the releases involved Ring-necked Pheasants. Of the other six species, none ever achieved more than six successes. Nor did the chance of Pheasants becoming established differ significantly from the other six species combined (c^2 test; df=1, p= .42). In the remaining analysis we treated all seven species together.

We grouped the months in which the release took place into four seasons: Winter (December, January, February), Spring (March, April, May), Summer (June, July, August), and Autumn (September, October, November).

Of the 412 of the 438 releases recorded the month of introduction. Success differed significantly between seasons (c^2 test; df = 3, p = .01). Contrary to our expectations, introductions in the winter time were *more* likely to be successful than those during the rest of the year (c^2 test; df = 1, p << .01; Table 2). For the remaining seasons, the proportion of successful introductions were essentially the same.

The release individuals came from two distinct sources. They consisted of birds that were either raised in captivity or were caught in the wild and then released. Of the 438 releases, 401 recorded the source of the released birds. Not surprisingly, birds caught in the wild were significantly more likely to become successfully established than birds raised in captivity (c^2 test ; df = 1, p << 0.01; Table 2).

It is possible that the effects of release season and source of birds may be confounding. For example, if all releases of wild-caught birds were in the winter we would not know whether the season or the source of the birds was responsible for increasing the chance of a successful introduction. We tested for this possible confounding effect by contrasting the probability of success of winter releases with those at other times for captive-raised birds. We found that captive-raised birds released in the winter were still more successful than at other times of year (c^2 test ; df = 1, p = 0.02; Table 2).

The last effect we will explore deals with specific differences in methods of species introductions. From the information in the FGIP reports, we were able to classify the type of the release. A *gentle* release was reported to have supplemental feeding or shelters constructed, whereas *direct* releases had no supplemental care. Of the 438 releases, 380 recorded this information. We

found that the chance that an introduction succeeded was not significantly different for these two different methods of release (c^2 test; df=1, p= 0.26).

b.The effect of propagule size.

To explore the relationship between propagule size and success it is possible to use a logistic regression on the binary success and failure data directly (Griffith et al. 1989). This type of regression *assumes* the shape of the curve rather than let us infer its actual shape from the data. Our motivation for analyzing the propagule size data is to explore the merits of the theoretical models previously described. For this, we need to look at the proportion of successes for equal size releases. This proportion of successful releases of similar sized propagules should be close to the probability of success predicted in the models described previously.

To obtain a continuous measure of the probability of success for a single introduction, we first grouped releases into sets with an equal number of releases in each. This set size was arbitrary, but we wished to select a set size in such a way as to minimize the number of releases excluded as a remainder. We chose sets of 54 and 108 releases, because these groupings excluded the fewest releases. For each set we then calculated the mean propagule size, and the probability of success calculated as the proportion of the releases that were successful.

Consider the case where we grouped releases into sets of 108. The smallest number of birds released was six, and the one-hundred-eighth smallest number of birds released was 75. Of the 108 releases included in this set, five were successful and thus the proportion of successful releases was 0.046. The mean propagule size for the releases within this set was 34.

It is possible to parameterize the logistic relationship between the proportion of successes, **P**, for a given size of release, **N** , in a number of ways. The form we chose was :

$$P = \frac{a}{e^{-aN} + b} - c \qquad (i)$$

Where **a, b**, and **c** are constants. As the size of the release increases, the proportion of successful introductions approaches an asymptotic limit to the probability of success, P_{max} , which can be shown to be:

$$P_{max} = \frac{a - bc}{b}$$

When N=0, P attains the value of

$$P_{N=0} = \frac{a}{1+b} - c$$

The parameter **a** determines the rate at which the probability of success increases at low propagule sizes and **c** is a constant of integration. Biological considerations suggest constraints on model parameters. This three parameter model does not necessarily estimate a zero probability of success when no individuals are released. Clearly, the probability of success should be zero when the numbers of individuals is zero or some relatively small size. To incorporate this constraint, we can use a two parameter model that constrains the probability of success to be zero at N=0. This forces

$$c = \frac{a}{1+b}$$

and so,

$$P = \frac{a}{e^{-aN} + b} - \frac{a}{1+b} \qquad (ii)$$

The maximum value of **P** is now:

$$P_{max} = \frac{a}{b(1-b)}$$

We used an iterative nonlinear regression method that locally minimizes the residual variation about the model parameters. The fits to the 54 point and 108 point groupings are very similar, and the two and three parameter models are so similar that it is impossible to see their differences at all but the smallest of propagule sizes. (Figure 2a shows the 108 point groupings, figure 2b, the 54 point groupings.)

In addition to analyzing the data with a logistic model that incorporates Allee effects, we also explored a model which only incorporates demographic accidents and environmental effects. We analyzed the data in the same way using the previously described simple birth-death process model. In this case the probability of success is:

$$p(n) = 1-(a)^{bn}$$

The parameter *a* in this case is the ratio of deaths to births, and *b* is proportional to the environmental effects experienced by the population. We show the results of these analyses in figure 2c and 2d. Table 4 compares this model with the sigmoidal model that includes Allee effects.

From our previous analyses, we know that an introduction of wild birds in the wintertime is more likely to be a success than an introduction of captive-raised birds at other times of year. Again, it is possible that the season and the source of birds might confound the effect of the numbers released. For example, the winter releases of wild-caught birds might have been larger than releases at other times of the year. In this case, we would not be able to determine the relative effects of these two factors. Statistically separating all

these effects is not simple. Nor can we run the logistic regression on subsets of the data (for example, on the releases of captive-reared birds outside the winter) because there would be too few successes within each subset.

What we can do, however, is to look at the propagule sizes for releases in the winter versus those for the rest of the year, and for captive-reared versus wild-caught birds. If the distribution of propagule sizes in these groups were very different, factors other than propagule size would be more important in determining success. This is not the case. On average, releases of wild and captive-raised birds, and releases during the different seasons, involve the same numbers of birds (Table 3).

5. Discussion

Factors other than propagule size are important in determining the success of game-bird introductions. We did not expect that releases in the winter would be more successful than at other times of the year. We did expect introductions of wild-caught birds would be more successful than ones made with captive-raised birds. Captive rearing may lead to inbreeding, and a loss of both genetic and behavioral adaptations which potentially lower an individual's fitness to survive in the wild. The difference in success of wild over captive birds is striking. While only one in seven captive releases are successful, nearly one half of the releases made with wild-caught birds are successful (Table 2). This result has considerable significance for attempts to re-establish populations that have become extinct either locally, or for which only captive populations exist. For example, translocations of species to areas where they have become locally extinct is likely to be more successful than introducing them from captive zoo populations after they are gone from the wild. This choice is not always possible, of course (Witteman et al. 1991).

In a parallel study to this one Griffith et al. (1989) compiled the results of questionnaires submitted to biologists who had moved both endangered species of birds and mammals and *native* game birds and mammals species within North America, Hawaii, Australia, and New Zealand. (All our releases were of *non-native* game birds introduced well outside their native range.) Their study showed that wild-caught animals were about twice as likely to be successful than captive-raised animals. They also found that larger propagule sizes were more likely to lead to success than smaller propagule sizes.

The logistic relationship between propagule size and probability of success is predicted by existing theory about the dynamics of small populations. Indeed, this theory was our motivation for analyzing these data. The relationship between the proportion of successful releases and propagule size, could be explained by statistically simpler models, including polynomial regressions. However, theory does not suggest or support the use of such alternative models. So it is worth considering the implications of the logistic model.

The highest probability of success is about 0.15 for even the largest game bird introductions (see Figure 2a, b). When about 200 individuals are released the probability of success is within 5% of this maximum value. So beyond about 200 individuals, the probability of success does not increase greatly and factors other than the propagule size must limit the chance of success.

The parameter **a** is measure of a species' risk from being at small numbers. With increasing propagule size, if **a** were large we would see a very steep approach of the probability of success to its highest possible value. If **a** were small, we would see a very gradual approach. When *a* is small, there will

be a large range of **N** over which an increase in the probability of success is observable. So on what should **a** depend?

The year-to-year variability of a population must be expected to play a major role in determining *a*. Species that have very variable densities will be often driven to the low population sizes for which susceptibility to Allee effects is high. Persistence for populations which must frequently recover from low levels will be lower than for ones which encounter these low levels less frequently. So very variable species are predicted to be more prone to extinction, (Wright and Hubbell 1983) and analyses of birds populations on islands show that they are (Wright and Hubbell 1983, Pimm et al. 1988). Comparably, highly variable species are likely to require the introductions of many individuals to insure that they are successful. In contrast, populations that do not vary greatly, may succeed with relatively small propagule sizes, they never encounter the exceptionally low levels that will almost certainly cause their extinction.

The inflection of the logistic curve represents the point at which the per-individual success of adding more individuals to the release propagule begins to decrease. For the three parameter model (equation *i*), the inflection point, and its corresponding population size, N, is:

$$P_{inf.} = \frac{a - cb}{2b} \qquad N_{inf.} = \frac{\ln\left(\frac{b(2a-bc)}{a+bc}\right)}{-a}$$

For the two parameter model (equation *ii*), the corresponding estimates are:

$$P_{inf.} = \frac{a}{2b(1-b)} \qquad N_{inf.} = \frac{\ln\left(\frac{b}{1+2b}\right)}{-a}$$

We estimate the inflection point as 75 or 74 (for the 108 and 54 point analyses respectively) for the three parameter model. The population size for the inflection point for both of the two parameter models is 74. The inflection of

this relationship may be interpreted as the propagule size at which the risk of extinction due to Allee effects become less important than the risk from environmental effects.

The reader may reasonably ask for a confidence interval about this value of 74. We cannot give one. The nature of the nonlinear regression plus the fact that the estimate comes from a complex function of estimated parameters prevents our doing so. Nor can we easily re-parameterise the logistic so that the inflection point appears directly as a single parameter in the model. (If we could, then the nonlinear procedure would also supply a standard error.) What we can do is ask whether a model with an inflection point describes the data better than one without. The models with an inflection points (figures 2a, b) provide visually compelling fits to the data. The models without inflection points (figures 2c, d) do not. Particularly at low propagule sizes, there is a systematic tendency for the data points to be first below and then above the predicted values. We conclude that a model with an inflection point is a better description of these data.

The logistic relationship also suggests an introduction strategy that maximizes each individual's contribution to the overall chance of successfully establishing a population. Consider the dilemma of a biologist who wants to successfully re-introduce a species. Should the introduction be of one large release (say, of 400 individuals) or two (or more) smaller releases in different places or at different times? For foreign game-birds the success may be only about 15% if a single release is the strategy (Figure 2). But if two releases of 200 individuals are chosen, then the chance of success for each is still nearly 15%. The chance of at least one of them succeeding *if the success of one*

release is independent of the success of the other, is nearly 28%. So, the better strategy is to make two releases.

Splitting one large release into two or more smaller ones does not always increase the overall chance of establishing a population. If this were always the correct choice, then the numbers of individuals in a release propagule could be split and split again. We know that four hundred independent releases of single birds will not have any successes! Simple algebra shows that one should always split the release when the number of individuals in each propagule exceeds the logistic inflection point. (Again, we assume the successes are completely independent). In the case of gamebirds released outside their native range, two independent releases of 75 individuals will have a better chance success than a single release of 150. Below this point, the probability of success is accelerating with increasing propagule size, and success is enhanced if we increase the numbers in any one release.

This result argues that we must evaluate possible Allee effects. Models that only incorporate environmental and demographic effects suggest a monotonic relationship between population size and the probability of success. These models lead to the conclusion that a higher overall probability of at least one population succeeding is achieved by always splitting one release propagule into two smaller ones. This is the *Noah hypothesis*: the notion that only two animals (one of each sex) enjoy the greatest *per capita* chance of success.

When the chance of success at different places and at different times are not independent, the decision whether to split the release is more complicated. In addition to the issues discussed previously, we would need to know how the expected success at one location at one time correlated with the expected

success at other locations and times. Is there any way to evaluate how independent are the different locations and times? The data show that 85% of introductions fail, even when the largest numbers of individuals are introduced. Yet we only included in our analyses species known to succeed at some place at some time. So we know that even when a species is going to succeed somewhere, that most individual introductions of even large propagules will fail. This suggests that the conditions needed for a successful introduction are scarce in time and space. At least for introductions of foreign gamebirds, different places and times often afford very different chances of success. If this result is general, then it is better to split a large release propagules into smaller ones. However, propagules should not be so small that Allee effects and demographic accidents are the principal cause of extinction. When sufficiently large propagules are available, attempting more releases will always increase the chance of finding at least one time and place where success is likely.

6. Summary

For gamebirds released outside their native range, we show that releases made in the winter are more likely to succeed than ones made at other times of the year. Introductions consisting of wild-caught individuals are much more likely to succeed than those made with captive-raised individuals. Theory predicts that environmental disturbances, demographic accidents and Allee effects should determine the fate of small populations. When these three factors are combined, the chance that a population will persist, or an introduction succeed, is a sigmoidal function of its initial size. Our study demonstrates this relationship for game-bird introductions.

Models which do not incorporate Allee effects (or are not logistic) predict that multiple small introductions will always have a overall higher chance of

success than a single large one with the same total number. This prediction is biologically unrealistic. However, if the relationship between population size and the chance of becoming successfully established has an inflection, the consequences of splitting one release propagule into smaller ones is clear. Above the population size of the inflection point environmental effects are more important than demographic accidents and Allee effects in determining an introduction's success. Two independent introductions with populations above this size will have an overall higher chance of establishing a population than a single large one.

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TABLE 1
Successfully Introduced Gamebirds

Common Name	Scientific Name	Missing	Failures	Persistents	Successes
Ring-Necked Pheasant	*Phasianus colchicus*	132	160	84	49
Black Francolin	*Francolinus francolinus*	6	18	14	3
Gray Francolin	*Francolinus pondicerianus*		4	5	7 4
Grey Partridge	*Perdix perdix*	0	10	0	4
Bamboo Partridge	*Bambusicola thoracica*	13	10	2	1
Chuckar Partridge	*Alectoris chukar*	10	6	10	1
Red Junglefowl	*Gallus gallus*	12	35	9	6
TOTALS		**177**	**244**	**126**	**68**

Table 1: Successful: population was reported as becoming established or developing a breeding population, **Persistent:** little breeding, population at progressively smaller numbers, **Failure:** species locally extinct in the release area, **Missing:** Inconclusive result, or not categorizable in the previous three categories.

The following species were never successfull: Galliformes: *Alectoris rufa, Alectoris graeca, Alectoris barbara, Ammoperdix grisgeogularis, Lophura leucomelana, Syrmaticus reevesi, Tetraogallus himalayensis, Francolinus erckelii* Tinamiformes: *Nothura darwinii, Nothura maculosa, Nothoprocta perdicaria, Eudromia elegans, Rhynchotus rufescens.*

TABLE 2

Effect of Source of birds and Season of release on Success

Source	Result	Season		Totals
		Mar. - Nov	Dec. - Feb.	
Wild	success	5	4	**9**
	Failure	8	2	**10**
Captive	success	43	13	**56**
	Failure	280	35	**315**
Totals	success	**48**	**17**	**65**
	Failure	**288**	**37**	**325**

TABLE 3

Distribution of $Log_{10}(N)$ by Source of birds and Season of release

	Log(Propogule size)				
Season	**Number of Releases**	**Mean**	**Std. Dev.**	**Min.**	**Max**
Mar. - Nov.	356	2.42	.599	.78	4.4
Dec. - Feb.	56	2.37	.585	1.0	3.9
Source					
Captive	382	2.42	.587	.78	4.4
Wild	19	2.32	.702	.90	3.9

TABLE 4

Results of logistic and non-logistic regression models

	Parameter	Estimate	Std. Error
Logistic (2 parameter)			
54	a	.0283	.00584
	b	.1552	.03634
108	a	.0287	.00240
	b	.1578	.01482
Logistic (3 parameter)			
54	a	.0258	.00997
	b	.1585	.04374
	c	.0048	.00531
108	a	.0265	.00436
	b	.1581	.01759
	c	.0098	.02332
Monotonic			
54	a	.1258	.00000
	b	.4210	.09132
108	a	.1258	.00000
	b	.4210	.11040

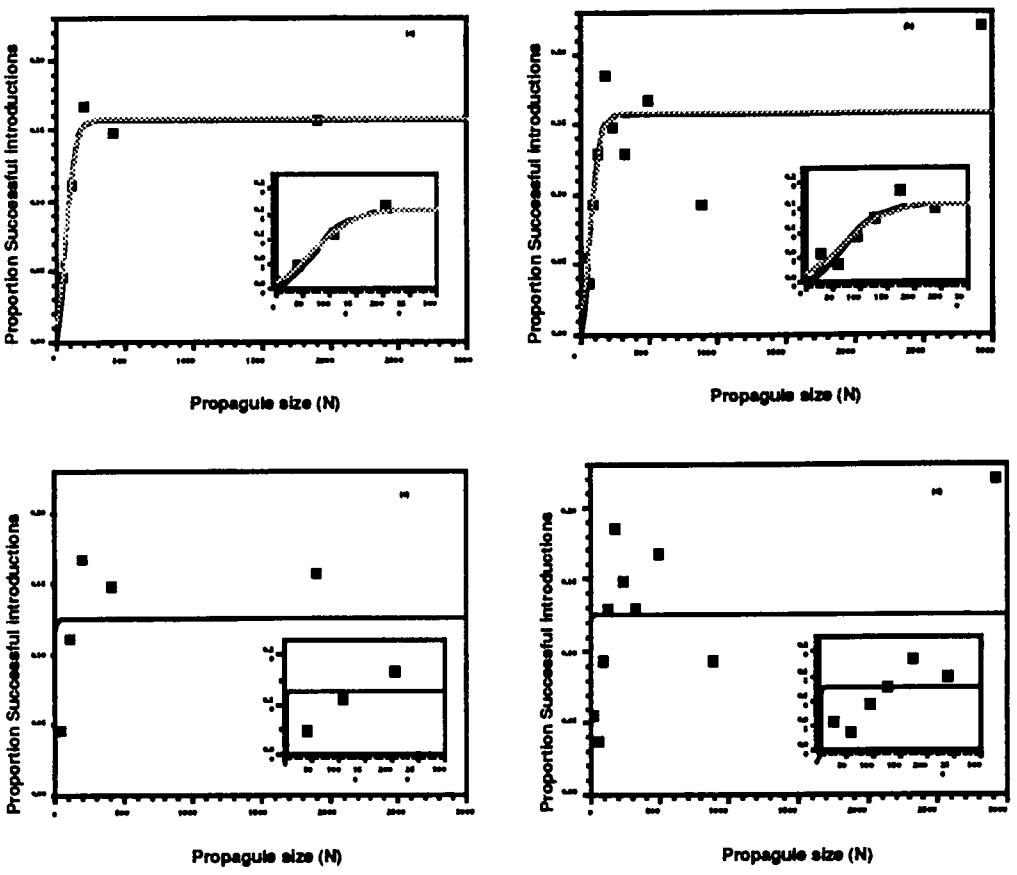


Figure 2: Logistic and non-logistic fits to the data.

The proportion of releases that were successful versus the propagule size for game birds introductions. In a and c the data were grouped into sets of 108 observations, and in b and d into sets of 54 observations. For the logistic regressions (a and b), both two parameter (solid lines) and three parameter (dotted lines) are plotted. Figures c and d represent the non-logistic models for these two groupings.

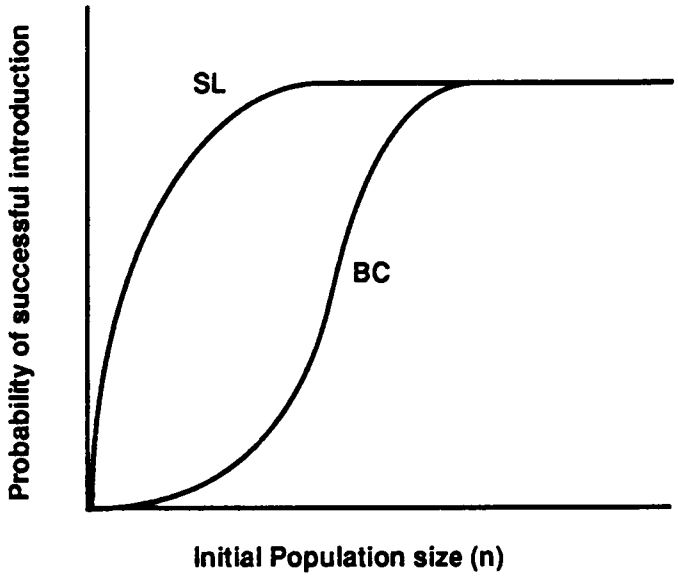


Figure 1.

The probability of successfully establishing a population , plotted as a function of the initial population size n. SL denotes the curve for the discrete stochastic birth-death model that encorporates a simple linear birth rate that assumes no Allee effects. The curve marked BC is for an equivalent model that incorporates an Allee effect in the birth rate.

PART 4
Scale dependence in edge effects: Hawaiian habitats and avifauna

1. Introduction

A relationship between area and species numbers has been suggested as a general ecological phenomenon ever since MacArthur and Wilson's (1967) pioneering work. The clearest demonstrations of the relationship between area and species number or abundance come from studies of oceanic islands (MacArthur and Wilson, 1967). The relationship is less clear when considering habitat "islands" within a continental land mass. In this case, the processes that determine the number of species and individuals may depend upon the habitat composition, spatial distribution of habitat, size of habitat islands, and species assembly processes (Drake, 1990). We will address the question of how the distribution and abundance of invasive, or foreign, animals and habitat affect the number of individuals and species of native Hawaiian forest birds.

At more than four thousand kilometers from the nearest continental land mass, the Hawaiian islands are the world's most isolated archipelago. Hawaii's endemic species are derived from a small number of initial founder species. Only fragments of the native habitat types, and coresponding fauna, are left after these two major eras of disturbance.

With the initial human colonization of the islands by the Polynesians, Hawaii experienced its first major wave of extinction (Kirch 1982). Over forty avian species alone perished as a direct result of human disturbance (Olson and James, 1982). Since the arrival of Christian missionaries to the islands, twenty species and sub-species of bird have become extinct, and an additional thirty or more have become endangered (USFWS 1983). The initial wave of extinction was likely due to introductions of feral animals, hunting, and habitat destruction in the lowland areas of the islands. In addition to these causes,

western man also introduced diseases, competitive and predatory species, as well as heightened the speed and level of habitat destruction (Berger 1981, Mountanspring and Scott 1985). The Hawaiian islands are often viewed as the worlds best example of invasion and extinction processes. In this paper I explore a number of hypotheses that relate the abundance and distribution of native and foreign species of bird to the size and quality of remaining Hawaiian habitat fragments.

2. Theory

A variety of factors may determine the native and non-native avifauna distribution and abundances in the Hawaiian Islands. The size and distribution of "good" habitat should be important in determining the number and distribution of native species. What constitutes good habitat and its effective size within each of the Hawaiian islands may depend on a variety of processes that operate on a wide range of spatial and temporal scales.

a. Habitat patch size.

Generally, there is a positive relationship between island size and the number of species present. Large islands should have more species than small islands. However, an island that is twice the size of another will have less than twice as many species. This species/area relationship is true only if the islands being compared have similar proportions and distributions of "good" habitat. Consider two similarly sized islands. If both have roughly the same area, but one has twice as much native habitat, the first island will likely have fewer species than the second. Equivalently, two islands with radically different sizes may contain a similar number of species if the area of a characteristic or important habitat is the same on both (figure 1a.)

b. Habitat quality

The quality of habitat patches also determines the *effective* habitat patch size. For example, a large patch of native habitat may consist of a mosaic of both low and high quality areas when viewed at intermediate or small spatial scales. At larger scales, this patch mosaic may hold relatively few species compared to a pristine habitat patch of equivalent size. In the same sense, a relatively small patch of pristine habitat may have an equivalent number of both species and individuals as a larger patch of low quality (figure 1b.).

c. Invasive effects

The number of species found on an island is related to the effective amount of habitat found there. The effects above describe the way that spatial and compositional characteristics of habitat patches themselves may be responsible in determining the number of species and individuals that they can contain. However, we must also consider how interactions with other animal species might decrease the effective patch size, or habitat "island" within an island. In the previous two cases we assume that native species depend upon a particular type of habitat. Outside that habitat patch there are no native species. Now consider what happens when the vacant area outside the patch harbors a number of invasive species.

i. Species-Habitat co-occurrence

A non-interaction model of habitat and species occurrences would explain the distribution of native and non-species by habitat composition alone. Native habitat patches would have native fauna and non-native habitats would have non-native fauna. In this model, habitat would be a nearly ideal predictor of faunal composition everywhere but the boundary between native and foreign habitats. At the edge a small number of native species and individuals would

be on the foreign habitat side, and a similar number of non-native species would be on the native habitat side. If there is no faunal interaction, we would expect the number of individuals and species outside their respective habitats to be few. In addition, the numbers of both native and non-native species and individuals should reflect their respective species pools and densities. However, for Hawaiian habitats and species of forest birds we suspect that this is not the case.

ii. Introduced pressure

Native species are likely to be unable to exploit non-native or *disturbed* habitat. There is, however, no reason to believe that non-native species will be unable to exploit either habitat equally. For example, some of the introduced birds found in Hawaii are from temperate climates. To these species, the difference between their native habitat and the tropical habitats found in Hawaii, is much greater than the difference they perceive between Hawaii's native and exotic tropical habitats. In this case, both native and non-native habitats are equally foreign to the non-native species. We would only expect the numbers of non-native species and individuals in native habitat to be less than in disturbed habitat if they compete with the native species. If this were the case, these non-native species may also prefer to keep a competitor-free zone within their foraging range. The effect of this on native species would be a zone of degraded habitat (henceforth *killing-zone*) which penetrates a fixed distance into the native habitat from the edge (figure 1c.). If that patch is relatively small, the *effective* area of the patch, (or the proportion that is not degraded by the invasive species), may be very small. If the patch size is relatively large compared to the distance this type of effect penetrates into native habitat, the proportion of degraded habitat is smaller (figure 1c.).

It is also possible that a killing-zone at the edge of a patch will not penetrate a fixed distance, but rather will follow some environmental contour or distribution. A particular disease (for example, avian malaria) may rely upon a vector or reservoir that is only found in island lowlands. The zone in this case may follow an elevational contour. It may be wide in some areas and very thin in others, unlike the fixed-distance band described above. Although unlikely, the types of killing-zone effects described may penetrate into disturbed side of the habitat boundary. In other words, the killing-zone is due to native habitat, and it penetrates and decreases the quality of non-native habitat.

d. Spatial scales of interactions

Although questions regarding habitat and species co-occurrences can be approached in a variety of ways and at different scales, I have chosen a measure that is consistent across all scales. I propose that the *proportion* of native individuals in an area of any size indicates the integrity of the forest bird community. Consider the case of two islands with the same number of both native and introduced species. If we were to measure the species abundance at the island-wide scale, habitat-patch scale, and single point scale we would expect to see a consistant decrease in the number of species for successively smaller areas. However, we may completely ignore important differences in the islands' relative species densities. For example, both islands may have ***n*** natives and ***m*** foreign species, but on one island the densities of the n species is high wereas on the other it is low. If , however, we were to look at the relative proportion of native and non-native individuals, we would not only be able to discern differences due to the islands' native and non-native species pool, but also those due to the species-density relationships for the islands.

Clearly, the effects caused by habitat composition and non-native species distribution should begin to determine the distribution of native species of Hawaiian forest birds. If we use the proportion of native individuals as an indicator of native community integrety, we should be able to explore the relative scales on which edge effects are important in determining species densities and distributions.

On the largest, or *macro*, scale we expect to find differences in species composition that are related to both characteristics of the islands or areas. Effects due to environmental characteristics such as elevation and large scale habitat composition, as well as the size of the introduced and native species pools, should be good predictors of the number of native species and individuals found within the area. Similar effects should be seen at some medium, or *meso*, scale within areas or islands. Portions of areas that have similar elevation and habitat composition should have equivalent proportions of native and introduced species and individuals. Finally, at the very smallest scale (ie, at the exact boundary of a habitat patch) the distribution of species types and individuals should agree with one of the two distributions described above: Either similar faunal and habitat types should co-occur, or one fauna will be excluded from the opposite habitat type, while the other is not.

3. Methods

Data collected during the *Hawaiian Forest Bird Survey* (henceforth HFBS) represent an effort of over 30 man-years of field work (Scott, et al., 1984). The modified variable circular plot (VCP) method was used to collect abundance and distributional data for Hawaii's avifauna. This method of census corrects a number of sample biases that would effect species' density estimates. The transects were arranged in such a way so that they included

only areas which included both native species of bird and habitat. Stations along transects were placed so that censuses at adjacent stations did not record individuals more than once (on average, 135 meters apart). The VCP method corrects for differences in species detectability for observations made in different habitat types. For example, if a small green bird such as the Anianiau is silent, it may have a very small chance of being detected in a patch of dense rain-forest, but a very high chance on a lava flow or in a clearing.

The scope of the survey was on all islands and in all areas with native habitats and species of bird (figure 2). Both the composition and distribution of native Hawaiian habitats are very different among islands and even within areas of the same island (areas are treated separately for Hawaii and Maui only). Hawaii, (or "the Big island"), with over eleven thousand point censuses, is nearly an order of magnitude more census area, than all other islands combined. Both physical characteristics, such as elevation and wetness, as well as habitat canopy and understory composition vary greatly among islands and areas (table 1.).

To quantify the integrity of the Hawaiian avian assemblages, we first grouped the number of individuals observed at each census station into native and non-native categories (table 2.). We then calculated the percent of native individuals (*henceforth PN*) as the proportion of all individuals that were native, for each of the stations that recorded habitat type (ie: 9,890 stations).

I regrouped the original 824 HFBS vegetational codes into categories that represent the basic characteristics of the habitats. Original vegetation codes were sorted into characteristic "wetness" regimes (ie: wet, mesic, or dry) as well as canopy types (native or exotic) and understory types (native or exotic). For some of the analysis exploring macro- and meso- scale effects, the

percent of native individuals was calculated for categories of either 500 or 1000 foot elevational categories, within each area or island.

4. Results

a. Macro-scale effects

I first explored the relationship between elevation and the percent of native individuals found in each of the areas. For this, I calculated the percent of native individuals for 1000 foot groupings for each area. We treated each wetness category separately, and only considered stations in each area and elevation that had only native canopies and understories (ie: N:N, canopy:understory). There is a strong positive relationship between elevation and the proportion of native individuals observed for wet, mesic and dry habitats (figure 3.). Other canopy and understory combinations produce similar elevation/individual relationships, but for all but N:X there are very few stations.

Next I explored the degree to which native individuals prefer habitats that have native rather than exotic canopies or understories. Although there are few areas with exotic canopy, every area and most elevations have both native and exotic understories under native canopies. I calculated the difference in the proportion of native individuals at stations that were N:N vs. N:X for each elevation, wetness type, and area. For most wetness types, elevations and areas, the difference is positive and on average greater than ten percent (figure 4). This suggests that habitat understory may be of crucial importance to individuals of native species.

b. Meso-scale effects

At the area and island scale Ifind a positive relationship between elevation and the proportion of native individuals. My next step was to determine if this relationship operates at smaller scales. The question is this:

what is the smallest *grain* size of habitat patchiness that is still important in determining the species composition of the Hawaiian avifauna.

To characterize meso-scale effects, we calculated the proportion of N:N stations within each 1000 foot elevational category. We explored aspects of each elevational categories habitat composition. In a similar to the way in which we calculated the proportion of native individuals for each elevational category within each area. This index of *habitat* integrity is a similar measure to the one we use to indicate avifauna assemblage integrity. For many elevational categories, wetness regimes, and areas, we find proportions of native habitat that range from nearly zero to unity. On the macro-scale, I already have evidence of global elevation, wetness and habitat effects. In addition to these effects, I also find a significant positive meso-scale relationship between proportion of native habitat and the proportion of native individuals.

c. Micro-scale effects

At the smallest scale, Ican look for differences between the proportion of native individuals between two adjacent census stations for a variety of edge types. From the previous analysis at larger scales, I would expect there to be a difference in the proportion of native individuals on the native and exotic habitat sides of an edge (ie: a decrease between the last native station, and the following exotic one). Equivalently, I would expect to see a difference in various types of edge transitions. For example, if I were to go from a point that is N:N (native canopy and understory) to another that is N:N. On average I would expect to find no difference in the proportion of native individuals between these two similar types of stations. If, however, I were to go from one type of station to a different type, for example from N:N to N:X we would expect to either see a increase or decrease in the proportion of native individuals. For a change of

canopy or understory edge we would expect to see a higher proportion of native individuals on the native habitat side of this type of edge.

For all edges within each area and elevational category, we calculated the magnitude and direction of the difference between the native and the non-native sides of the edges. In addition, we calculated the changes in all adjacent pair-wise transition types (ie: transition to similar type or different type). At the station, or micro-scale, we found no consistent magnitude or directional trends, for either characterization of edge type transitions, within area and elevational groupings.

5. Discussion

At the largest scale, there is a relationship between elevation and the proportion of native individuals. This relationship is consistent for both areas/islands and within a variety of habitat types and wetnesses. If we compare differences in the proportion of native individuals between forests with native understory and those with exotic understory we find a difference that is positive. If native understory were equally important to introduced species, we would expect their numbers to increase by an equivalent proportion. They do not. This suggests that the "nativeness" of a habitat is important to native species, but not to not-native species. If true, this result agrees with the *introduced pressure* hypothesis described above.

In addition to confirming macro-scale effects, we find that increases in the proportion of native individuals within an elevational category are related to similar increases in proportion of native habitat. In this case meso-scale habitat composition is a good predictor of the proportion of native individuals among different areas and islands, but for the same elevation and wetness categories.

Although we expected to see a relationship between the proportion of native individuals and the side of habitat edge, or the type of habitat transition, we found none. In nearly every area, elevation and wetness category, the change in PN associated with going from the native to non-native side was equally likely to be positive or negative in magnitude. A similar lack of consistent relationship was found when comparing transitions to the same habitat type with transitions to a different type. Though relatively uninteresting of themselves, these two results suggest that the edge effects operate on larger than micro- , or station-to-station scales.

6. Summary

The integrity of a native community is potentially determined by a variety of mechanisms, which are likely to operate on different spatial scales. Both island size, as well as patch size, distribution and quality *within* an island, are important in determining the number and distribution of species. When faced with the potential effects of invasive predators, competitors or diseases, we would expect both fewer native individuals and species. For the Hawaiian islands we have found evidence these effects at both macro- and meso- scales.

At the largest scale, there are differences in the proportion of native individuals due to elevation and understory composition. At meso-scale we see that habitat -block, or grain size of the patch, is positively related to the proportion of native individuals. At the smallest scale (between two census stations) we see no effect on the proportion of native individuals of habitat type or habitat transition type.

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Table 1
Physical and Habitat characteristics of Areas[1] and Islands

Area or Island	Number of stations	Average[2] Elevation	# Wet	#Mesic	#Dry	#NN	#NX	#XN	#XX
Kau	867	4461	579	178	89	815	26	5	0
Hamakua	2449	3863	1731	536	141	1886	342	134	46
Puna	669	2258	513	31	88	518	93	20	0
Kona	2844	4408	418	986	1390	1211	1020	466	76
Kohala	211	3707	177	28	0	134	52	9	10
Kipu	451	5604	0	30	407	284	48	102	0
Mauna Kea	343	7619	0	0	320	0	255	65	0
Kaui	140	4147	129	5	1	134	1	0	0
Molokai	572	2689	337	105	91	297	126	34	76
Lanai	77	2551	36	33	3	23	13	16	20
Maui	1267	4082	715	112	278	784	212	21	62
Total	9890			0	4635	2044	2808	6086	2188

[1] The island of Hawaii has large and distinctive areas which were treated seperately in the majority of analysis.
[2] Averages for areas and islands reflect mean census-station elevation.

Table 2
Native and Introduced Species Lists

Introduced Species	Scientific Name	Occurrence*
Black-headed Munia	*Lonchura malacca*	Ka
Common Myna	*Acridotheres tristis*	All
Eurasian Skylark	*Alauda arvensis*	Mo,La,Ma,Ha
House Finch	*Carpodacus mexicanus*	All
House Sparrow	*Passer domesticus*	All
Japanese Bush-Warbler	*Cettia diphone*	Mo,La,Ma
Japanese White-eye	*Zosterops japonicus*	All
Lavender Fire-finch	*Estrilda caerulescens*	Ha
Melodious Laughing-thrush	*Garrulax canorus*	Ka,Mo,Ma,Ha
Northern Cardinal	*Cardinalis cardinalis*	All
Northern Mockingbird	*Mimus polyglottos*	All
Red-billed Leiothrix	*Leiothrix lutea*	Ka,Mo,Ma,Ha
Red-cheeked Cordonbleu	*Uraeginthus bengalus*	Ha
Saffron Finch	*Sicalis flaveola*	Ha
Spotted Munia	*Lonchura punctulata*	All
Warbling Silverbill	*Lonchura malabarica*	Mo,Ma,La,Ha
White-rumped Shama	*Copsychus malabaricus*	Ka
Yellow-fronted Canary	*Serinus mozambicus*	Ha

Native species	Scientific Name	Occurrance
Akepa	*Loxops coccineus*	Ha,Ma,Ka
Akiapolaau	*Hemignathus munroi*	Hi
Anianiau	*Hemignathus parvus*	Ka
Apapane	*Himatione sanguinea*	All
Common Amakihi	*Hemignathus virens*	Ha,Ma,Mo,Ka
Akoekoe	*Palmeria dolei*	Ma
Elepaio	*Chasiempis sandwichensis*	Ha,Ka
Hawaii Creeper	*Oreomystis mana*	Ha
Hawaiian Crow (Alala)	*Corvus hawaiiensis*	Ha
Omao	*Myadestes obscurus*	Ha
Iiwi	*Vestiaria coccinea*	Ha,Ma,Mo,Ka
Kauai Creeper	*Oreomystis bairdi*	Ka
Kauai Oo	*Maho braccatus*	Ka
Maui Creeper	*Paroreomyza montana*	Ma
Maui Parrotbill	*Pseudonestor xanthophyrus*	Ma
Nukupuu	*Hemignathus lucidus*	Ma,Ka
Ou	*Psittirostra psittacea*	Ha,Ka
Palila	*Loxioides bailleui*	Ha
Poo-uli	*Melamprosops phaeosoma*	Ma
Puaiohi	*Myadestes palmeri*	Ka

* Island abbreviations: Ha:Hawaii, Ma:Maui, La:Lanai, Mo:Molokai, Ka:Kaui

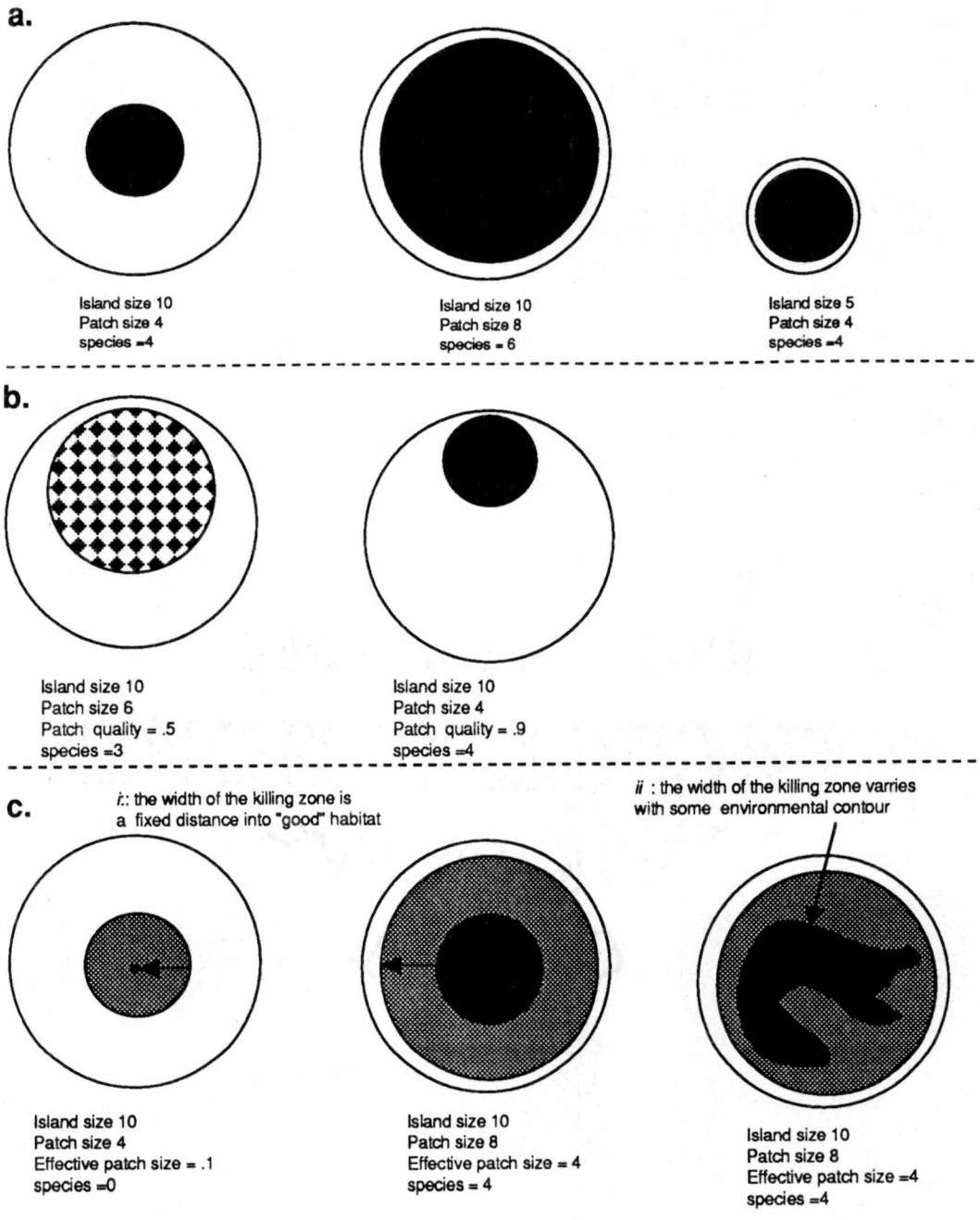


Figure 1: Patch size, quality and distance effects

(a)Patch size to island size, (b) Effective patch size due differences in habitat quality (c) types of habitat degredation {Killing-zone} effects

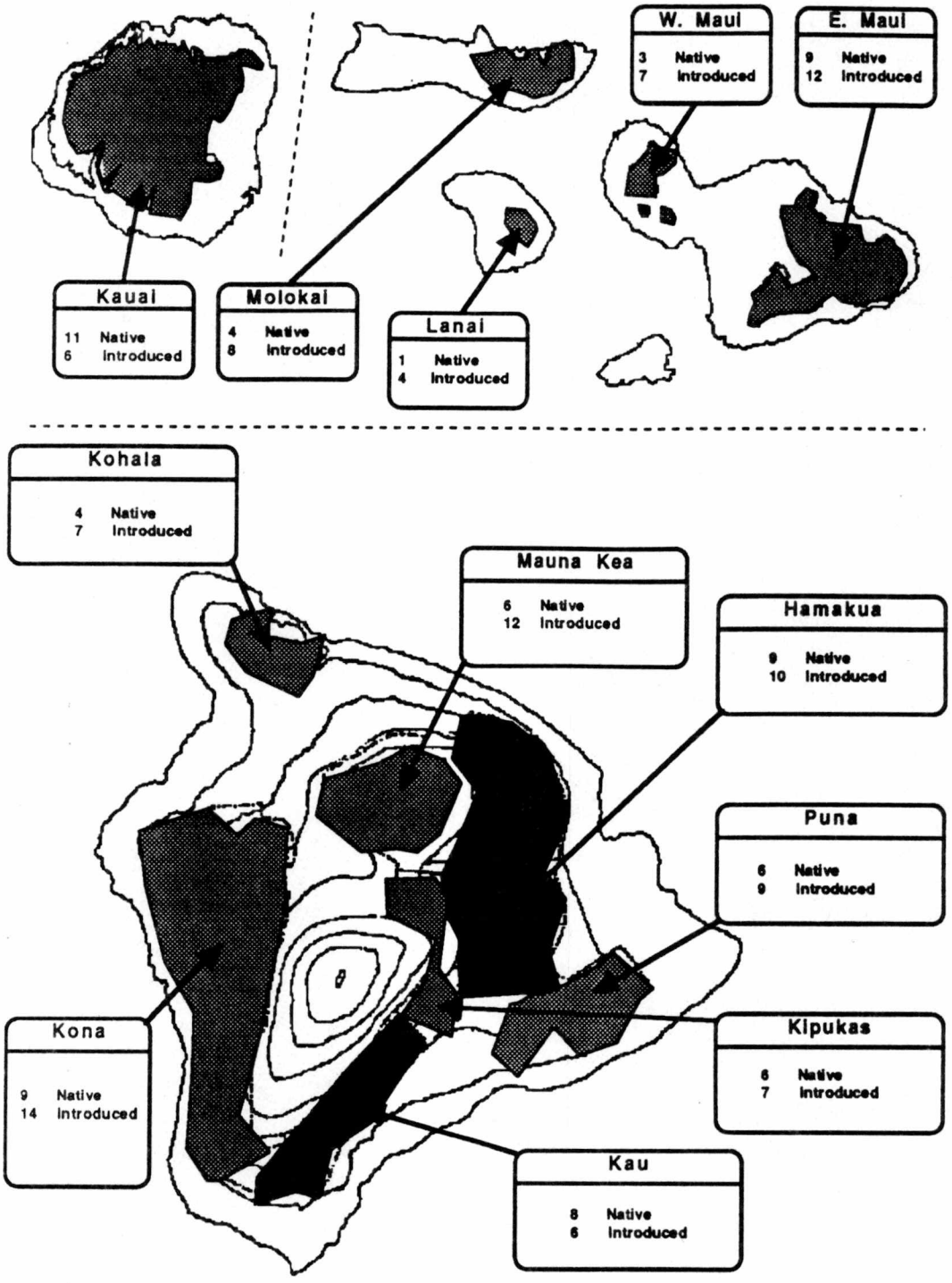


Figure 2: Areas censused

Shaded areas represent areas censused by the Hawaiin Forest Bird survey. Numbers of native and introduced species are limited to species encountered during the census.

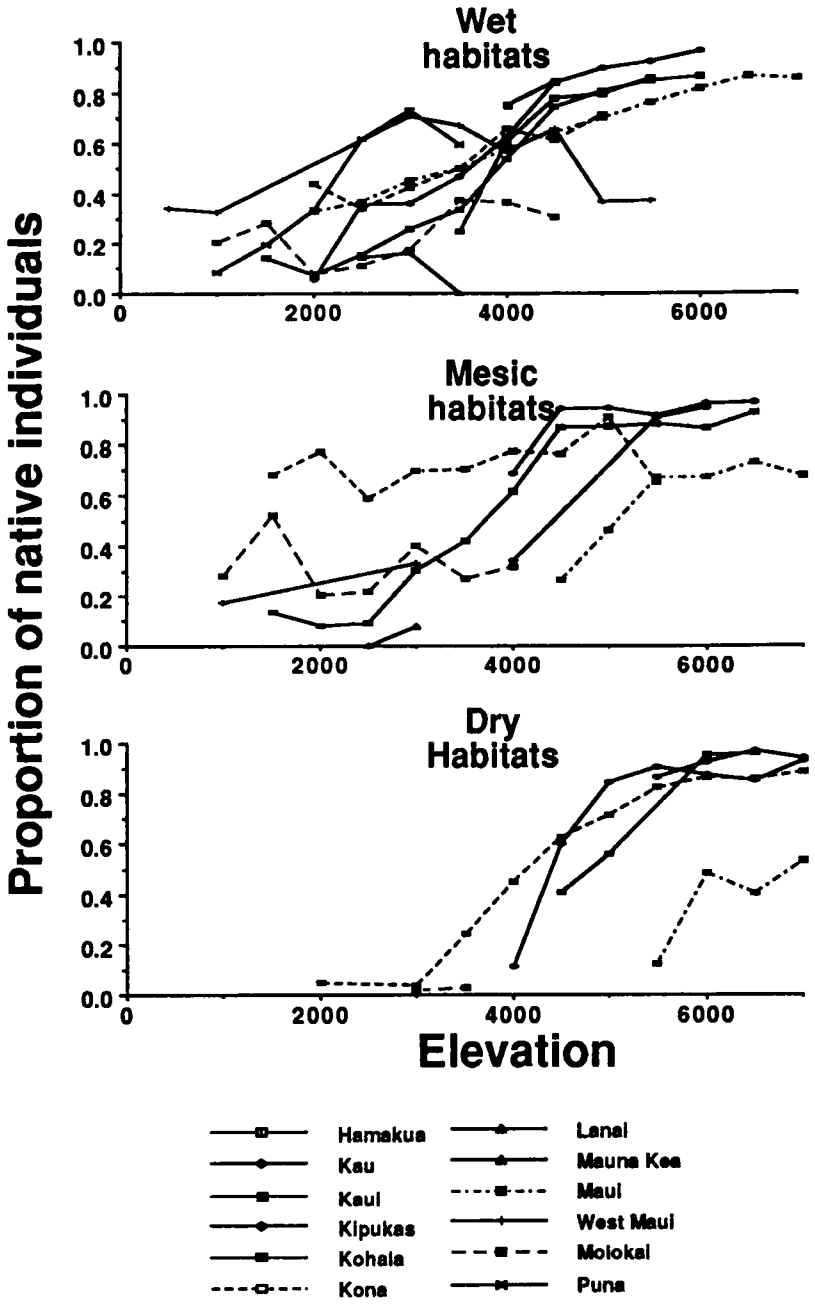


Figure 3: Proportion of native individuals for Native forest

Only stations with both native canopy and understory were included in the analysis. Each line above represents either an area or island shown in figure 2.

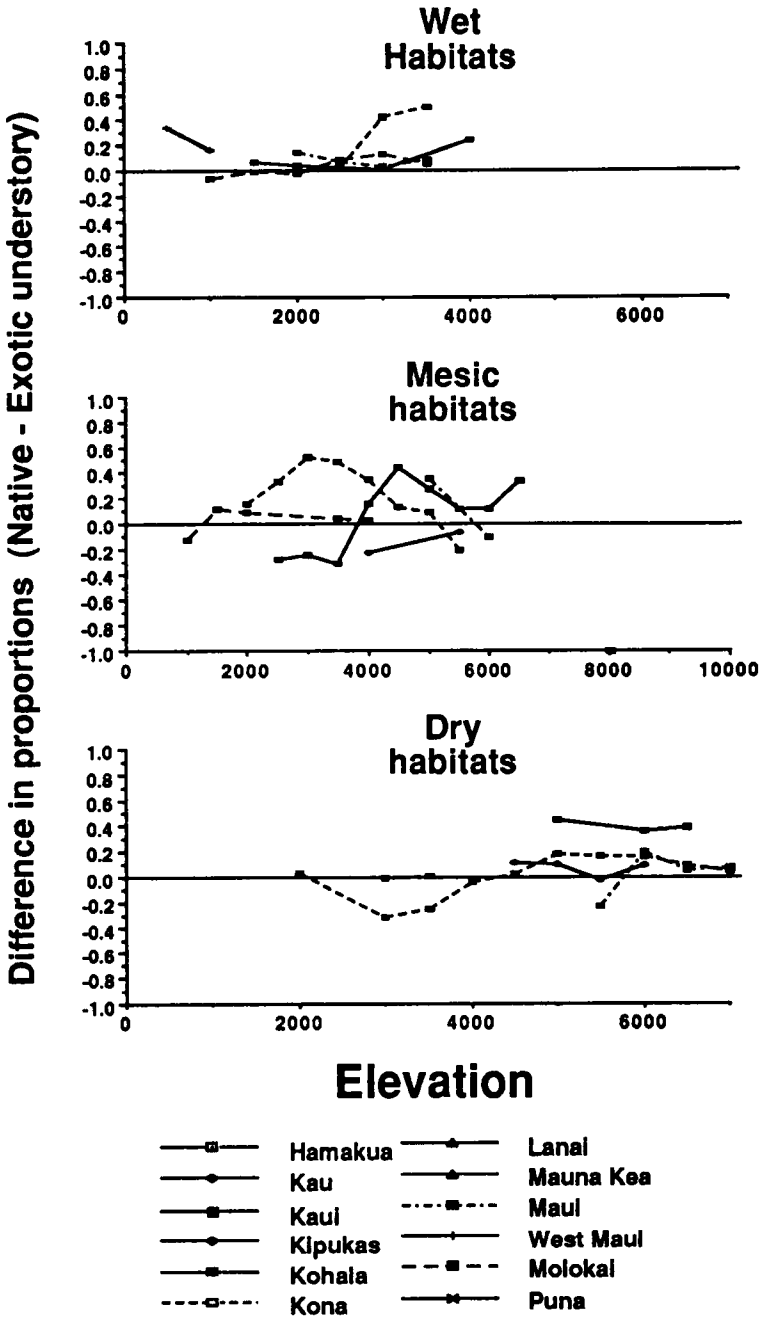


Figure 4: Differences in the proportion of native individuals for N:N compared with N:X * stations

*N:N, and N:X designates Canopy:Understory, (Native or eXotic). Each line above represents either an area or island shown in figure 2.

PART 5
The decline and restoration of the Guam Rail, *Rallus owstoni*

1. Introduction

The Guam Rail, *Rallus owstoni,* is known historically only from Guam with no closely related forms nearby in Micronesia (Baker 1951, Ripley 1977). Baker (1951) speculates that the Guam Rail may have been more widely distributed in former times. *R. owstoni* is a large rail (200-300 gms) with a dark brown head, neck, back, rump, tail, legs, feet and bill. The wings, lower breast, abdomen and under-tail coverts are black and white barred. Extensive areas of gray occur on the neck, upper breast and superciliary stripe. Adult rails have a bright red eye. Plumages of both sexes are similar, though males are larger than females (Baker 1951, Jenkins 1979). *R. owstoni* was distributed over much of Guam in all habitats except wetlands (Baker 1951, Beck and Savidge in press) although Jenkins (1979) considered both savanna and mature mixed forest marginal habitat. On Guam, it was an opportunistic omnivorous feeder that appeared to prefer animal over vegetable matter. It was known to eat gastropods, skinks, geckos, insects, and carrion as well as seeds and palm leaves (Jenkins 1979).

The Guam Rail was a year-round ground nester with a peak occurring during the rainy season. Both sexes shared in the construction of a shallow nest made of loose grasses and in the incubation of the eggs which lasted about 19 days (Jenkins 1979). The typical clutch consisted of three to four eggs but the number of clutches per year on Guam was unknown (Jenkins 1979). The 172 broods observed in the wild ranged from one to four with an average of two. One family group that was observed foraging in the wild consisted of two adults, several immatures and three chicks (R. E. Beck, Jr. and E. P. Morton, unpublished observations).

2. Decline of the Guam Rail

Prior to the 1960's the Guam Rail was abundant island-wide with their population estimated to be in the tens of thousands (Lint 1968). By 1982, a survey conducted by the Division of Aquatic and Wildlife Resources of the Department of Agriculture (DAWR), making use of tape recorded play-back of rail calls, found rails restricted to two small discontinuous populations in northern Guam (Aguon 1983). A repeat of that survey in 1983 found an 80% decline from the previous year. By 1984 only approximately 20 rails remained in northern Guam with the possibility of a few scattered isolated individuals elsewhere (Beck 1988). The Guam rail was listed on the U.S. Endangered Species List in 1984 (USFWS 1984a, 1984b). In 1987, came the last confirmed observation of a Guam Rail in the wild (Beck 1989).

The story of the decline of Guam's forest birds (see particularly Savidge 1987) is one of the most spectacular examples of the damage caused by an introduced species (Pimm 1987). The spatial and temporal distribution of the introduced brown tree snake (*Boiga irregularis*) was well-correlated with the decline of Guam's native birds. Forest bird communities containing up to ten species lost all of those species, with the decline starting in the middle of the island, then the south, with the forests at the far north of the island holding intact communities the longest. When in 1982 it became apparent that if population trends already in evidence continued, many if not all of Guam's native forest birds would soon be extirpated, DAWR made the decision to develop a captive breeding program for Guam's 5 remaining endemic species, The Guam Rail, Guam Micronesian Kingfisher, *Halcyon c. cinnomomina*, Rufous fronted Fantail, *Rhipidura rufifrons uraniae,* Guam flycatcher, *Myiagra freycineti,* and the Bridled White-eye, *Zosterops c. conspicillatus* (Beck 1988). Sadly, by July

1983, the Bridled White-eye and by October 1983, the Rufous-fronted Fantail and Guam Flycatcher were so rare that captive breeding of these species had to be discontinued (Beck 1988).

3. Captive Breeding

Efforts to captive breed the kingfisher and rail were then accelerated and with the assistance of Larry Shelton representing the American Association of Zoological Parks (AAZPA) and Aquariums, a cooperative captive breeding program was organized with the initial participation of the Philadelphia Zoological Garden (Shelton 1986a, 1986b, 1986c) the Smithsonian Institution's National Zoological Park (Derrickson 1986a, 1986b) and the New York Zoological Society's Bronx Zoo (Shepard 1985). By the end of 1983 there were four rails in captivity at the DAWR's fledgling captive breeding facility on Guam (Beck 1988).

Sexual maturity occurs at only 4 months of age and breeding is year-round. Although this high fecundity allowed a potentially fast growing captive population, aggression between potential mates limited the number of feasible pairings. The first successful breeding of the rail as a part of the captive breeding program occurred at the DAWR's facility on April 17, 1984 (Beck 1988). The first breeding of the rail at mainland U.S. zoos occurred in September 1984 at the National Zoological Park (Derrickson 1986a, 1986b). From an initial founder population of 19, there are at present over 150 birds in captivity at 18 zoos in the U.S.

With continued effort, the Guam rail could be maintained in zoos almost indefinitely. Although captive populations are useful as species reservoirs, they necessarily lack important features of wild populations. Unless particular attention is paid to the problem, captive populations can quickly loose genetic

variability, for the total size of the captive population is necessarily small. Whatever the size of the captive population, behavioral adaptations to the wild may be lost (Kleiman 1980). In short, re-establishing and maintaining a wild population should be a high priority for any captive breeding effort (Conway 1980).

For any re-introduction using a small captive population we would want as broad a cross-section of the genetic variation of the founder population as possible going back out into the wild. At the same time, we would not want to detract from the captive populations' ability to continue to produce individuals for release. Management efforts for the Guam rail have tried to reduce the potential behavioral and genetic losses in the captive population (Derrickson 1986a, 1986b). For the Guam Rail, mDNA comparative methods have been used to determine the amount of genetic variation in the captive population (Haig pers. comm.). The captive breeding effort has attempted to maintain the genetic variability of the initial wild-caught birds.

More difficult is the problem of the loss of behavioral adaptations, for unlike genetic variability, these cannot be quantified simply. Some of the important of this loss is suggested by a recent study (Witteman and Pimm, see chapter 3) of game bird introductions. When such introductions involve wild-caught birds moved to new locations, they are about four times more likely to succeed than introductions using captive-reared birds. While I cannot eliminate a genetic explanation for this result, it seems likely that the loss of behavioural adaptations may be the principal cause of the difference. The captive breeding program for the Guam rail has attempted to avoid the loss of wild behaviors by minimizing the rails contact with humans and proceeding with establishing a wild population as soon as feasible.

4. The Rota introduction

a. The choice of location

We lack a detailed knowledge of its habitat preferences. Common sense suggests that the best strategy will involve releasing the rails in different places and seeing how well they fare. In the short-term, we might expect to follow the individual birds and learn what habitats they chose.

b.The number releases and the number of birds released

In the case of the Guam rail, there is necessarily a limit to the number of individuals that can be taken from the captive population for release. In deciding how many birds to release, into how many different locations, and on how many occasions, the guiding principles are those that relate to the problem of minimizing the chance of population extinction. Both theoretical insights and empirical studies can help us with the necessary decisions.

Both *environmental disturbances* and *demographic accidents* appear to be important in determining the fate of small wild populations (Pimm and Diamond 1988). At extremely small numbers, breeding may produce only individuals of one sex, all the individuals may die in the same year from independent causes, or individuals may never even find a mate. These are demographic accidents, and by releasing more individuals, we minimize the chance that they will prevent a successful introductions. Environmental disturbances, (for instance, a major typhoon), result in many individuals dying of the same cause. As such, they can cause even very large populations to become extinct or a very large introduction to fail. The obvious way to minimize such effects is to introduce individuals to different places. For instance, it is

likely that some parts of the islands will fare better than others (in the example of the typhoon, some parts of the island may be better sheltered.) This is a strategy of spreading risk and it also helps to minimize the risks associated with our lack of a detailed knowledge of the rail's habitat preferences.

The difficulty is obvious. With a fixed number of birds available for release, we cannot release large numbers of birds (to minimize the risk of demographic accidents), to large numbers of places (to minimize the risk of environmental disturbances). So what is the optimal solution and how do we find it?

We have used two approaches. The first (Pimm *et al.* 1988) examined the fate of several hundred small populations of about a hundred species of birds on islands off the British coast. Using an indirect and technical argument that space prevents our repeating here, we estimated that populations above seven breeding pairs were more likely to fail because of environmental disturbances than demographic accidents and below seven pairs, the reverse was true.

An alternate approach (see chapter 3) examined the success of several hundred introductions of gamebirds into the United States (Witteman and Pimm, in preparation). We considered only those species that were eventually successfully introduced. Interestingly, even for these species and even when large numbers of individuals were released, most introductions failed. This result suggests that the severity of environmental effects varies considerably, so choosing the right place and time for an introduction is important. On average about seven releases were required before one was successful.

The relationship between success and the numbers of individuals introduced was logistic, that is, with increasing numbers, success first

accelerated and then reached a plateau. The inflection point is where the per individual cost of becoming successfully established is minimized (around 75 individuals for the gamebirds), and the maximum success rate was about 15%. This relationship also suggest a strategy for optimizing the chance of a successful introduction. If several hundred individuals are available for release, several smaller releases in different places and at different times can have a higher probability of establishing at least one population. When the total numbers of individuals released falls below 75, splitting the release into smaller ones decreases the overall probability of success.

The optimal number for gamebird releases must be about 75 individuals, for reasons already explained. This is roughly comparable to the optimum result based on the island study, that is, seven breeding pairs. Seven pairs (14 individuals) must be on the low side for an optimal release, for with seven breeding pairs, there would certainly be some non-breeding birds in the population. Seventy-five must be on the high side, because some individuals would disperse and others would be non-breeders. At the very least, these estimates (between 14 to 75 individuals) suggest that we have enough rails to attempt an introduction. If the optimal size for an introduction were an order of magnitude larger, for example, it would not be possible with the number of birds we now have.

In short, we estimated that the best way to introduce the Guam rail would be to split a large number available for release into smaller propagules, but not so small that the numbers fall to levels where demographic accidents are the principal cause of extinction. On the other hand, if only very few individuals were available, the release would have to be postponed until a larger of individuals become available. The more releases attempted, the better the

chance of hitting the right time and place. Captive breeding efforts are such that we expect to be able to release about 30 per year, enough for one release and close to the optimum number if the birds were to remain near each other and form a breeding population.

5. First Rota Releases

I released the first Guam rails on Rota between December 1989 and early February 1990. Appropriately, S. Dillon Ripley participated in this first release. On Rota the birds were held for two days at a holding facility at the release site. During this time they were weighed and measured and all individuals had color leg bands and harness-mounted radio transmitters attached. The transmitters were of both solar and battery types and weighed between 4% and 7% of the rails' body weight. The rails were fed a reduced portion of the feed used in the Guam breeding facility and a supplement of live-caught insects. This supplemental feeding began on Guam, and was intended to enhance the foraging abilities of the rails after release into the wild.

It became clear that use of radio transmitters will be critical in ascertaining the birds disposition; there were only two confirmed sightings of rails one week after the release. Unfortunately, of the 22 birds released, 8 (36%) carried transmitters that failed and so we have no idea of the birds fate. Obtaining reliable transmitters is now a major concern. Of the birds we could track, there seemed to be little evidence of site fidelity, destroying any hopes that we could establish a viable population in the area we chose. The birds often moved along roads following their release suggesting that the birds were seeking more open habitats than the one into which we released them. In choosing roads, the birds were vulnerable to traffic and three birds were killed by vehicles. The other certain major cause of mortality was cat predation.

Although the initial mortality was discouraging, it was by no means unexpected. Sources of mortality such as vehicular kills and cat predation can be prevented with appropriate measures. Currently, efforts to control feral cats are being made and alternative sites are being considered that have less traffic. It is less obvious what measures are necessary to create a wild population in which both encounters between individuals will be frequent enough for mating. Our plans call for additional releases of Guam Rails on Rota over the next several years until a breeding population is established. The experience gained from these releases will accomplish several important goals. The Guam Rail will have been returned to the wild at the earliest possible moment to a snake free environment. A source of wild rails for possible future translocation to Guam will be established on Rota. Release techniques perfected on Rota will be available for future use on Guam when *Boiga irregularis* is controlled there.

Acknowledgements

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vita

I was born, (not hatched - as some people think) in Pasedena California (where little old ladies are from) in the year 1962. Went to Catholic grammar school; I have not-so-fond memories of Penguins with rulers whacking my hands. I must not have been permanently damaged by the experience, because when our family moved to Blue Jay (Calif. , go the nowhere and take a left) in the tail end of the Sierra Nevada Mts. I was put into an MGM science class, - it was a blast. We then moved to San Diego when I was about ... 12? or so... . Did the Penguin and ruler rutine until High School.

First lucky break, the Catholic High school was cool, and the teachers rad. Did the Wrestling routine for four years, and took the City and County titles for my weight class the last two years. Also did the track thing, 440 yard. Took city when I was a Senior.

Somehow I ended up going to UCSD. Had an atmosphere more like a country-club than a university. Worked the whole time at SIO-IGPP-AOG with the most awsome group of Engineers and scientists. Did two years, then went to work at HIMB on coconut island in Kaneohe Hawaii for a couple, published my first paper on "diurnal planulation of the hermatypic coral, Pocillopora damicornus" and did some cool stuf with microcomputer data loggers.

Decided to finish up the degree thing at UCSD in 1985. Taught a couple of Electrical engineering classes (PASCAL programming), a bunch of Biology classes, and finally ended up with a degres in Sociology and Ecology-behavior-and-evolution in 1987 ish. How I ended up working on endangered species through UTK was just luck.

Went to another little island in the middle of nowhere (Rota) to do the field conservation part of the Ph.D thing. I like little remote islands, as long as they have good things in the rainforest to eat (like breadfruit, papaya, mango, ... my mouth is watering...)

In the future I plan ....

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don't forget that the best revenge on poverty, is eating well.