Dynamics of Bird Communities, Populations, and Individuals

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ABSTRACT

This thesis contains three empirical research pieces and one literature review. The empirical work explores questions in behavioral, population, and community ecology. One empirical study draws on experimental data specifically collected for this thesis. The other two use different long-term capture-recapture datasets collected by other researchers. The first study asks whether an experimentally manipulated environment affects mixed-species flock formation among birds wintering in Black Rock Forest, New York. It discusses the mechanism of mixed-flock formation and explores its possible adaptive benefits. The second study looks for evidence of short-term and long-term memory in the capture histories of Common Terns (Sterna hirundo) breeding in Great Gull Island, at the Eastern end of Long Island Sound. Inter-annual dependence among Common Tern captures operates predominantly on short-term memory. The final empirical study examines the pace of understory bird species loss in artificially isolated forest fragments in the central Amazon, Brazil. It reports that fragments with up to 100 ha in area lose one half of their initial number of species in less than twenty years. This diversity of empirical studies touches on a wide variety of ecological questions while drawing information from one taxonomic group—birds. Finally, a review examines the use of a popular term—habitat ‘fragmentation’—in the ecological literature. There are more than sixteen different measures of fragmentation, the majority of which do not distinguish basic components of landscape change, such as habitat area and configuration. I explore the implications of such terminological vagueness upon the study and management of landscape change.
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To my godsons

Vasco and Sebastião
Introduction

This thesis combines four chapters: the first three are research papers, and the fourth is a literature review. Chapter one draws on data originally collected for the thesis; chapters two and three are based on existing long-term data sets (> 10 years). The different data sets share a common structure – they all monitor the occurrence of birds through time, in particular locations. The first follows approximately 200 individuals of seven species in their inter-specific associations during three consecutive winters; the second monitors a population of Common Terns (> 47,000 individuals) breeding in one colony for thirty years; the third follows a community of 164 species occurring in artificially isolated rainforest fragments throughout thirteen years. All research questions focus on the change of an occurrence-related variable through time; hence, the title of the thesis.
Many birds, in a wide variety of ecosystems and geographical locations, forage in groups of different species. The formation of such mixed-species flocks is usually explained by hypothetical increases in foraging efficiency or anti-predator protection. In chapter one, I manipulate the availability of food and the presence of predators affecting a group of wintering North American forest birds, and measure the formation of mixed-species flocks among them. The study takes place in Black Rock Forest, New York – one hour away from Morningside Heights. There are no evident predator presence effects at the time scale of the experiments but the artificial food supply leads to an increase or to a decrease in flocking, depending on the spatiotemporal pattern of food addition. In light of the observations, I argue that birds will look for safety in flocks composed of any number of species, as long as they do not have to forgo too many foraging opportunities.

Most mark-recapture monitoring programs register a limited number of encounters with each individual animal. The Common Tern data set is exceptional, not only in its duration and number of marked individuals, but also in its large number of individuals with many encounters. This type of data permits the detailed investigation of temporal patterns in individual detection. The second chapter asks whether long-term memory plays a relevant role in the capture histories of Common Terns. Given a pattern of captures (or their absence) during increasingly long past periods, what can I say about the present probability of capturing an individual? The data were collected in a massive volunteer effort led by ornithologists Helen Hays and Joe DiCostanzo from the American Museum of Natural History. Tern captures took place in Great Gull Island, at the eastern end of Long Island Sound, New York. Here, I focus on a subset of 7,388 birds known to be alive
for seven or more years. The answer is that short-term memory dominates the capture process.

Habitat loss and the isolation in remaining habitat patches represent a serious threat for many species all over the world. In some circumstances, species-area relations offer a theoretical prediction of how many species may be lost from a patch (at equilibrium) after a given reduction in area. There is no theoretical expectation, however, of how fast species disappear. Chapter three offers one empirical answer. I estimate the time to loose one half of the initial number of understory bird species in artificially isolated forest patches of different sizes. The data came from the Biological Dynamics of Forest Fragments Project, Amazon, Brazil. This study was conducted in collaboration with Gareth J. Russell, Philip C. Stouffer, Richard O. Bierregaard, Jr., Stuart L. Pimm, and Thomas E. Lovejoy. We published a slightly different version of this text in the Proceedings of the National Academy of Sciences of the USA (vol. 100, no. 24).

Fragments of up to 100 hectares in area take at most sixteen years to loose one half of their species. Comparison with related estimates from larger fragments in Africa suggests that a ten-fold gain in time requires a thousand-fold increase in area.

Chapter three – the last research study – estimates local species extinction under habitat loss and isolation, a phenomenon of landscape change that is usually termed ‘fragmentation’. Given the popularity of the term in ecological and environmental circles I decided to review its use in the scientific literature. Chapter four reports the findings. There are more than sixteen different measures of fragmentation. Inconsistent use of the term causes very substantial disagreements about the purported effects of the
phenomenon. I emphasize the importance of drawing a quantitative distinction between
two consensual components of fragmentation: habitat loss and change in habitat
configuration. I also examine the established ways of assessing and generalizing the
effects of fragmentation. A number of studies take unconventional approaches to the
problem and I highlight their methodological innovations. Together, the established ways
and the unconventional approaches reveal a few clear research tasks within the pressing
but ill-defined problem of fragmentation.

Why does it matter that we understand the dynamics of individuals, populations, and
communities of birds? The answer to this question is almost as broad as the answer to
“why does it matter that we understand organism ecology?” Ecologists study the
dynamics of organisms, populations, and communities both for the sake of solving
scientific puzzles and for the better management of wildlife and natural resources. The
last two chapters of this dissertation are geared towards application in management
problems. The first two chapters address scientific questions without immediate
management implications.

A number of factors guided the choice of questions. I applied to graduate school with a
keen interest in studying community ecology. When faced with the difficult problem of
defining a community, I decided to focus on a set of species that sustained evident, non-
trophic, inter-specific interactions. Hence, the interest on mixed-species flocks of birds.
With the first attempts to collect my own field data I realized how most ecological
phenomena at the population level take place at a time scale of, at least, years or decades.
This observation made me acutely aware of the importance of long-term data sets and
motivated collaborations with the Great Gull Island Project, and the Biological Dynamics of Forest Fragments Project. The two collaborations addressed different questions but they required similar skills in data sharing, database management, and the analysis of large data sets. Finally, after conducting three empirical studies on a variety of data sources, I focused on the methodological question of how ecologists use one particular term – fragmentation. This chapter complements the empirical orientation of the first three articles, but it also works as a methodological clarification for the applied question of bird species decay in tropical forest fragments.

It is not by chance that all empirical chapters focus on birds. Most of my fieldwork experience prior to graduate school was in ornithology. As a result, throughout my education I had an inclination to apply biological questions to ornithological problems. Birds are well known and relatively easy to monitor. These advantages make them privileged study objects for behavioral, population, and community ecology. Despite this empirical focus on a single taxonomic group, I shall frame my questions and discuss the results with a view to application to other groups.
Do birds of a feather flock together? An experimental study of hetero-specific flocking

INTRODUCTION

There are even mixed-species groups of foraging seabirds in Antarctic waters (Silverman and Veit 2001).

In North America, groups of Black-capped Chickadees (*Poecile atricapillus*) and Carolina Chickadees (*Poecile carolinensis*) often associate with a long list of species during the non-breeding season. Species joining these Parid flocks include White-breasted Nuthatch (*Sitta carolinensis*), Red-breasted Nuthatch (*Sitta canadensis*), Tufted Titmouse (*Baeolophus bicolor*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*Regulus calendula*), and Brown Creeper (*Certhia americana*) (Morse 1970, Smith 1991). The flocks vary in size and composition, but they usually include up to ten individuals of less than five species. The flocks almost always include Black-capped or Carolina Chickadees (Morse 1970, Smith 1991, Dolby and Grubb 1998) which are often part of one family group (Smith 1991). The associations can last from a few minutes to a few hours; they are evident to the field observer because flock members move together, exchange calls, and stay within close distance to each other.

Why do Parid flocks form? Among Neotropical birds, species that forage in mixed-species flocks all the time have higher survival rates than species that forage alone or in pairs (Jullien and Clobert 2000) – this statistical relation provides relevant insights on life history evolution, but it is no proof that mixing increases a bird’s chance of surviving. As far as I can tell, there has been no demographic assessment of the survival value of mixed-flocking in any group of birds. While there is no evidence of a direct survival advantage, it appears that participation in mixed-flocks affects a bird’s nutritional
condition. In two different experiments, Thomas Grubb and colleagues removed Tufted Titmice and/or Carolina Chickadees from their study woodlots and measured feather growth (as an indication of nutritional condition) in a set of remaining birds. According to their observations, White-breasted Nuthatches did worse in the absence of both Parids (Dolby and Grubb 1998); but Carolina Chickadees did better in the absence of Tufted Titmice (Cimprich and Grubb 1994). These studies underscore two important points: (1) mixed-flocking may affect survival indirectly, when the changes in nutritional condition are strong enough; and (2) the effects can be different (and even opposite) for different species.

Just how mixed-flocking affects survival or nutritional condition is a more elusive question. The traditional answers fall in two broad groups: increase in foraging efficiency, and increase in anti-predator defense (Morse 1970, Diamond 1981). Note that these two answers may overlap to some extent. A flock member’s foraging efficiency may increase because it steals food or copies foraging locations from its flock mates; but it may also increase because the company and vigilance of the mates allow it to allocate less time for predator detection and more time for feeding. Additionally, if intra-specific competition is strong in comparison to competition between species, mixed-flocking may be a strategy to obtain safety benefits while paying a relatively low cost for competition (Terborgh 1990).

There are likely no direct food rewards from joining mixed-flocks of Parids. Captive Chickadees are known to copy foraging sources and techniques from hetero-specific aviary mates (Krebs 1973). The foraging niches of different species in North American
flocks of Parids do overlap to a certain extent (Morse 1970); there is no evidence, however, that such overlap is greater when birds are in a flock than otherwise – as would be expected if they were joining for a direct foraging reward. In fact, a removal experiment points in the opposite direction: the foraging niches of Carolina Chickadees and Tufted Titmice overlap more – not less – when Titmice are removed than when they are present (Cimprich and Grubb 1994). It is more likely that the Parid mixed-flock members who obtain a benefit, do so through a decrease in time spent searching for predators (Sullivan 1984).

It is important to clarify the way in which one asks a ‘why’ question about mixed-species flocks. ‘Why’ questions about any behavior can take two distinct forms:

‘what is the behavior good for?’ – function or survival value – and ‘how does the behavior work’ – mechanism or causality (Tinbergen 1963). For a matter of choice or constraint, mixed-species flock studies have often addressed these two facets as one, by articulating observations of mechanism into explanations of function (Berner and Grubb 1985, Klein 1988, Poulsen 1995). Such an approach can be insightful but it also has pitfalls: as behaviors become complex, it becomes difficult to establish links between mechanism and function. This is true in the same sense that understanding the mechanism of current flow in a microchip may not help one find out what it is used for.

In this study, I focus on the mechanism of mixed-flock formation. I manipulate food availability and predation risk while measuring the frequency of mixed-flock formation. In the discussion, I explore the implications of the mechanism in the function of flocking, without implying a direct connection between them.
The study is structured around four questions. The first two aim at whether the observed flocks and inter-specific interactions are real, as opposed to being random encounters of independently moving birds. The first question asks whether the means and variances of observed group sizes differ from what should be expected if birds occurred at random and independently of each other. In the second question, I ask whether mixed-species flocking is higher than expected if the observed groups of birds from the same species were to occur randomly and independently of each other.

The last two questions are directly aimed at the mechanism. Question 3 asks whether the frequency of mixing between species changes according to the availability of supplemental food presented in two distribution patterns, and according to predation risk, manipulated with a trained predator. The final question asks whether mixing changes according to the movements of Black-capped Chickadees, the most abundant species in the flocks.

**STUDY AREA AND EXPERIMENTAL DESIGN**

**Study area**

I observed mixed-species flocks in Black Rock Forest, a 1,500 ha private research area on the Hudson Highlands, Orange County, New York. Black Rock is one hour away from New York City, on the end of a patch of contiguous forest of more than 20,000 ha extending southwards through the West Point Military Academy and the Bear Mountain and Harriman State Parks. I established two study sites within the limits of the research
forest: Stone House (SH), and Aleck Meadow (AM). The sites are approximately one kilometer away from each other and at least one kilometer from the closest inhabited house (and home bird feeder). The arboreal vegetation on the study sites is mixed coniferous-deciduous, dominated by Sugar maple (*Acer saccharum*), Red oak (*Quercus rubra*), and Eastern hemlock (*Tsuga canadensis*). Both sites are in the close vicinity (<50m) of water reservoirs. Stone House is at a higher altitude (~380m) than Aleck Meadow (~310m) and more exposed to the sun. Temperatures during fieldwork days ranged from –19 to 21ºC, with a mean of 0ºC.

At each site, I established one 800m-long observation transect along a dirt road. Each transect was subdivided in 32 sections of 25m labeled with numbered markers. I placed a feeder in each section, locating consecutive feeders on opposite sides of the road. Feeders were left empty or stocked with various amounts of black-oil sunflower seed, depending on the stage of the study.

**Experimental design**

This study was designed to assess the independent and combined effects of food availability and predator pressure upon the frequency of mixed-species flock formation. I intended to follow a two-by-two design combining food and predator manipulations to represent four states of nature: 1) *Baseline* (no predator, and no food supplementation); 2) *Full feeders* (inexhaustible food supplementation); 3) *Predator with empty feeders* (trained falcon flying close to foraging flocks); and 4) *Full feeders with predator* (combination of 2 and 3). As in any field study, there were methodological surprises and
unexpected constraints. As a result, the executed design differed from the intended one in three main ways: First, I could not obtain sufficient data on state 3; Second, the baseline state was represented by two different treatments - no manipulation at all, and low food manipulation; Third, I introduced a new state, random low food to assess the effects of food distribution.

The rationale of the design follows a comparison of the two sites during three consecutive periods. During the first and second periods the two sites are treated in the same way: Both receive the same treatment during a given period and both change treatment from period 1 to period 2. By the third period, one of the sites changes treatment for a second time but the other remains in the same state. This design was the reference throughout the project and I applied it whenever possible (table 1.1). I performed nine field experiments on two sites over three consecutive winters: 1999-2000, 2000-2001, and 2001-2002. One field season (winter) included three experiments separated by two to three weeks. Each experiment had two or three periods of approximately five days. I apply the term sample to a site-period combination. For example, one experiment with three periods (on two sites) contains six samples. When necessary, I refer to samples with a code of two letters (the initials of the site), and three digits (the season, experiment, and period). The code AM231, for example refers to the first period of the third experiment of the second season in the Aleck Meadow site.

The target length of a period is five days, but I adjusted this timing so as to balance the number of observations across periods. In four of the experiments it was impossible to complete three observation periods with enough observations. In these cases, I performed
two slightly longer periods, starting with both sites in the same state (baseline), and ending with the application of different treatments in each site.

Throughout the study, I evaluated the birds’ response to the experiments and adjusted the manipulations accordingly. These adjustments were meaningful but limited, so as to incorporate the methodological lessons of each season without losing comparability between seasons. All treatments are defined on the bottom of table 1.1.

Early in the first season, I realized that birds spent more time in the upper canopy (and were more difficult to see) when the feeders were empty. The trained falcon could not fly more than three meters above ground – too low to represent a threat for canopy feeding birds. This convinced me that a predator manipulation without food would be ineffective – as a result, I invested more effort in the other treatments.

During the second year, I tried to solve the problem of empty-feeder bird secrecy by replacing the baseline treatment with a low-food treatment. This meant adding a small portion of the food available at full feeders (~1%) and distributing it through a smaller number of more sparsely distributed feeders. The objective was to attract the birds’ away from the canopy without giving them an unlimited food supply. In fact, the birds (mostly chickadees) were capable of exhausting the daily low food supply in less than two hours. I expected them to keep visiting empty feeders throughout the day but that did not happen. After a few days of habituation, the birds were checking all the feeders in the early morning and then resuming their canopy foraging for the rest of the day. Nevertheless, I performed the low food with predator manipulation by flying the predator mostly during the beginning of the day.
Table 1.1. Experimental Calendar.

<table>
<thead>
<tr>
<th>Season</th>
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<th>Site 2: Alleck Meadow</th>
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<td></td>
<td>Food</td>
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<td>1</td>
<td>1</td>
<td>Nov 27 – Dec 1</td>
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<td></td>
<td>2</td>
<td>Dec 2-6</td>
<td>Full feeders†</td>
<td>–</td>
<td>Full feeders</td>
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<td>3</td>
<td>Dec 7-12</td>
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<td>–</td>
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<tr>
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<td>1</td>
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<td>Merlin‡</td>
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<td>Merlin‡</td>
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</table>

* No treatment. Baseline corresponds to no predator and no food treatment.
† Thirty-two 400ml feeders at 25m intervals along an 800m observation transect. All feeders are kept stocked throughout the period.
‡ Approximately seven daily flights of a trained Merlin (*Falco columbarius*) within sight of flocking birds foraging within 25m of the observation transect.
|| Same as ‡ with an American Kestrel (*Falco sparverius*).
§ Thirty-two empty feeders along transect: Every evening, starting on the eve of the first day, eleven regularly spaced feeders are stocked with 10ml of seed each. Stocked feeder locations shift 25m per day.
¶ Thirty-two empty feeders along transect: Every hour from 8:00am to 3:00pm eight randomly selected feeders are stocked with 2.5ml of seed. Each feeder is stocked twice per day - once in the morning and once in the afternoon.
The third-season plan introduced two changes. First, I abandoned the low-food treatment and went back to baseline as the departure point of the experiments. Second, given the considerable unreliability and cost of the predator manipulation I decided to focus on food manipulation only. The first experiment started off with a bleak prospect – when I changed the treatment from baseline to full feeders, there were no changes in mixing on either site. At this point I had noticed some contradictory results in year 1 and 2 (such as similar changes in treatment leading to significant effects in opposite directions) and was very eager to obtain a reliable strong change in mixed-flock formation. I could only be sure of understanding something about the flocking mechanism if I where able to tweak it according to my knowledge. In year two, I had learned that chickadees would systematically search the feeders for a predictable low amount of food and then resume their natural foraging. What would happen if that low amount of food were unpredictable? To address this question I introduced a new experimental treatment: random low food. Daily, a field assistant would add approximately the same amount of food as in the low food treatment. This amount, however, was divided in smaller portions (2.5ml) and added to feeders in randomly selected sections throughout the day.

METHODS

Data collection

Every year by the second half of October, at the beginning of the field season, I set up one trapping station in each study site. A station consisted of a platform with three or four
Potter traps baited with black-oil sunflower seeds. For the first two weeks after set up, I left the traps locked open and supplied with food. After this initial period of habituation, I visited the sites weekly and captured birds with traps and with mist-nets placed near the feeding stations. Trapping visits lasted until one week before the beginning of the first experiment. I marked all captured Black-capped Chickadees, White-breasted Nuthatches, and Tufted Titmice with one aluminum USGS band and a unique combination of three plastic color bands.

During the experiments, an observer walked back and forth along the transects four times per day between 7:30am and 4:30pm. For the first two experiments of the first season I collected the data alone, alternating transect runs between sites, so that each site was visited twice per day – once in the morning and once in the afternoon. From then on, I obtained the help of a second observer; together we performed four transect-runs per day, per site. Every day, we changed the starting site and the starting section (1 or 32) of the transects, so as to maximize the variety of observer-time-location combinations. We stopped the observations whenever it rained heavily.

While running the transects, we noted the presence of any Black-capped chickadees, White-breasted nuthatches, Tufted titmice, Downy woodpeckers, Golden-crowned kinglets, Brown creepers, and Red-breasted nuthatches. On every observation, we recorded the number of individuals of each species, as well as their color-band combinations (when there were any). We also recorded the time and transect section where the birds were first seen, followed by the time and transect section where they were last seen or abandoned by the observer. All information was taped into a small
hand-carried tape-recorder. We tried to extend every observation to a minimum of three minutes. Some observations were shorter than the target time (down to a few seconds) because the birds moved away, others were much longer (more than twenty minutes).

**Operational definitions**

Every *observation* contains one or more *encounters* with individual birds. When encountering only one individual I speak of a *singleton* observation, when encountering more I speak of a *group*. For a set of individuals to be considered a group, they must fulfill at least two of the following three conditions: 1) To be moving in the same direction; 2) To be within at most ten meters of the closest group member; and 3) To be in calling contact with the other members of the group. If, at any given moment, the observer can see two separate groups of birds he/she records only the group that is closer to his/her location. There are no simultaneous observations of different groups of birds at the same site.

Each group can be subdivided in two different ways. First, it can be split according to species. For example, a group of three Chickadees and one White-breasted nuthatch contains two same-species subgroups: one Chickadee subgroup of size three, and one Nuthatch subgroup of size one. Note that, in this case, even though the nuthatch subgroup has size one, that nuthatch is not considered a singleton. The second type of subdivision splits the group in *pair-wise encounters*. A group of three birds, for example, contains three pair-wise encounters; a group of four would contain six. A pair-wise encounter may be homo-specific (if it involves individuals of the same species), or heterospecific (if it
involves two different species). I measure heterospecific flocking (or mixing) as the ratio of heterospecific pair-wise encounters to the total number of pair-wise encounters. This measure can be applied to any set of observations.

**Data analysis**

The field data translate into a matrix of observations with rows representing observations and columns representing birds. Some columns stand for individually marked birds, hence, their elements can only take the values of zero (for absence) or one (for presence). Other columns represent unidentified birds of a given species – these may be filled with any integer number from zero to \( n \), representing the number of unidentified individuals. From the matrix of observations, I extract a triangular matrix of pair-wise encounters. This matrix’s rows and columns (in equal number) correspond to the birds listed as columns in the observation matrix. The triangular matrix only has non-zero values below the diagonal: an element \( A_{ij} \), with \( i > j \), indicates the number of times bird \( i \) was seen in a pair-wise encounter with bird \( j \). Every sample has its own matrix of observations and triangular matrix of pair-wise encounters. The analysis described below uses these two matrices to ask questions about experimental periods. The questions focus on one sample at a time, on pairs of consecutive samples from the same site, or on sets of samples from both sites pooled by treatment.

The first three questions of this study (see introduction) are addressed with a common analytical procedure: first, define a statistic of interest to be measured from the data; second, use the data to simulate a random distribution of the statistic according to some
pre-determined constraints; and last, compare the observed statistic with the simulated
distribution. Question 1 asks whether the mean and variance of the group sizes observed
in any given sample differ from those expected at random. Simulation 1 generates the
random expectation by operating on a matrix of observations: It keeps the column totals
constant, and randomly permutes the encounters in each column across observations.

Each simulation returns a group size frequency distribution. After running 1000
simulations I obtain mean group size frequencies per class and from those estimate a
mean and variance of the expected group size. Simulation 1 illustrates a scenario where
individual birds are encountered randomly and independently across a fixed number of
observations – it breaks all intra- and inter-specific ties among birds. This includes all ties
within any observed group of birds. I test the null hypotheses of equality of observed and
expected variances using an F-test (Sokal and Rohlf 1995). For comparing means, since
the variances are often significantly different, I use a Welsh’s adjusted t-test (Zar 1996). I
also test the composite null hypotheses of equality of variances and equality of means
across all samples, using a sequential Bonferroni adjustment (Rice 1989).

Question 2 asks whether the mixing observed in a given sample is significantly different
from that expected at random. This is a question about heterospecific flocking; therefore,
while simulating a random expectation, one should leave the intra-specific group
structure intact. Simulation 2 operates on a matrix of observations and keeps the column
totals constant; however, it does not treat individuals independently of each other.
Instead, it permutes same-species subgroups across observations, breaking inter-specific
ties but leaving intra-specific ones as observed. From each simulated matrix I obtain a
triangular matrix of pair-wise encounters, and one measure of mixing. I draw an expected
distribution of mixing measures using 1000 simulations, and then compare it with the observed mixing. To test the null hypotheses of no difference between observation and expectation, I use a two-tailed test where the $p$-value is two times the proportion of the expected distribution falling on the tail-side of the observed value. To test the composite null hypothesis of no difference in any of the samples, I apply a sequential Bonferroni adjustment to the $p$-values (Rice 1989). Additionally, I plot the observed against the expected values and indicate the significance of each period’s displacement from the expectation using a one-tailed test.

Given two mixing values derived from two observation matrices, question 3 asks whether the difference between them is significantly greater than zero. Suppose one has observation matrices with dimensions $[r_1, c]$ and $[r_2, c]$. Simulation 3 joins the two matrices into one with dimensions $[r_1+r_2, c]$, randomly permutes the rows, and finally extracts two simulated matrices with $c$ columns and $r_1$ and $r_2$ rows, respectively. After performing 1000 simulations I draw a distribution of simulated differences between matrices. If the observed difference is greater than 95% of the simulations I reject the null hypotheses of no change (one-tailed test). I apply simulation 3 for comparing consecutive sample of the same site and experiment, as well as for comparing matrices that pool all the samples with a given treatment. I make three different comparisons between pooled matrices. First, I pool all ‘no food’ and all low food samples and compare them with the pooling of all full feeder samples. Note that I do not include random low food samples in this comparison. Second I compare all the no predator samples (from sites and experiments with predator manipulation) and compare them with the pooled predator samples. Finally I compare the pooled samples without random low food (again, drawing
only from the experiments and sites with random low food in any of the samples) and compare them with the pooled random low food samples.

Finally, I ask whether Chickadee movement has any relation to mixing. Every observation of one or more Chickadees starts and ends in a known transect section. If starting and ending sections are the same, displacement is zero; otherwise, it is greater than zero. Using all the observations in a given sample, I draw a distribution of chickadee displacements. Subsequently, I fit a lognormal function to this distribution. My measure of movement is the mean of the lognormal fit to observed displacements. To examine the relation between movement and mixing I perform a linear regression of mixing on movement, using each sample as a data point. Since mixing is a proportion, I logit-transform the mixing measures before running the regression.

RESULTS

There are a total of 7,205 observations collected in 46 samples. These include 27,581 encounters with individual birds: 63% with Black-capped chickadees, 16% with White-breasted nuthatches, and 13% with Eastern tufted titmice. The remaining 7% include encounters with Downy woodpeckers, Golden-crowned kinglets, and Red-breasted nuthatches. The large number of encounters corresponds to a much smaller number of individuals. Combining both sites over all seasons, 55% of the encounters involved birds with color bands. These included only 129 chickadees, 24 white-breasted nuthatches, and 38 titmice.
Observed group size variance is larger than expected at random under simulation 1 (see standard deviations in Fig. 1.1). Thirty-six of 46 samples show a significant difference between observed and expected variances, with the observed value always being the largest one (F-test for comparison of variances with sequential Bonferroni adjustment and $\alpha = 0.05$). I reject the composite null hypothesis of equal variances. Not surprisingly, given the constraint on the total number of observations, the observed and expected group size means are never significantly different, even before Bonferroni adjustment of the test results (Welch’s approximated Student’s $t$-test with $\alpha = 0.05$). The group size frequency distributions reveal that singletons and large groups appear more frequently than predicted by simulation 1 – thus the difference in variances.

Fig. 1.1. Relation between observed and expected values of the group size mean (circles) and standard deviation (triangles). Expected values follow independent random permutation of individual observations.
I also reject the composite null hypothesis that, in all samples, observed and expected mixing is the same. Mixing tends to occur more often than expected under simulation 2 – where I break interspecific ties but leave intra-specific subgroups intact. The observed mixing differs significantly from the expectation in seventeen of 46 samples (two-tailed randomization test with sequential Bonferroni adjustment and $\alpha = 0.05$). Figure 1.2 shows the significance of one-tailed departures from expectation on a period-by-period basis (no adjustment). An overwhelming majority of significant departures corresponds to mixing above the expectation. Only two samples, corresponding to random-low food treatments, show significantly less mixing than expected.

**Fig. 1.2.** Relation between observed and expected mixing under simulation 2 (random permutation of same-species subgroups.) The diagonal line indicates where observed and expected values are equal; empty circles show periods where the observed flocking was not significantly different from the expectation; filled circles show significant deviations from expectation under a two-tailed test ($p < 0.05$.)
Fig. 1.3. Mixing at the Stone House (continuous line) and Aleck Meadow (dashed line) sites throughout the study. The symbols identify experimental treatment: baseline (○), low food (●), low food with predator (●!), random low food (●?), full feeders (●), full feeders with predator (●!). Changes in mixing between consecutive periods are tested with one-tailed permutation tests. The asterisks indicate significant increase or decrease (* = p<0.05, ** = p<0.01, *** = p<0.001.)
The experimental results explain part of the variation in mixing. The y-axis coordinate of each symbol in figure 1.3 indicates the level of mixing for a particular sample. The asterisks between symbols indicate significant changes between consecutive periods at the same site (one-tailed randomization test). First, I will focus on transitions between consecutive samples in the same site and ask whether mixing increases or decreases (regardless of significance) in association with given changes in treatment. Mixing varies continuously between zero and one and, as it is, the outcome of all transitions was either an increase or a decrease in mixing. Two thirds of the fifteen transitions from baseline (or low food) to full feeders result in increased mixing. Two of three transitions from ‘no predator’ to predator treatment result in an increase as well (regardless of food manipulation). Finally, two of three transitions to random low food show a decrease in mixing. These qualitative results do not favor either outcome in any of the treatments. In fact, for full feeders, predator, or random low food treatments, the observed partition of outcomes could easily result from a binomial process with equal probabilities of increase and decrease.

Simulation 3 allows a quantitative comparison between consecutive samples but the quantitative results are only slightly different from the qualitative pattern described above. There are five significant changes associated with food abundance transitions – four of these are increases. There are no significant changes in mixing associated with predator additions. Finally, of the two significant changes associated with random low food both are decreases.
To better illustrate the aggregate effect of treatments, I applied simulation 3 to pairs of matrices that pool samples according to treatment (see methods). Figure 1.4 shows the results. There is no significant difference between pooled periods with and without predator. Pooled periods with full feeders, however, show significantly more mixing than pooled periods with no food or low food ($p < 0.001$). Despite the slight increase associated with the first random low food treatment (SH313), the pooled random low food samples had significantly lower mixing than the pooled no food or full feeder treatments from the same sites and experiments. Note that SH313 is exceptional among the random low food samples because, in this case, the birds did not consume the seeds in

Fig. 1.4. Mixing comparisons between three pairs of pooled matrices with and without one particular treatment: full feeders (●), predator (†), and random low food (○). The no-treatment (×) matrices pool all no-treatment samples from the sites and experiments that included the corresponding treatment. To be conservative, I exclude all random low food periods from the full feeder comparison. Asterisks indicate a significant difference (‘***’ = $p < 0.001$.)
most feeders until the last day of observations – probably because they did not notice that the feeders had any food at all. In the other two random low food samples (SH322 and AM332), the chickadees checked all feeders regularly and removed most or all the seeds every day. I consider the random low food treatment in SH313 to have been ineffective.

Fig. 1.5. Mixing with respect to Chickadee movement. Symbols indicate samples with different food-treatment and site combinations: Stone House with no food, low food, or random low food (○); Stone House with full feeders (●); Aleck Meadow with no food, low food, or random low food (○); Aleck Meadow with full feeders (●). The two points on the lower right-hand corner of the graph correspond to the effective random low food treatments. Table 1.1 displays the results of linear fits to the data on this figure.
Table 1.2. Linear regression fits to the relation between mixing \( (y) \) and chickadee movement \( (x) \). I fit lines \( y=a+bx \) to two different sets of samples: all samples, and all but the two effective random low food treatments (SH322 and AM332). The numeric values indicate intercept \( (a) \), slope \( (b) \), the proportion of variation in flocking that is explained by variation in movement \( (R^2) \), and the probability value associated with the null hypotheses of a slope equal to zero \( (p) \).

<table>
<thead>
<tr>
<th>Data</th>
<th>( a )</th>
<th>( b )</th>
<th>( R^2 )</th>
<th>( p )</th>
</tr>
</thead>
<tbody>
<tr>
<td>All samples</td>
<td>-0.120</td>
<td>-0.939</td>
<td>0.3202</td>
<td>0.0001</td>
</tr>
<tr>
<td>All but random low food (SH322 and AM332)</td>
<td>-0.025</td>
<td>-0.501</td>
<td>0.1171</td>
<td>0.0330</td>
</tr>
</tbody>
</table>

Chickadee displacement varied considerably but it was exceptionally high in the two effective random low food samples. Figure 1.5 shows these two extreme points on the lower right-hand side of the graph. The linear regression of logit mixing on mean displacement per observation (mean of the lognormal distribution fitted to displacement distribution) shows a moderate but significant \( (p < 0.05) \) relation between chickadee movement and mixing. The relation is more significant \( (p < 0.001) \) and it has a higher coefficient of determination \( (R^2 \approx 0.320) \) if it includes the effective random low food samples. When I remove those samples \( R^2 \) decreases to \( \approx 0.120 \), but the regression is still significant \( (p < 0.05, \text{table 1.2}) \).
DISCUSSION

Measuring hetero-specific flocking

My measure of mixing reflects the extent to which all birds co-occur with heterospecific flock mates. This is a relative measure, because it looks at all observed pair-wise encounters and quantifies what proportion of those encounters involve individuals of different species. The pair-wise approach is inspired by Morse’s follower-followed matrices (Morse 1970). Triangular matrices in Morse’s study displayed the number of times species \( i \) had followed species \( j \); here, they count the number of pair-wise encounters between individuals of species \( i \) and \( j \) in flocks. One could measure mixing in many different ways: for example, by looking at one species at a time and asking what proportion of encounters fall in monospecific flocks, heterospecific flocks, or singleton observations (Berner and Grubb 1985). This approach, however, raises a complicated problem. By taking species apart, one risks overlooking one very real constraint: one species’ choice of company depends on the choices of individuals from other species as well as on its own. To preclude this problem, I chose a broader measure of mixing, one that looks at the aggregate behavior of individuals from all flocking species. This measure also has the advantage of being flexible. Depending on the question, one may restrict it to subsets of birds defined on the basis of species or any other criterion. Additionally, the measure provides a quantitative way of distinguishing between temperate mixed-flocks, numerically dominated by one or a few species (Morse 1970, Smith 1991), from those larger tropical flocks with many, and more evenly distributed,
species (Munn 1985, Jullien and Thiollay 1998). The tropical flocks should show the highest level of mixing.

**Are flocks real?**

Beyond the question of the level of mixing, there is a legitimate question of whether the groups are real or not. Do we observe animals that deliberately associate with each other, or do we merely run across chance encounters of independently moving elements? Often, the sight of animals from different species following each other as they forage is so compelling that one promptly rules out the possibility of a chance encounter. In many instances, however, the limits and/or the movement of the group are not so obvious – that is when chance encounters become more plausible (Waser 1982). I addressed this problem by comparing my observations with two different ‘chance’ scenarios: the first, assuming that all *individuals* from any species occur randomly and independently of each other; the second, assuming that *conspecific groups* of each species occur randomly and independently of each other. In both cases, the observations differed significantly from the expectation. I take the results as evidence of two processes: group formation, and mixing. First, individuals (regardless of species) are forming groups. Second, individuals from one species are actively joining individuals from a different species. Having confirmed the reality of these two processes, I proceed to examine the influence of experimental treatment on mixing.
Superabundant food

There was significantly more mixing during the pooled full-feeder samples than during the pooled no-food plus low-food samples. How did this happen? First, groups of chickadees shifted from foraging mostly on tree canopies to foraging on the feeders. They were joined by White-breasted nuthatches and, occasionally, by Titmice – all eating or caching seeds from the feeders. Birds would frequently concentrate on a feeder for a few minutes and subsequently move to a different feeder without emptying the first. In full-feeder samples there was always a choice of stocked feeders without birds. Therefore, I considered those concentrating around a feeder as genuine groups rather than aggregations of birds attracted by a common food source (Morse 1970). Occasionally, a group would simultaneously visit two feeders, in which case, if its elements remained in calling contact and sufficiently close to each other, I would still consider it a group.

Chickadees foraging in the canopy could also be accompanied by Nuthatches or (more rarely) by titmice. However, this happened more often during full feeder samples. Some birds that never used the feeders also joined the flocks. Downy woodpeckers, Brown creepers, and Golden-crowned kinglets would also follow Black-capped chickadees and White-breasted nuthatches as they moved from feeder to feeder along a transect. This confirms that some birds join mixed-flocks without receiving any direct foraging benefit. If group membership allows Woodpeckers, Creepers, or Kinglets to allocate relatively more time to foraging, they may get an indirect foraging benefit. It is doubtful, however, that they are finding richer food patches, and quite certain that they are not copying the Chickadee and Nuthatch foraging sources or techniques. These changes were strong
enough to generate a significant increase in flocking in the pooled data but not so consistent as to generate the same response in every experiment.

How to interpret this result in the light of previous field experiments? In Ohio, Berner and Grubb (1985) observed lower participation in flocks among birds with access to a superabundant food supplement. From this they concluded that birds join flocks as a means of increasing foraging efficiency. Their bird community is similar to that of Black Rock Forest – with Carolina chickadees (*Poecile carolinensis*) instead of Black-capped chickadees. There are two important differences between the Ohio study and mine: first, they measure mixing on a species-by-species basis, as the proportion of encounters in mixed-species flocks; second, they add food in one single superabundant source. Many birds that occur along Berner and Grubb’s observation transect will not have a food supplement in their home range, but they may easily travel to the nearby feeder. Black-capped chickadees are known to travel away from their home ranges to visit feeders (Brittingham and Temple 1988, Brittingham and Temple 1992); it is very likely that Carolina chickadees behave in a similar manner.

The difference between the two studies can be due to differences between study areas, species, or the measure of hetero-specific flocking. If that is the case, there may be little to learn from a comparison. There is a plausible alternative, however, that may provide an insight on the mechanism of flock formation. In Berner and Grubb’s supplemented samples, birds could be making frequent trips between their usual foraging grounds and the only available bird feeder. In this scenario, it would be more difficult for individuals of different species to meet and stay together as a flock. Nevertheless, such decrease in
hetero-specific flocking is no proof of a direct foraging benefit of associating with hetero-specifics. Instead, it can be seen as evidence of the cost of keeping up with fast moving flock mates.

The cost of keeping up

To further explore the possibility of a speed limit in flock formation, I designed the random low food treatment. This treatment aims at increasing the movement of the most abundant flock species: the black-capped chickadee. In both sites, when chickadees realized the potential reward in apparently empty feeders, they took to visiting all feeders in a site, systematically, moving back and forth along the transects. A group of ten chickadees could exhaust a 25-seed reward in less than a minute; therefore, their movements were fast. The sharp decline in mixing during random low food treatments shows that not all species keep up with the chickadee’s pace. This applied to species that do not use feeders, as well as to those that do (e.g. White-breasted nuthatches and Titmice). White-breasted nuthatches occasionally got some seeds, but they would not take part in the chickadee’s systematic searches. The negative relation between chickadee movement and mixing is very obvious if we compare random low food samples with the remaining samples. The relation still applies, however, if we remove the random low food samples and focus on the less extreme circumstances (see fig. 1.5 and table 1.2).

Looking at both full feeders and random low food treatments, we see that an increase in food availability may associate with either an increase or a decrease in mixing. The sign of the change seems mediated by the distribution of the food supplement and its effects
on chickadee movement. The abundance and distribution of food does play a part in the mechanism of flock formation. I found no evidence, however, that an increase in foraging efficiency is a necessary function of mixed-flock participation.

**Safety**

How can one interpret the predator manipulation results? After finding no evidence of a direct foraging benefit, is there any hint that mixed-flocks function as a source of anti-predator defense? There are several reasons to expect such function: both theoretical and empirical. The simplest reason is the theoretical expectation of safety in numbers (Hamilton 1971). In the face of a non-selective predator attack, an individual in a group will always be at lower risk than an individual that is alone. A second reason is that grouping may lead to improved predator detection (Lima 1995a). Lima described the mechanism of predator detection in mixed flocks of sparrows in much detail (Lima 1995b). Empirical studies of North American flocks of Parids and accompanying species suggest that both Downy woodpeckers (Sullivan 1984) and White-breasted nuthatches (Dolby and Grubb 2000) take more risks in the presence of hetero-specific flock mates than when foraging alone. The case for an anti-predator function is extremely plausible, at least for some of the species. Why is it then that I saw no changes in mixing under predator manipulation? There was no evidence that predator presence affects the mechanism of flock formation.

Did I choose the right predator? Merlins (*Falco columbarius*) and American Kestrels (*Falco sparverius*) are not effective predators of woodland birds (Sodhi et al. 1993,
Smallwood and Bird 2002). Unlike Sharp-shinned hawks (*Accipiter striatus*), they are not adapted for attacking or pursuing small birds in forested areas (Bildstein and Meyer 2000). Sharp-shinned hawks, however, are much more difficult to train – I could not find a falconer to work with a Sharp-shinned hawk in this project. Since Merlins and Kestrels are known to occasionally attack chickadees (Smith 1991), I trusted that they would represent a credible threat. Indeed, experimental predator flights elicited consistent alarm reactions from flocking individuals. Birds gave alarm calls, fled the area, or froze for a few seconds (or minutes).

If the predator was right and there is an anti-predator function, how could the mechanism not reflect such function? To explore this possibility, it is useful to regard flocks as refuges (Sih 1992, 1997). When a bird is in the refuge (flock), it receives a safety benefit and pays a foraging cost. The foraging cost is incurred either by having to share food or by following hetero-specifics into sub-optimal foraging areas. There are at least three ways in which this scenario might be compatible with the absence of response to predator manipulation: good predator tracking, overestimation of risk, and lack of plasticity. With a good tracking of predation risk, birds could return to their ‘usual’ behavior shortly after predator flights. Waite and Grubb reported Tufted titmice resuming activity within less than ten minutes of a simulated predator attack (Waite and Grubb 1987). In one occasion, we performed repeated Merlin flights between two points 25 meters apart, within sight of a group of Chickadees visiting a feeder. On its flight, the Merlin would pass within less than five meters of the feeder. After six flights and less than ten minutes the Chickadees resumed visits to the feeder, despite the presence of the predator. Seven daily flights along a transect that spanned the area of three flock ranges would result in, at most, two
or three predator encounters per individual per day. This would give the birds considerable time to resume their regular activity after a stressful encounter. Considering that we never made observations within sight of the predator, it is conceivable that, within a five-day manipulation period, the behavior could appear indistinguishable from predator-free behavior.

Indifference to the predator manipulation could also result from a consistent overestimation of predation risk (Abrams 1994) – the second explanation. Birds would always behave as if the safety benefit of being in a flock were higher than what it actually is. In such scenario, our introduction of a predator might not change the already high perception of risk, and the flocking behavior would not change. The third explanation – lack of plasticity – implies that birds cannot adjust their flocking decisions to the level of predation risk. This seems plausible if one considers the potentially high cost of acquiring predation risk information (DeWitt et al. 1998). Flocking could still vary according to environmental constraints such as food availability and distribution, but there would be no plasticity in the face of changes in predation risk.

**Mechanism and function**

The dilemma of a flock member is how to eat without being eaten. By deciding to stay in, or out, of a flock a bird may incur costs and benefits both in foraging success and in safety. In mixed-species flocks, the costs and benefits may be different for different species. One may learn about a behavior’s function by watching it unfold in an experimental setting. While doing so, however, it is important to maintain the distinction
between mechanism and function (Tinbergen 1963). I have shown that food availability affects the mechanism of mixed-flock formation, but I found no evidence of any direct foraging reward in flock participation. There may be indirect foraging benefits deriving from increased safety; however, in a world without predators, flocking would be much less rewarding.
Inter-annual dependence in capture histories of Common Terns (*Sterna hirundo*): determining and interpreting the order of a two-state Markov chain.

The Common Tern (*Sterna hirundo*) is a widespread seabird that breeds along the eastern coast of North America and elsewhere in the Northern Hemisphere. North American Common Terns migrate to the neo-tropics every winter, as far south as Argentina, and return during the spring to nest in colonies comprising from fewer than ten to more than 10,000 breeding individuals (Burger and Gochfeld 1991). The present study draws on thirty years of live-trapping and banding data from one of the largest North American colonies, in Great Gull Island, New York. As adult breeders, Common Terns tend to return to the same colonies where they were born (Austin 1949); nevertheless, there are
frequent exceptions to this philopatric behavior (Austin 1949, DiCostanzo 1980, Burger and Gochfeld 1991, Nisbet 1996). As much as twenty percent of a given year’s breeding population in Great Gull Island may consist of birds that either hatched elsewhere or were seen breeding in other colonies at some point of their lives (Helen Hays, unpublished data). Inference of colony choice, however, is based on the fallible process of detection. Presence in the breeding site is a necessary but not sufficient condition for detecting an individual. Furthermore, individuals may be trap-happy (more detectable) or trap-shy (less so) depending on their past experience (Williams et al. 2002). Just as the past breeding experience and hatching location may affect colony choice, the past trapping experience may affect future detection. The sequence of captures and non-captures of a living Tern at a given colony reflects a combination of factors that include colony choice, current probability of detection, and past trapping experience.

What is the role of history in a Common Tern’s capture? Does an individual’s capture in a given colony depend on the history of captures during previous years? I ask this question by focusing on individuals that are known to be alive for a given period of time and treat their capture histories as two-state Markov chains. To understand the role of history, I ask what is the order of those chains.

A second question relates to the pattern of inter-colony exchange of individuals. It is not clear whether the non-philopatric birds observed in Great Gull Island are the result of short-term colony change, or whether they are caused by a more permanent re-establishment in a new colony. I will address this problem by comparing the transition
probabilities in the Markov chains representing the capture histories of immigrant and native birds breeding at Great Gull Island.

Markov chains have already been applied to the study of animal behavior sequences (Cane 1978). Data for such studies are usually collected in periods of observation on a time scale of minutes to hours. For example, Altmann (1965) categorized the stream of Rhesus Monkey social behavior as a series of discrete behavioral states (i.e. slaps ground, sniffs at, sucks digit, etc.). He modeled the sequence of states as a Markov chain and assessed its order by comparing the uncertainty associated with predictions of the current state based on the knowledge of one, two, and three previous states. In a similar example, Nelson (1964) studied sequences of courtship behaviors in the characid fish Corynopoma riisei and described their temporal pattern as a first-order Markov chain. Nelson found no significant second order effects.

Markov chains were also used as a tool for studying the importance of history in the dynamics of species composition in both plant and animal communities. Usher (1987) modeled plant succession as a Markov chain. He described the vegetation of sites with different succession ages and attributed time intervals to states, depending on the plant species that was dominant at each interval. After aggregating data from several sites, he found significant second-order effects. That is, in a discrete-time model of plant succession, Usher found that the state occupied at a given time step is influenced by the state occupied in the preceding step and by the state occupied two steps before. Tanner et al. (1996) used a similar approach to assess the impact of history on the dynamics of
species composition of a coral reef. They found changes through time in the probabilities of transition from state to state but they did not find significant second order effects.

Animal behavior and community dynamics are often conceived as continuous-time processes that are not easily translated in a series of discrete events. This results in a variety of criteria for: 1) defining a catalogue of states (Cane 1978); and 2) splitting continuous time into a series of discrete-time steps. The behavior of an animal can be subdivided into a variable number of states depending on how much detail the researcher wants to convey. The chosen level of detail may hide or reveal certain temporal patterns. Similarly, the state occupied by a plant community sample may depend on the researcher’s decision to classify states based on single-species dominance, multi-species dominance, or ordination techniques (Usher 1987). Once a catalogue of states is defined it may happen that some states last longer than others (Altmann 1965). When that is the case, there may be alternative ways of partitioning time for long lasting states. A fine partition will convert long lasting states into several transitions from a state to itself, thus changing the perception of temporal patterns. The applications of Markov chains to capture histories of breeding animals with seasonal reproduction, like the Common Tern, is free of these methodological problems. First, there is virtually no subjectivity in the definitions of ‘captured’ and ‘not captured’. Second, individuals are declared ‘captured’ or ‘not captured’ during a time step that is a discrete breeding season, bounded by periods with no breeding activity at all.

A capture history is a vector of ones and zeros indicating whether a bird was captured as an adult breeder or not, in a given colony, for a sequence of time steps. Every adult
breeder ever captured in a colony has its own individual capture history and each element of the history corresponds to one breeding year. Birds are captured with traps placed on top of chicks hatched in their nest. In this study, a ‘1’ means that the adult bird was present in the colony, it hatched at least one chick, and it was captured. A ‘0’ has three possible meanings: 1) the bird was alive and away from the colony; 2) it was alive and present but did not hatch any chicks; and 3) it was alive, present, and hatching chicks but was not captured. All captures took place in Great Gull Island between 1969 and 1997. Fieldwork and database management were conducted by a large team of researchers and volunteers led by Helen Hays and Joe DiCostanzo from the American Museum of Natural History.

If there were no trap responses and birds were to switch colonies randomly every year, the capture of one individual in a given colony in year $i$ should be independent of its capture or non-capture in year $i-1$. A more plausible situation is that in which birds are more likely to return to a colony if they nested there last year. This should result in a capture pattern in which the individual probability of being captured in year $i$ is higher when the bird was also captured in year $i-1$ than when the bird was not captured in year $i-1$. If the effect of capture in a given year is carried on for a longer period it may generate a stronger pattern, in which the higher the number of consecutive times a bird shows up in a colony, the more likely it is to return the next year. This would be equivalent to the probability of being captured in year $i$ being higher for birds that were captured in years $i-1$ and $i-2$, than for birds captured in $i-1$ but not captured in $i-2$. The latter scenario is plausible, provided that the total number of presences is kept within the limits of the birds’ life span. Similar time-dependent patterns may arise from trap response. One can
conceive more complex scenarios by blending different types of time-dependence regardless of their cause. For example, for a group of birds that were captured in year $i-1$ the probability of not being captured in year $i$ may be influenced by the presence in year $i-2$, whereas for a group of birds that were not captured in year $i-1$, the probability of being captured in $i$ may be independent of what happened in $i-2$. Hestbeck et al. (1991) report on a case in which presence of wintering migrant birds in year $i$ was dependent on presence/absence in year $i-2$.

All the examples above make some statement about how the presence-absence of an adult breeder in a colony is or is not influenced by its own presence-absence in the same colony $n$ years in the past. The objective of the present analysis is to understand which pattern of year-to-year influence is more compatible with what we know about the capture histories of both immigrant and native Common Terns at Great Gull Island. The order of a Markov chain of captures reveals how far back into the past the memory of the system goes. In other words, if presence-absence now is influenced by what happened in the past, how far back in the past can we find such influence?

**METHODS**

Great Gull Island is located on the eastern entrance to Long Island Sound and hosts one of the largest colonies of Common Terns in North America. Terns are known to have bred on Great Gull as far back as the 19th century (Heilburn 1970). By 1897, a fort was built on the island, marking the beginning of a drastic reduction in tern numbers. By the mid-1940s the colony was completely abandoned. In 1949, the fort was deactivated and
the American Museum of Natural History and the Linnaean Society of New York took charge of the island. The first breeding terns reappeared in 1955, and the colony grew up to approximately 2,000 nests in 1969. Between 1969 and 1980, the colony size varied between 1,600 and 3,000 nests. In 1981 it entered a period of growth that peaked above 8,900 nests in 1991. From 1992 to the present, the colony size varied between 5,300 and 10,000 nests. The availability of breeding ground has increased due to mechanical clearing of vegetation since 1980, and the introduction of the plant-eating meadow vole, *Microtus pennsylvanicus* in 1981 (Hays 1984).

The sign of year-to-year changes in the total number of immigrant breeding adults matches the sign of changes in colony size; however, the proportion of breeding adults that are immigrants does not remain constant throughout the study. If one looks only at birds whose hatching location is known, the proportion of captured Great Gull Island breeders that are immigrant varies between one and 24 percent, depending on the year. Between 1972 and 1980 the percentage remained under 5%. After 1981 the proportion of immigrants started to increase, peaking at approximately 24% in 1985 and decreasing again to 17% in 1989. From 1990 to 1997, the percentage of immigrants remained between 14% and 17%. The proportion of immigrants in years prior to 1972 is unknown due to the lack of adult breeders that had been first captured as nestlings. These values must be interpreted with caution since they are influenced by banding effort outside Great Gull Island, which is not known to this study.
How were the data generated?

I drew the capture information from yearly lists of the band numbers of Common Terns trapped as breeders on Great Gull Island. Such lists are compiled during the field season, as marked birds are recaptured and unmarked birds are assigned new band numbers. Following each season, the current year’s data are matched with similar data from previous years. Band numbers corresponding to birds originally marked in places other than Great Gull Island are checked against U.S. Fish & Wildlife Service records to obtain the location and age of first capture. The end result is a second list of band numbers containing a more detailed description of each individual’s passage through the colony in a given year. Such description is based on a number of variables including the year, age, and location of the first capture of each individual. The age information tells whether a bird was first captured as an adult breeder, or as a hatchling. From here on, we will designate as “known-age” any bird that was first captured as a hatchling. Location at first capture can be at Great Gull Island or at an unspecified location off the island. This study is based exclusively on capture histories of known-age birds captured as breeders on Great Gull Island and hatched either there or elsewhere. I generated capture histories with a Matlab program that reads through the yearly band number lists and writes the repeated incidences of the same band under the corresponding row and column of a capture history matrix. Such matrix has one row per individual band number, and one column per year.

The variation of capture effort during the study is a potential source of sampling error. Irregularities in the capture effort may produce capture history patterns that are not a result of the birds’ behavior. The rate of success in capturing both members of each
breeding pair was used as a measure of capture effort per year. This measure consists of the number of pairs with both members captured, divided by the number of pairs with at least one member captured. The level of effort was relatively constant during the period 1979-94, in contrast to lower and more variable effort before 1979 and after 1994. The slope of the least squares line fitted to the logit transformed capture effort data for 1979-94 ($b = 0.054$) is less than one third of the slope for the period 1969-78 ($b = 0.186$). The adult capture information used in this study refers exclusively to the years 1979-94.

**Assessing the Order of a Markov Chain**

The methodology for assessing the order of a Markov chain follows three steps: 1) Sampling sets of capture histories from the capture history matrix; 2) Counting transition frequencies in each capture history set; and 3) Testing for independence between current and past states in the capture history Markov chains.

Each set of capture histories has a limited number of year-to-year steps. At a given step, each capture history can be assigned to a unique transition type depending on the currently occupied state and the state(s) occupied from 1 to $n$ years in the past. The integer $n = 1, 2, 3 \ldots$, defines the order of the transition. Transition frequencies will depend on the number of capture histories assigned to each type. A *step* in time is identified by the letter $i$, which always corresponds to the current year. A *transition type* is identified by a vector of ones and zeros. The last element of the vector indicates the state in the current year, while the previous $n$ elements indicate the past states. The symbol ‘+’ designates any state. For example, the vector (+,0,1) would designate a type
of second-order transition including all birds that were absent in year $i-1$ and present in year $i$ regardless of their state in year $i-2$.

Each step in a capture history set can be represented by a contingency table with rows identified by past states and columns identified by current states. A chi-square test indicates whether some transitions from past states to current states are more likely than others. If the examination of a sequence of steps of order $n$ leads to rejecting the null hypothesis of independence between past and current states, it follows that the capture history subset can be represented by a Markov chain of order $n$ or higher. The procedure continues by testing for independence with transitions of order $n+1$. If eventually it is not possible to reject the null hypothesis of independence between past and current states, then the order of the chain has been found, subject to the limited accuracy attainable with a finite amount of data. The following paragraphs provide finer details of the method.

To achieve comparability between different steps in a given set of capture histories, it is important that all the individuals represented in the set be alive throughout all steps. This constrains the analysis to sets of birds that hatched in the same season and survived up to a common minimum number of years. By conditioning on individuals that are alive throughout the whole sampling period we exclude the effects of survival probability. The temporal pattern in each set of capture histories depends exclusively on the probability of capturing breeding individuals at Great Gull Island. All the individuals included in the analysis were first banded as hatchlings; therefore, we can tell the age of every bird at any time step in a capture history set. We picked seven years as the common minimum life span for the birds included in each set. This value is a compromise between the
sample size and the number of transitions. Higher values would decrease the sample size due to fewer and fewer birds surviving up to the required age, while lower values would reduce the number of steps that can be examined in each set and limit the relevance of the data. A preliminary run of the method with ten years as the common minimum life span produced a pattern of transition probabilities very similar to the one reported here. The choice of a seven-year span increases the number of birds in the analysis without considerable loss of temporal information. Under this selection criterion, every capture history set will provide information on 7-\(n\) steps of order \(n\). In some steps, transitions will be concentrated in one or a few cells of the contingency table. When this is the case, chi-square tests are inapplicable and will not be performed.

Table 2.1 shows a sample of transition frequencies for orders 1, 2, and 3 in the capture history set of the 1984 cohort of native birds. The current year is \(i = 1991\). Cell (2,1) in table 2.1(a) indicates that 120 individuals were not captured in 1990 but were captured in 1991. Similarly, cell (3,2) in table 2.1(c) states that eleven individuals from this group were captured in 1988, not captured in 1989, captured in 1990, and finally not captured in 1991. For every transition of order \(n\), there are \(2^n\) possible past states. For each past state, there are two possible current states: 0 and 1.

The operational question, formulated with a chi-square test, is the following: given a current state, are capture histories more likely to have occupied a certain state in the past? For transitions of order 1, this amounts to testing the null hypothesis:

\[
H_0: \quad \frac{N_{11}}{N_{1+}} = \frac{N_{01}}{N_{0+}}
\]
Table 2.1. Sections a, b, and c, show transition counts in 1991 for orders 1, 2, and 3. The data come from native birds of the 1984 cohort known to survive up to seven or more years. The columns indicate the state in the current year, $i=1991$. The rows indicate the states in the past 1, 2, and 3 years for orders 1, 2, and 3 respectively.

<table>
<thead>
<tr>
<th></th>
<th>1st order (a)</th>
<th>2nd order (b)</th>
<th>3rd order (c)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>current</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>past</td>
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<tr>
<td>1</td>
<td>781</td>
<td>58</td>
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<tr>
<td>0</td>
<td>120</td>
<td>44</td>
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The subscripts ‘11’ and ‘01’ indicate first-order transitions types, namely from captured in the past to captured now, and not captured in the past to captured now. $N$ stands for the number of individual capture histories with the type of transition given in the subscript. The ‘+’ signs indicate any state; therefore, $N_{1+} = N_{101} + N_{111}$.

The null hypotheses for the second-order tests are:

$H_0^1: N_{111}/N_{11+} = N_{011}/N_{01+}$

$H_0^2: N_{101}/N_{10+} = N_{001}/N_{00+}$

Third-order tests evaluate the hypotheses:
$H_0^1$: $N_{1111}/N_{111+} = N_{0111}/N_{011+}$

$H_0^2$: $N_{1011}/N_{101+} = N_{0011}/N_{001+}$

$H_0^3$: $N_{1101}/N_{110+} = N_{0101}/N_{010+}$

$H_0^4$: $N_{1001}/N_{100+} = N_{0001}/N_{000+}$

For first-order chains, with $n = 1$, we calculated expected values as the product of the row and column totals divided by the grand total. For order $n > 1$ the tests are based on sub-tables of two rows each, so that the expected values are based on the row and column sums of the sub-table corresponding to each null hypothesis. The number of degrees of freedom is 1 for each first-order test or for any sub-table test when $n > 1$. The chi-square value and degrees of freedom for a higher-order test ($n > 1$) are the sum of chi-square values and degrees of freedom, respectively, for the corresponding sub-tables. Whenever there is at least one cell in a sub-table or first order table with an expected value of $N < 5$ the distributional assumptions of the chi-square test may not apply and it is sensible not to perform the test. In such cases we cannot sum the sub-table chi-square values to obtain the overall chi-square; however it may still be possible to draw conclusions from other sub-tables in the same higher-order test. For example, in table 2.1c it is not possible to test the second and third sub-tables (rows 3 to 6) and hence there is no overall chi-square value; nevertheless, it can be observed that the first and last sub-tables (rows 1-2 and 7-8) do not deviate significantly from the expectations.

The significance level of each test was evaluated by considering, simultaneously, all tests of similar transitions in all cohorts and years. To do this, I performed a sequential
Bonferroni adjustment (Rice 1989). Such procedure addresses the composite null
hypotheses that in all transitions of a certain type the current state is independent of the past state. The adjustment technique takes into account that given a true composite null hypothesis the probability of encountering at least one component transition test that shows a significant deviation from independence increases with an increasing number of component tests. I performed adjustments over nine groups of transitions tests separately for native and for immigrant birds: three groups of tests assess overall independence at the first, second, and third-order transitions; two groups assess independence at the level of the sub-tables in the second-order transition; the last four groups of tests are directed at the four types of sub-tables of the third-order transitions. Each group has a different number of component tests affecting the adjustment. In all the cases where an adjusted $p$ value was below 0.05, I rejected the composite null hypothesis and concluded that at least some of the transitions do not show independence between current and past states.

**Estimating Transition Probabilities**

The chi-square test results are complemented by the calculation of transition probabilities. Whenever a test shows significant deviation from independence, the transition probability indicates the direction of such deviation. The meaning of the transition probabilities is easily understood from examination of table 2.1. We calculated first-order transition probabilities at each time step by dividing the number of observations in a cell by the row total (Bishop et al. 1975):

\[
P_{11} = \frac{N_{11}}{N_{1+}}
\]

\[
P_{10} = \frac{N_{10}}{N_{1+}}
\]
\[ P_{01} = \frac{N_{01}}{N_{0+}} \]
\[ P_{00} = \frac{N_{00}}{N_{0+}} \]

\( P_{10} \), for example, is the probability that a bird is not captured in a certain year given that it was captured the year before. Transition probabilities for higher-order transitions are calculated in a similar way. This information is especially relevant for comparing immigrant birds with birds that hatched on Great Gull Island.

**RESULTS**

The procedure explained above requires a large sample size. Table 2.2 shows the number of individuals from each cohort and hatching location included in the analysis. The label ‘\( N (7+) \)’ indicates birds who showed up as breeders on Great Gull Island seven or more years after hatching. Natives outnumber immigrants, and the temporal variation in sample size is smaller for immigrant than for native birds. Beneath each \( N (7+) \) value the ‘%’ value indicates what proportion of the cohort total captured individuals is represented in the sample; that is, the number of birds that hatched in the given year and location and were captured as breeders on Great Gull Island at least once in their lifetime. These percentages decline towards the later years for both immigrant and native birds. Such decline may result from higher capture effort increasing the number of birds that show up only once early in their lifetime. In the first years of table 2.2, the percentage of birds classified as 7+ is clearly higher for immigrants than for natives; towards the end of the period, they become more similar.
Table 2.2. Sample sizes for each cohort of birds included in the data set. Natives are birds that were first banded as hatchlings in Great Gull Island. Immigrants hatched elsewhere. The sample sizes are shown in the rows labeled N (7+): number of individuals in a given cohort with a life span greater than or equal to 7 years. The rows labeled % indicate what percentage of all birds hatched in a given year and captured at least once as breeders in Great Gull Island had a life span of 7 or more years.

<table>
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<tr>
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<th>76</th>
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<th>78</th>
<th>79</th>
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<tr>
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<tr>
<td>N (7+)</td>
<td>258</td>
<td>165</td>
<td>188</td>
<td>159</td>
<td>258</td>
<td>574</td>
<td>322</td>
<td>612</td>
<td>1003</td>
<td>334</td>
<td>807</td>
<td>1162</td>
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<td>71</td>
<td>71</td>
<td>70</td>
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<td>64</td>
<td>60</td>
<td>64</td>
<td>52</td>
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<tr>
<td>Immigrants</td>
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<tr>
<td>N (7+)</td>
<td>75</td>
<td>47</td>
<td>135</td>
<td>163</td>
<td>130</td>
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</table>

In Great Gull Island, known-age Common Terns are first captured as adult breeders at an average age of 3.7 (±1.6 s.d.) years (N=23,900). Figure 2.1 shows the average age at first capture for the cohorts analyzed in this study. On average, earlier cohorts have an older age of first capture. This is partially due to many Common Terns living longer than the duration of the study; individuals hatched earlier have a higher chance of being first captured late than individuals hatched towards the end of the study – who may never be captured at all. The average age at first capture for all known age birds captured at least once up to their seventh year (regardless of the time of last capture) shows a similar, but less steep, trend. The average age at first capture is higher for immigrants than for natives in all cohorts. Assuming a null hypothesis of equal averages between the two hatching
locations, there would be a $(0.5)^{12}$ chance of finding the pattern shown in figure 2.1; I reject the null hypothesis with $P<0.001$.

The observed age at first capture results in a predominance of non-captures during the first 2-3 years after hatching. Such predominance seriously limits the possibility of hypothesis testing on early first-order transitions. Similarly, cohorts with small sample sizes have very few non-captures during the last years. This leads to a scarcity of expected $(0,0)$ transitions, again making it sensible not to perform the tests.

**Fig. 2.1.** Average age at first capture as adult breeder for native (white) and immigrant (shaded) known age birds. The error bars extend to one standard deviation above the average. Total sample size is 12,031 birds. The number of birds accounting for each bar range from 47 immigrants on the 77 cohort, to 2,286 natives on the 87 cohort.
Table 2.3a shows the chi-square test results for the first-order transitions of native birds. Only thirteen of 57 first-order tests do not show significant deviation from independence at the table level. Of the remaining 44 significant cases, nineteen have a Bonferroni adjusted \( p < 10^{-4} \). I therefore reject the composite null hypothesis that the state in year \( i \) is independent of the state in year \( i-1 \) for all transitions. In most transitions, the probability of being present in year \( i \) does depend on whether the bird was present or absent in year \( i-1 \). In the cohort of 1979, exceptionally, no transition shows a significant deviation from independence. Note, however, that four of five tests for that cohort have unadjusted \( p < 0.05 \). Also, 1979 has the cohort with the smallest sample size of all.

Table 2.3. Chi-square test results for first- (a), second- (b), and third-order transitions (c) of native birds. Column labels indicate cohorts. Row labels indicate years after hatching and (when appropriate) past states. To obtain the current year of each transition sum the corresponding numerical row and column labels. For second- and third-order transitions rows are grouped, respectively, in sets of three and five. The significance level for the whole transition is in bold face at the first row of each set. The remaining rows show significance levels for the sub-tables with the past states indicated by the row labels. Asterisks denote Bonferroni adjusted significance at the level of the whole table: \( * = p < 0.05 \); \( ** = p < 0.01 \); \( *** = p < 0.001 \); \( **** = p < 0.0001 \). When the deviation from independence is not significant, the table shows the component test \( p \)-value without Bonferroni adjustment. Blank spaces indicate transitions with insufficient data. The cells enclosed in boxes correspond to the examples in table 2.1 (continued next page).
<table>
<thead>
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<td><strong>b) 2nd</strong></td>
<td>76 77 78 79 80 81 82 83 84 85 86 87</td>
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<td>c) 3rd</td>
<td>76 77 78 79 80 81 82 83 84 85 86 87</td>
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<th>76 77 78 79 80 81 82 83 84 85 86 87</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>++</td>
</tr>
<tr>
<td>7</td>
<td>++</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>i-2,i-1</th>
<th>76 77 78 79 80 81 82 83 84 85 86 87</th>
</tr>
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<tbody>
<tr>
<td>7</td>
<td>++</td>
</tr>
</tbody>
</table>
Second-order results show the inverse pattern; table 2.3b shows only a few transitions with significant table-wide deviation from independence. There were 36 cases where both sub-tables of a second-order transition could be tested. Among these, only ten showed a significant aggregate deviation from independence ($p < 0.05$). The sub-table results show that all such cases were matched by a significant table-wide deviation in the transitions of type $(+,0,+)$.

Conversely, there was not a single case of adjusted significant deviation in a total of 39 tested transitions of the type $(+,1,+)$—there is no evidence to reject the composite null hypotheses of independence for these transitions. When a bird was captured in $i-1$, its probability of capture in $i$ was not dependent on whether it was captured or not in $i-2$. When a bird was missed in $i-1$, in some cases, its probability of capture in $i$ did depend on its state in $i-2$. The latter observation leads to rejection of the composite null for the $(+,0,+)$ transitions.

There are only three third-order transitions with a large enough number of native bird captures to test deviations simultaneously in the four sub-tables. In all such cases (table 2.3c), the summed chi-square value is low enough that one can never reject the composite null hypothesis. Of the 44 sub-table tests, only three have adjusted $p$-values that show significant deviation from independence. I perform the adjustments separately for each of the four types of sub-tables (see table 2.1). If the component tests are judged one at a time, with the non-adjusted $p$ values, there are only six cases with significant deviation ($p < 0.05$). There is not enough evidence to reject the composite null hypothesis of independence in the third-order transitions.
Table 2.4. Chi-square test results for first- (a) and second-order transitions (b) of immigrant birds; structure equivalent to table 2.3.

<table>
<thead>
<tr>
<th>Order</th>
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<th>81</th>
<th>82</th>
<th>83</th>
<th>84</th>
<th>85</th>
<th>86</th>
<th>87</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) 1st</td>
<td></td>
<td></td>
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<td>0.051 **</td>
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<td>4</td>
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<tbody>
<tr>
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<td></td>
<td></td>
<td>0.724 ****</td>
</tr>
</tbody>
</table>

Despite the relative scarcity of data, immigrant and native birds show similar patterns. Only four of 47 first-order immigrant transitions fail to deviate significantly from independence at the table level (table 2.4a). Among the 43 significant deviations, 33 have an adjusted $p<10^{-4}$. I reject the composite null hypothesis of independence for all first-order transitions.

I also reject the immigrant-bird composite null of independence for second-order transitions (table 2.4b). Four of five sum chi-square values are high enough to show adjusted significance with $p<0.05$. Examination of sub-tables leads to the same
conclusion as in native birds: all deviations are due to transitions of the type (+,0,+).
There is not a single case of table-wide significant deviation involving (+,1,+) transitions.

The number of immigrant captures is not high enough for testing all sub-tables in any third-order transition. I could only test eight third-order sub-tables: five were of type (+,1,1,+); two were (+,0,0,+); and one was a (+,0,1,+) transition. I found only one case of significant table-wide deviation from independence, a transition of type (+,0,0,+). The other seven tests showed non-significant deviation ($P > 0.05$), even prior to Bonferroni adjustment. I cannot reject the composite null hypothesis of independence. The five tests of (+,1,1,+) transitions suggest that the current state and the state in year $i-3$ are independent when the bird is present in both years $i-2$ and $i-1$.

Both immigrant and native birds show significant deviations from independence in all first-order transitions and in one type of second-order transition. The current state of a bird always depends on the state it occupied last year and, in some cases, it also depends on the state occupied two years ago. The transition probabilities represented in figures 2-4 illustrate a more precise meaning of this dependence. I test the null hypothesis of no difference between transition probabilities between groups using a non-parametric test for comparing two means (Mann-Whitney U). Figures 2.2 and 2.3 illustrate only those transitions with enough data for chi-square testing.

Any bird is more likely to be captured in a given year if it was captured the year before. This is true for both native ($p \not= 0$; fig. 2.2a) and immigrant birds ($p \not= 0$; fig. 2.2b). The probability of a (1,1) transition for immigrants and for natives is indistinguishable ($p=0.237$; filled circles, fig. 2.2); however, among those birds not captured in year $i-1$,
natives have a higher probability of being captured in year \(i\) (\(p=10^{-13}\); open circles, fig. 2.2).

Figure 2.3a, b illustrates the result that in second-order transitions of type (+,1,+) the current state is independent of the state in year \(i-2\). If a bird is captured in year \(i-1\), its probability of being captured in year \(i\) is not affected by the state occupied in \(i-2\). Here, the Mann-Whitney test seems to contradict the previous results by suggesting that birds captured in \(i-2\) are indeed more likely to be recaptured, both among native birds (\(p=0.0030\); fig. 2.3a) and among immigrants (\(p=0.0059\); fig. 2.3b). The appearance of figure 2.3 and the scarcity of data for immigrants should inspire caution about the latter result. If a difference exists it is several orders of magnitude smaller than that found for
first-order transitions. The probability of a transition of the type (1,1,1) is not
distinguishable when native and immigrant birds are compared ($p=0.0553$; filled circles,
fig. 2.3a, b). Among those birds missed in $i$-2 and captured in $i$-1, immigrants seem to be
less likely to return in $i$ than native birds ($p=0.0011$; open circles, fig. 2.3a,b). Again, this

Fig. 2.3. Second-order transition probabilities for native (a,c) and immigrant (b,d) birds.
Pannels a and b show second-order transition probabilities of type (+,1,1) with filled circles representing $P(1,1,1)$, and open circles representing $P(0,1,1)$. Pannels c and d show transition probabilities of type (+,0,1) with filled circles standing for $P(1,0,1)$ and empty circles for $P(0,0,1)$.
result is based on only eight immigrant transitions and the magnitude of the difference is hardly comparable to that in first-order transitions.

The differences among transition probabilities of type (+,0,+) are clearer. Native Common Terns that are not captured in \( i-1 \) are more likely to be captured in year \( i \) if they were captured in \( i-2 \) (\( p=10^{-11} \); fig. 2.3c); immigrant birds show a similar pattern (\( p=10^{-5} \); fig. 2.3d). Immigrants that were captured in \( i-2 \) and not captured in \( i-1 \) are as likely to return in year \( i \) as natives with the same past states (\( p=0.4283 \); filled circles, fig. 2.3c, d). In contrast, among birds not captured for two consecutive years (\( i-2, i-1 \)), immigrants are the least likely to be captured in the third year (\( p=10^{-6} \); open circles, fig. 2.3c,d).

**DISCUSSION**

The data analyzed here include only a proportion of the individuals in the original capture lists. The 7,373 known-age birds represent 21% of all adult breeders captured on Great Gull Island from 1979 to 1994 (of known age, unknown age, immigrant, or native). The same sample (7,373) comprises 41% of the known-age breeders captured during the stable-effort period (1979-94), and 61% of the known-age birds captured in that period and belonging to the cohorts included in this study (1976-87). Discrimination between hatching locations reveals that immigrant birds are slightly better represented than natives: the current analysis includes 66 % of 3,157 immigrants hatched in 1976-87 and captured in 1979-94 (1,543 birds); the equivalent percentage of native birds is 60%. I consider these individuals to represent the long-term capture pattern of the population.
A second concern is that quality, rather than quantity, of data may lead to biased results. Many birds are left out of the analysis because their last capture occurs too early (before age seven). Death seems the most plausible explanation for early disappearance, but other explanations – such as permanent emigration, permanent trap avoidance, or permanent breeding failure – may be equally important. Could memory play different roles in the analyzed birds and in those birds that remain alive but are consistently not captured? Take the colony choice scenario, for example: a bird breeding successfully in another colony might become increasingly likely to return there after a string of successful breeding seasons. This scenario could result in an undetectable long-term memory effect. Nonetheless, if such effect took place it should also apply to birds breeding successfully in Great Gull Island; in which case it would be detectable by the current approach. Likewise, in a trap-response scenario, some birds could get increasingly better at avoiding traps as they accumulate trap-avoidance experience throughout the years – they could also have one bad trapping experience and consistently avoid being trapped until the end of their lives. This possibility would be undetectable here. Capture failure due to permanent trap-shyness is a possibility (Nisbet 1978); indeed, the inclusion of such once-seen-forever-lost birds in the data set would predictably result in more higher-order deviations. I argue that those birds fall outside the scope of the study. The central question is about the role of memory in the capture pattern of birds that are known to be alive; therefore, I feel justified in excluding those individuals that are almost never seen (and not known to be alive) to focus on the large proportion that regularly shows up in the records.
Reviewers of previous versions of this manuscript recommended the use of a capture-recapture method. Arguably, by explicitly distinguishing probability of capture and probability of survival, such approach could operate on the whole data set (without excluding any birds). Some capture-recapture models account for history-dependent capture probabilities; i.e. the probability of being captured in a given occasion depends on having or not having been captured in the past (Sandland and Kirkwood 1981, Pradel 1993). These models do not try to distinguish between first-order and higher order dependence in capture probability; rather, they aim at estimating survival parameters under the unavoidable constraint of fallible detection. The question I pursue here, however, is one of assessing patterns of detection under the constraint of uncertain survival. The latter constraint, it turns out, is quite avoidable – given the large number of individuals that are repeatedly captured until late in their lifetime. This is why I simplify by conditioning on individuals known to be alive. Capture-recapture modeling is the fundamental tool for analyzing animal trapping data; nonetheless, in the particular context of this paper, the separate estimation of capture and survival probability would add an unnecessary level of complexity.

First-order effects dominate the pattern of inter-annual dependence. The only significant higher-order effect is found in some transitions of type (+,0,+). Both immigrant and native birds that are absent in year $i-1$ are more likely to be captured in year $i$ if they were also captured in year $i-2$. The length of a string of consecutive captures does not change the probability of a subsequent recapture. This observation rests on the lack of significant departure from independence in the second- and third-order sub-tables of type (+,1,+), and (+,1,1,+) respectively: there were no differences of probability between transitions
A second-order Markov chain is sufficient to explain the sequence of captures and non-captures of Great Gull Island Common Terns, but the second-order effects are scarce and restricted to one type of transition.

In the context of behavior sequences, higher order effects provide a measure of an animal’s memory (Altmann 1965). One cannot be sure of the process operating behind the observed pattern – it must be a combination of different elements that condition the detection of a bird in Great Gull Island. These include inter-colony migration, breeding failure, and any type of trap response. Memory could conceivably affect any of the elements, but we do not know which. What we do know is that the resulting capture pattern does not give evidence of long-term memory.

An in-depth study of colony choice requires a mark-recapture approach over data from different colonies (Spendelow et al. 1995). The current results, however, merit a speculative comment in the context of colony choice. A string of past captures does not increase the probability of a subsequent capture any more than one past capture. This observation contrasts with Austin’s (1949) conclusion that ‘attachment to a site increases with each additional occupancy’. If such increase is taking place, it must be masked by the effects of breeding failure and trap response. Figure 2.2 does suggest that the strength of the first-order effect may increase, as individuals grow older. It is possible that given a capture in year \( i-1 \), the probability of capture in year \( i \) is higher for older than for younger birds; however, our data do not support the idea that the probability of capture in year \( i \) increases with each additional past capture.
Any bird’s probability of being captured in a given year is higher when it was captured the year before. This is not surprising when applied to native birds – and agrees with the prior observation that once having nested, terns tend to return from year to year to the colony of previous occupancy (Austin 1949). What is not so obvious is that immigrant birds should behave in the same way with respect to Great Gull Island. The probability of a (1,1) transition for immigrants and natives was indistinguishable. Since the age at first capture is older for immigrant than for native birds, I believe that most immigrants have bred elsewhere before appearing in Great Gull Island. Why do they keep returning to Great Gull Island?

Most inter-colony migration events observed by Austin consisted of the first breeding attempts of young adults, or of birds that, having failed one breeding attempt in the natal colony, made a second attempt at a different site during the same season (Austin 1949). Apparently, we have observed a different phenomenon. Immigrants are recaptured in Great Gull Island with the same probability as natives. This suggests that we are in the presence of a relocation of birds, rather than a short-term reversible inter-colony migration. Such relocation may have been triggered by the increased availability of nesting space on Great Gull Island after 1980 and by habitat destruction in coastal colonies (Burger and Gochfeld 1991).
Rates of species loss from Amazonian forest fragments

Humid tropical forests, harboring at least half of all species (Myers 1992, Pimm 2001), are disappearing rapidly due to fire, selective logging, and clear-cutting (Nepstad et al. 1999). Only about half their pre-industrial area remains (Myers 1992, Pimm 2001), divided into fragments that are often very small (Gascon et al. 2000, Peres 2001). Twenty years ago, Tom Lovejoy engineered an experiment to follow species numbers before and after fragment isolations (Bierregaard et al. 2001). When this experiment began, there was controversy over whether the equilibrium theory of island biogeography would extend to forest fragments. The theory explained the widespread pattern that islands surrounded by water hold fewer species the smaller they are and the more distant they are from mainland sources of immigrants (Diamond 1972, Terborgh 1974). That forest
fragments – habitat “islands” surrounded by a “sea” of cattle pastures (Lovejoy et al. 1986) – also hold few species is no longer controversial (Willis 1979, Robbins et al. 1989, Rosenzweig 1995), but another question is pressing (Daily 2001) and unanswered: how fast do fragments lose their species?

The Brazilian Government’s Medida Provisória MP2.166-67 (a presidential decree pending approval into law) requires that clearing of private properties in the Amazon leave 80% (originally 50%) of the forest intact. A collaborative effort between Brazil and the US, the Biological Dynamics of Forest Fragments Project (BDFFP) (Debinski and Holt 2000, Bierregaard et al. 2001) ensured that clearing for cattle ranching in the Manaus free-trade zone would leave predetermined forest “islands” in a “sea” of pasture. Between 1980 and 1990 the project established 11 fragments 80 km north of Manaus, two of approximately 100 ha, four of 10 ha, and five of 1 ha (table 3.1). At isolation time, fragments were separated from continuous forest by at least 100 meters of cleared land. Here, we analyze the understory mist-net captures of birds up to 13 years post-isolation. We use data from the ten fragments that were isolated before 1990.

Fragmentation in the central Amazon takes place against a background of very extensive, continuous forest. Any cleared surface larger than a forest gap is a radically contrasting landscape feature likely to limit the movement of animals (Develey and Stouffer 2001). This often results in well-isolated forest fragments, where recolonization is too slow to compensate for local extinction on a management time scale. The BDFFP sites result from such a drastic process of isolation, making them good sources of information on local species loss.
Table 3.1. Fragment characterization and \( t_{50} \) values. The actual fragment areas in hectares, as measured from an aerial image, differ slightly from the target areas. ‘\( S_0 \)’ is the initial number of species.

<table>
<thead>
<tr>
<th>Fragment/Location</th>
<th>Area (ha)</th>
<th>Start year</th>
<th>Isolation year</th>
<th>( S_0 )</th>
<th>( t_{50} ) min.</th>
<th>uniform</th>
<th>( t_{50}=0.1 ) runs-test</th>
<th>jackknife all</th>
<th>jackknife initial</th>
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<td>2.8</td>
<td>1979</td>
<td>1980</td>
<td>90</td>
<td>3</td>
<td>3.3±0.9</td>
<td>5.0±1.4</td>
<td>5</td>
<td>4.4</td>
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<tr>
<td>1112/Cidade</td>
<td>1.6</td>
<td>1981</td>
<td>1983</td>
<td>73</td>
<td>2</td>
<td>3.0±0.8</td>
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<td>15.7</td>
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<tr>
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<td>1980</td>
<td>1984</td>
<td>86</td>
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<td>2.5±1.0</td>
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<td>1984</td>
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<td>2.4±0.9</td>
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<td>7.3</td>
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<td>1983</td>
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<td>5</td>
<td>5.8±0.8</td>
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<td>1980</td>
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<td>1983</td>
<td>101</td>
<td>7</td>
<td>8.4±1.3</td>
<td>10.4±1.4</td>
<td>&gt;9</td>
<td>5.3</td>
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<td>1980</td>
<td>1984</td>
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<td>11.0</td>
<td>1982</td>
<td>1983</td>
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<td>1990</td>
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<td>1982</td>
<td>1983</td>
<td>111</td>
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<td>11.7±1.4</td>
<td>12.2±1.4</td>
<td>&gt;10</td>
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</tr>
</tbody>
</table>

THE DATA

Sampling lasted from 1979 to 1993. Birds were captured in mist-nets extending for 100 m in 1ha fragments and 200 m in 10 and 100ha fragments. Nets touched the ground and were placed in the interior of the fragments in approximately the same locations throughout the duration of the study. 1,087 mist-netting days, distributed among the sites, produced >21,600 captures. Each newly captured bird was given an individually numbered band. Our analysis ignores all the same-day recaptures but does not discriminate between first captures and recaptures on subsequent days. The data include captures of each species in each site from 1979 to 1992, containing information on 164 bird species: mostly flycatchers, antbirds, tanagers, woodcreepers and foliage-gleaners.
Over one half (95) of the species belongs to one of the four families: *Tyrannidae* (32), *Thamnophilidae* (21), *Furnariidae* (22), and *Emberizidae* (20). The remaining species are distributed among 24 different families. Our sample includes 40% of the regional bird species list (Cohn-Haft et al. 1997). Species from open fields, inundated areas, and the high canopy are the most consistent absences. The families *Icteridae*, *Hirundinidae*, *Apodidae*, *Psittacidae*, and *Cracidae* are regionally well represented but do not appear in our data set. We also have no data on any *Charadriiformes* or *Ciconiformes*, and only a few captures of *Falconiformes*.

For a given site $i$, we list species $j = 1, 2, \ldots$ in rows, time intervals $t = 0, 1, \ldots$ in columns, and fill in each cell with the corresponding captures $N_{ijt}$. Each row in the data matrix is the time series vector $N_{ij}$ of the number of captures of that species over time. Time is divided into years or into netting days, depending on the method. Because the number of netting days varies from year to year, we complement each site’s year-based matrix with a vector $E_t$, containing elements $E_{it}$ that record the number of net hours or “effort” in each year $t$. Netting days within sites represent approximately the same effort; therefore, when dividing time into days, we do not need to measure effort. For simplicity, we will drop site and species subscripts except where necessary. Unless otherwise specified, the equations that follow refer to the data for one species at one site.

**THE PROBLEM OF MISSING SPECIES**

The number of species and individuals recorded in each fragment (especially prior to fragmentation) measures not only those occurring exclusively therein, but also those
using the area for varying amounts of time. Some individuals are residents, while others are transients. In determining species loss we must interpret the changing captures of each species both before, and after, a fragment’s isolation. Some variation may stem from unequal trapping effort, but we know the effort, so we can correct for it. In addition, if we assume perfectly isolated fragments, an absence followed by a presence is taken to mean the species was present but not detected. But how do we interpret the absences that follow the final capture? Is the species truly missing, or are we failing to detect it? If fragment isolation is not perfect, some species may disappear from a fragment but return later. Should all temporary absences be regarded as detection failures? First, we ask what would be the minimum number of species present through time if isolation were perfect and there was no possibility of recolonization. Then, we maintain the assumption of perfect isolation and use two methods for estimating the number of species through time. The first is a Bayesian approach developed by Gareth Russell specifically for this study. It has the special feature of predicting the number of species in each fragment for a period of time after the end of the sampling period. I employ several variants of this method and compare the results. The second method is a variant of a runs-test, obtained from the literature. Finally, knowing there was secondary growth of varying extent around fragments (Lucas et al. 2002), I withdraw the assumption of perfect isolation and explore the consequences with a jackknife estimation of the number of species in each year. After using these different methods involving a variety of assumptions, I ask whether this variety alters the basic conclusions.
INFERRING DECAYS UNDER PERFECT ISOLATION

The minimum

Many species in our dataset show signs of having gone extinct. For example, in fragment 1202, we caught 7, 6, 4, 3, 5, 2, 1, 0, 0, 0, 0, 0, and 0 *Formicarius colma* from 1980 to 1992. This pattern of consistent presence followed by consistent absence suggests the bird was extinct by 1987, the year it first went missing. *Method 1* assumes that all species go extinct immediately after the last sighting. This assumption provides an absolute lower bound on times to extinction and hence a baseline against which to compare other methods.

*Method 1* makes the extreme assumption that species are extinct immediately following their final capture and never return. The opposite extreme would be to assume that no species ever really disappears from any fragment. In this case, the apparent absence of many species after fragmentation might be explained by individuals becoming extremely trap-shy once their habitat is fragmented, or as their numbers decline. This seems very unlikely. Most often, nets were opened at a given site fewer than 7 days per year and never opened for two consecutive days in the same site. There were always at least two weeks between consecutive nettings at one site — often the interval was one or two months. During 1990, netting was interrupted for seven months. There was no increase in captures per unit effort during the subsequent period.

Instead, abundant evidence shows that small fragments retain few species (Andrén 1994, Stratford and Stouffer 1999). Between the extremes of immediate extinction and eternal
hiding, there is a plethora of models of how long a species persists after its last observation. They invoke different assumptions about detection and isolation. The following two methods assume perfect isolation. Both estimate the number of species present each year using capture information for all years.

**The Bayesian method**

**Introductory information.** Depending on the site, there are up to three and a half years of pre-isolation data, the rest being post-isolation. In the Bayesian method, I combine all pre-isolation data in one single time period and treat it as a year with its corresponding combined effort. This period will be designated ‘year’ 0 \((t = 0)\), and years after isolation will be referred to as years 1, 2, …, etc.

At the core of the Bayesian method there is a product of likelihood and prior probability functions. The likelihood is the probability of the data given a model of choice. In this case we use two alternative two-parameter models of population decay to extinction. The priors define the distributions of the parameters (time of extinction and a proxy of population size) that we expect prior to looking at the data. Our objective is to estimate time to extinction \((t_e)\) for each species in each site, and from that information obtain one species decay curve per site.

**Two models of population decay.** Each model describes the change in the unknown true population size \(n_t\) from \(n_0\) just prior to fragmentation, to zero at time \(t_e\). Model 1 (*linear decay*) assumes a linear decay of the unknown true population size \(n_t\):
\[
 f_{\text{lin}}(n_0, t_c, t) = \begin{cases} 
 n_t = n_0 \frac{n_0}{t_c} & 0 < t < t_c \\
 n_t = 0 & 0 < t_c \leq t 
\end{cases}
\] (1)

Model 2 (*step decay*) assumes that \( n_t \) remains constant until the moment of extinction.

\[
 f_{\text{step}}(n_0, t_c, t) = \begin{cases} 
 n_t = n_0 & 0 < t < t_c \\
 n_t = 0 & 0 < t_c \leq t 
\end{cases}
\] (2)

Many reviewers of previous drafts of this text understandably took issue with the second model, labeling it unrealistic. That is why we decided to consider an alternative. Our data, however, are strikingly compatible with a step decay. Figure 3.1 shows bar charts of one measure of abundance, the number of captures per unit effort, over time, for each species in site 2206. We assume that this measure is a function of \( n_t \). Visual inspection shows that for many species, captures per unit effort remain relatively constant until the species disappears. Gradual declines are rare. Data which, in raw form, appear to show a gradual decline, often do not do so when capture effort is taken into account. For example, the capture record of *Formicarius colma* mentioned above appears to be a gradual decline. But when effort is taken into account, the numbers become \( (0.0046, 0.0029, 0.0037, 0.0030, 0.0067, 0.0031, 0.0030, 0, 0, 0, 0, 0) \). In fact, comparison of likelihood values shows that for any given site, the step model fits better than the linear decay model in approximately 75% of the species. (A convex model, such as an exponential decay, performs worse than the linear model.)

**Likelihood calculations.** We assume that the more individuals of a species that are truly present in a patch, the more individuals of that species will be caught in the nets. In our
Fig. 3.1. Bar charts of the number of captures per unit effort, over time, for each of 92 species in site 2206. All species were best fit by the step decay model, except those whose names are in bold face, which were best fit by a linear decay. Isolation takes place between the first and second time intervals.
model, capture rate per unit of effort, $c_t$, is directly proportional to the true number of individuals in a patch, $n_t$. Thus, $c_t$ behaves according to the same function as $n_t$ above, with $c_t$ replacing $n_t$, and $c_0$ replacing $n_0$. We call these functions $g_{\text{lin}}$ and $g_{\text{step}}$. The actual number of individuals caught will depend, of course, on the effort. We assume a linear increase in captures with effort (the data show this to be reasonable), and we assume that actual captures are distributed as Poisson ($\mathbb{P}$) where $\mathbb{E} = c_t E_t$. Thus, we can obtain the probability of a given observation using

$$P(N_t|c_0, t_e, E_t) = \frac{e^{\mathbb{E}c} [c_t E_t]^{N_t}}{N_t!} = \frac{e^{\mathbb{E}g(c_0, t_e, t) E_t} [g(c_0, t_e, t) E_t]^{N_t}}{N_t!}$$

(3)

where $g$ is either $g_{\text{lin}}$ or $g_{\text{step}}$ as appropriate.

The probability of an entire time series of captures ($N$) for one species is

$$P(N|c_0, t_e, E) = \prod_{t=0}^{T} P(N_t|c_0, t_e, E_t).$$

(4)

We can thus generate a joint likelihood surface for $c_0$ and $t_e$. Figure 3.2 shows the likelihood surfaces for *Formicarius colma* in site 1202, for the linear decay model (left) and the step decay model (right). Both surfaces are zero for $t < 7$, because the species is known to be present up to and including year six after isolation. The linear model shows a rapid climb to a peak at $t = 9$, and a decline thereafter. $c_0$ peaks at $\sim 0.005$, indicating an expected number of captures before isolation of 0.005 $\mathbb{P} 1514 \approx 7.5$. The step model peaks at $t = 7$, the year immediately following the final capture, and a subsequent decline
that is almost as rapid. $c_0$ peaks at \(~0.004\), indicating an expected number of captures before isolation of $0.004 \times 1514 \approx 6.0$. Recall that for these data, the step model fits much better.

**Three priors for $t_e$.** Now that we have an expression for the likelihood of the model parameters, we need expressions for the prior probability functions of $c_0$ and $t_e$. We have no prior information on what $c_0$ should be, so we use an uninformative prior, $P(c_0) = U[0,1]$. The range [0,1] encompasses all likely values of $c_0$, which tend to be in the range 0–0.007 for these data because the efforts $E_t$ are measured in the 100’s and 1000’s of net-hours.

All priors for $t_e$ are based on the idea of a species-specific, time-invariant, probability of extinction, $\mu$. From various studies we know that species differ in how prone they are to extinction (Pimm et al. 1988, Karr 1990, Laurance 1991, Stouffer and Bierregaard 1995,

**Fig. 3.2.** Likelihood surfaces for *Formicarius colma* in site 1202 for the linear decay model (a), and the step decay model (b). The horizontal axes show time of extinction ($t_e$), and initial number of captures per unit effort ($c_0$).
Duncan and Young 2000, Sekercioglu et al. 2002). On the other hand, studies of small bird populations on islands roughly the same size as these fragments (Russell et al. 1995) find that annual turnover, and hence mean yearly extinction probability, is clustered around $\mu = 0.1$. The fixed $\mu$ prior ($\mu = 0.1$) assumes that all species have the same probability of going extinct. It takes the form

$$P(t_e) = (1 - \mu)^t = 0.9^{t_e}.$$  \hspace{1cm} (5)

With the Uniform $\mu$ prior, we assume that any value of $\mu$ is equally probable, i.e., that $\mu$ is uniformly distributed on $[0,1]$, which, by integrating $(1 - \mu)^t$ over all $\mu$ gives

$$P(t_e) = \frac{1}{t_e + t_e^2}. \hspace{1cm} (6)$$

The mean $\mu$ in this case is 0.5, and the prior for $t_e$ therefore drops off much more quickly with time than for $\mu = 0.1$ (figure 3.3). Finally, we assume that $\mu$, while not constant, has some centrally weighted distribution between 0 and 1. A Beta distribution is suitable, which gives the following general form for a prior for $t_e$:

$$P(t_e) = \frac{\Gamma(\alpha + \beta)\Gamma(\beta + t_e)\Gamma(1)}{\Gamma(\alpha)\Gamma(\beta + \alpha + t_e)} \hspace{1cm} (7)$$

where $\Gamma$ is the Gamma function, and $\alpha$ and $\beta$ are parameters of the Beta distribution governing $\mu$. We call this the “Beta $\mu$” prior. Using $\alpha = 2$ and $\beta = 18$ gives a distribution with a mean of 0.1 and a standard deviation of $\approx 0.06$. (The Uniform $\mu$ prior above is a special case of the Beta $\mu$ prior with $\alpha = \beta = 1$.) Figure 3.3 shows the three priors.
Bayes’ equation. We can now use Bayes’ equation to construct a joint posterior probability function for $c_0$ and $t_e$, given the data:

$$
P(c_0, t_e | N, E) = \frac{P(N | c_0, t_e, E)P(c_0)P(t_e)}{\int \int P(N | c_0, t_e, E)P(c_0)P(t_e) dc_0 dt_e} \quad (8)$$

The bounds of the integral are defined by the choice of prior, and the denominator is constant for each site and species combination. Figure 3.4 shows two probability surfaces corresponding to the first six years of data from the record of *Formicarius colma* in fragment 1202. The left surface uses the “$\mu = 0.1$” prior for $t_e$. The right surface uses the Uniform $\mu$ prior for $t_e$. 

Fig. 3.3. Prior probability for time of extinction, $t_e$, assuming $\mu=0.1$ (a), uniform $\mu$ (b), and Beta distributed $\mu$ with a mean of 0.1 (c).
We want to know when species go extinct, i.e., the value of $t_e$, so we numerically integrate over $c_0$ to obtain a probability function for $t_e$ alone: $\Pr(t_e|N, E)$. Figure 3.5 shows the functions corresponding to the *Formicarius colma* data mentioned above.

**Fig. 3.4.** Posterior probability surfaces for a dataset consisting of the first six years of data on *Formicarius colma* in fragment 1202. The left surface uses the fixed $\mu$ prior (a) and the right surface uses the uniform $\mu$ prior for $t_e$ (b). The horizontal axes show time of extinction ($t_e$), and the initial number of captures per unit effort ($c_0$).

**Fig. 3.5.** Posterior probability functions of $t_e$ obtained from integrating the probability surfaces of Figure 3.4 over $c_0$. The left function corresponds to the fixed $\mu$ prior (a) and the right to the uniform $\mu$ prior for $t_e$ (b).
Decay curves: sampling from $\Pr(t_e|N, E)$. Once we have $\Pr(t_e|N, E)$ for all the species in a site, we generate a set of species loss curves. Each curve is obtained by drawing one $t_e$ from each of the species-specific $\Pr(t_e|N, E)$ distributions. The set of $t_e$’s provides a sequence of losses of species. We generate 1000 loss curves, and from these, the mean and 95% boundary curves.

Figure 3.6 shows the mean curves for all three prior distributions for $t_e$ and both decay models (i.e., there are six curves). As expected, for any given prior of $t_e$, the square decay model produces a steeper curve. The $t_e$ priors “Beta $\mu$” and “$\mu=0.1$” result in broadly similar curves as they use the same mean $\mu$ value; the “Uniform $\mu$” has a mean $\mu$ of 0.5 and results in a faster initial decay. Because the results with the “Beta $\mu$” prior did not
differ substantially from those with “\( m = 0.1 \)”, we focus only on “\( m = 0.1 \)" (figure 3.7, table 3.1) and “Uniform \( m \)” (table 3.1), both under the step decay model.

**The runs test method**

Each decay curve has a corresponding \( t_{50} \): the time at which the number of species drops below 50% of the initial number. From our 1000 curves, we therefore have 1000 \( t_{50} \)'s from which we obtain a mean and 95% bounds. These mean values produce the scaling relation illustrated in figure 3.8.

The application of Bayesian methods in ecology elicits statistical controversies that we do not intend to resolve here (Dennis 1996). *Method 3*, one frequentist alternative to *method 2*, is a computationally simple version of a runs test. If we assume that captures per species follow one particular distribution, then it is possible to calculate the probability of obtaining a run of a certain number of captures along a series of consecutive capture occasions, just as, when rolling a die, we can calculate the probability of obtaining, say, five ‘ones’ in a row. In the species-extinction context, the interesting question is: if one species is present at one site throughout a whole series of capture occasions, and if we know the probability of detecting 0, 1, 2, …, \( n \) individuals at any occasion, what is the probability of getting a run of \( t \) occasions with 0 captures? More precisely, what is the probability of observing a run of zeros of a certain length at the end of a series? If there is a high probability associated with one terminal run of zeros, then we will believe that the species is still there, but we failed to detect it. If the observed run has a low probability,
we will suspect that the species was actually not present throughout the whole series and interpret the run of zeros as evidence of extinction.

One vector of capture records for a given species at a given site, N, contains a total of C captures that may take place over a number of days \(1, 2, \ldots, T\). Let the last capture occur at day \(T - D\). \(D\) can be anywhere from zero to \(T - 1\), and when \(D > 0\), this indicates a run of zeros of length \(D\) at the end of the vector. Our aim is to convert \(N\), a vector of captures, into \(P\), a vector of probabilities \(P_t\) that the species is extant at any day \(t\). Since we are considering perfect isolation, species can go extinct only once, and this has to be after the day of their last capture. The runs test in Burgman et al (Burgman et al. 1995) give the following probabilities:

\[
P_t = \frac{1}{T} \left\{ \begin{array}{ll}
\frac{t - D}{T} & \text{if } T - D < t \leq T \\
0 & \text{otherwise}
\end{array} \right.
\]

(9)

Summing \(P_t\) values across species in a site we obtain an expected number of species at day \(t\). The yearly values shown in figure 3.7 are drawn from the first day of netting in each year.

Solow (1993) used this approach in inferring extinction from presence/absence data, and Burgman et al (1995) adapted it for use with frequency data. Both cases treat capture success as a stationary Poisson process, implying constant density until the moment of extinction, just as in the step decay model above. Solow did formulate a variant for testing extinction with declining populations (Solow and Helser 2000), but we have seen
that a model of gradual population decline does not fit the data on most species. We therefore feel justified in applying Burgman’s approach to our frequency data.

FOREST RECOVERY ALLOWS RECOLONIZATION

Jackknife estimates

Finally, we withdraw the assumption of perfect isolation and estimate the number of species in any given year based exclusively on that year’s data. In this approach, because it allows extinctions and recolonizations to occur from year to year, the knowledge of how many species were seen over the sampling period does not help us define a lower bound for their numbers. Increased realism comes at a price. We must assume community closure, i.e., that the number of extinctions and colonizations over one year is negligible with respect to the changes taking place between years. To the best of our knowledge, there is no satisfying goodness of fit test for closed capture models. We also assume that species-specific capture probabilities are constant — each species keeps its particular capture probability throughout the year — and that captures are independent events.

The jackknife operates by comparing $q$ estimates of the parameter of interest — in this case $S$, the number of species — obtained by repeatedly excluding $k = 1, 2, \ldots, q$ data points from the sample. Here, ‘data points’ mean ‘netting days’ and we proceed by comparing four or five estimates of $S$ depending on the number of netting days available. When a year-site combination has only four or fewer netting days we exclude it from this
analysis. The jackknife estimates can be obtained by re-sampling or by a tedious
derivation of the estimators. The software package *Capture* (Rexstad and Burnham
1991), available under *Mark* (White and Burnham 1999), follows a closed form solution
developed by Ken Burnham for estimating the size of closed populations with
heterogeneous individual capture probabilities (Burnham and Overton 1979). Here, we
apply the same procedure to a ‘closed’ community with heterogeneous species capture
probabilities.

First, the data matrix is summarized as a vector $F$ of frequencies $f_d$ indicating the number
of species that were seen exactly $d = 1, 2, \ldots, t$ days. If $I$ is the observed number of
species, then

$$I = \sum_{d=1}^{t} f_d.$$

Not all species are captured in all days; therefore, if community closure applies, we must
be missing species in some of the visits. It follows that $I$ is necessarily a negatively biased
estimate of the true number of species, $S$. The higher the difference between individual
days’ species lists, the higher the bias. Bias correction proceeds by obtaining $k$ different
jackknife estimators of the true number of species according to

$$\hat{S}_k = I + \sum_{d=1}^{k} \mathbb{D}_{dk} f_d,$$  \hspace{1cm} (10)

where the $\mathbb{D}_{dk}$'s are constants defined as functions of $t$ for each value of $k$ (Burnham and
Overton 1979). This estimator has variance
\[ \hat{\text{var}}(\hat{S}_k) = \sum_{d=1}^{l} (\ell_d + 1)^2 f_d \hat{S}_k. \]  

(11)

For example, there were seven netting days during 1989 at site 2108. The number of detected species was fifteen, with frequencies \( f_1 \) to \( f_7 \) respectively of 6, 3, 2, 2, 0, 2 and 0.

The values of the first five jackknife estimates are:

\[
\begin{array}{ccc}
 k & \hat{S}_k & \hat{se}(\hat{S}_k) \\
 1 & 20.1 & 3.09 \\
 2 & 22.6 & 4.85 \\
 3 & 24.1 & 6.57 \\
 4 & 25.0 & 8.19 \\
 5 & 25.4 & 9.48 \\
\end{array}
\]

At this point, Mark looks for the first pair of adjacent \( S \) estimates that are significantly different from each other (working from \( k = 0 \) up) and uses an interpolation algorithm to obtain a final estimate of the number of species and its standard error (Burnham and Overton 1979):

\[ \hat{S} = 18, \quad \hat{se}(\hat{S}_J) = 3.5 \]

We assign confidence intervals to \( \hat{S}_J \) assuming that \( (\hat{S}_J \square S) / \hat{se}(\hat{S}_J) \) is approximately a standard normal deviate (Burnham and Overton 1979). Figure 3.7 shows the final estimates and their confidence intervals.
RATES OF SPECIES LOSS

Methods 1–3 produce curves (figure 3.7) that yield $t_{50}$ values, the time it takes to lose half the initial number of species (table 3.1; figure 3.8). Methods 2 and 3 yield such similar results that we omit the latter in figure 3.8. The jackknife estimates, however, produce only a set of points with confidence intervals. In this case, we obtain the $t_{50}$’s by fitting an exponential curve to each fragment’s set of points. We fit curves in two ways. First, we use all points, from the year before isolation to the end of sampling. This returns a $t_{50}$ that neglects the possible historical effects of relaxing isolation. A second, generally better fit, uses fewer data points. It starts the year before isolation and ends the year before the number of species begins to recover. The resulting $t_{50}$ illustrates how fast species would disappear, had the isolation held constant throughout the study period. The aggregate result of the four methods allows some general conclusions.

(1) On average, smaller fragments start with fewer species than larger ones, as expected by the species-area relationship. This tendency is perceptible ($z \approx 0.07$) but not very pronounced, as expected from different-sized samples of a continuous biota (Rosenzweig 1995).

(2) The number of species drops quickly. A slightly higher than expected number of species in the first year after isolation is likely due to the temporary presence of refugee birds from the recently destroyed adjacent forest (Bierregaard and Lovejoy 1988). An occasionally steeper drop in some methods at the end of the survey is due to species not captured in the very last survey year; the most recent capture will be deemed ‘final’, and
the species therefore extinct. Our sample of fragment interior locations does not detect species that regularly use deforested areas — a small proportion of the regional avifauna (Cohn-Haft et al. 1997). The quickly dropping initial number of species reflects a fast loss of forest-dependent birds. Fragments in areas that have been patchy for a long time, at the confluence of different biota, lose species more slowly than the fragments in our sample (Sekercioglu et al. 2002).

**Fig. 3.7.** Plots of species loss for all fragments according to four different methods: minimum under perfect isolation, Bayesian with $\mu = 0.1$ and step decay, runs-test, and jackknife estimates. The orange bars indicate the timing of isolation.
(3) Species differ greatly in their probabilities of extinction. For example, *Cyphorhinus arada*, *Sclerurus caudacutus*, and *Myrmornis torquata* consistently disappear early from all fragments, whereas *Phaetornis supercilliosus*, *Glyphorynchus spirurus*, and *Mionectes maconelli* remain present until the end of the sampling period. On a log graph, this heterogeneity of extinction probabilities results in a concave species-loss curve, with interesting implications for conservation. An initial, transient, high rate of vulnerable species loss means that infrequent surveys taken long after fragmentation may only record occasional extinctions of long-lasting species. From this, one might infer a spuriously long time for species losses (Diamond 1972). Conversely, surveys soon after fragmentation may mistake the slowing rate of extinction for its cessation, and so underestimate the continuing but slow decline in species numbers. Drawing inferences about the exact shape of the curves in figure 3.7 is complicated when, with the Bayesian method, we assume a priori probability distributions. There is also the problem of forest re-growth around fragments: the jackknife estimates suggest that species numbers may not be declining more slowly towards the end of the sampling period, they may actually be increasing. We will address species differences in the probability of extinction and the role of re-growth on re-colonization elsewhere.

(4) Despite different assumptions, the $t_{50}$ estimates are broadly similar. Smaller fragments lose a given proportion of species more quickly than larger ones (table 3.1; figure 3.8). The $t_{50}$ estimates are shortest when we estimate them from the initial decay of the jackknife estimates. This suggests that fragmentation would have had more drastic effects if there had not been some forest re-growth (Stouffer and Bierregaard 1995).
Figure 3.8 also shows rates of species loss for generally larger forest fragments at Kakamega, Kenya (Brooks et al. 1999). This study has significant differences in methods, species, and history. It assumed exponential decay from an initial to a final, equilibrium number of species, both estimated from species-area relationships. The initial estimate employed parameters typical of areas within continuous forest, the final those typical of long isolated forest fragments (Rosenzweig 1995). The empirical datum is the number of species observed a known time after forest isolation. In calculating a half-life for the numbers of species lost, the Manaus study assumes that fragments will eventually lose all their species. This cannot be far wrong, given the rapid loss and the extreme disparity between pre- and post-fragmentation areas. (If the fragments retained some species, then
$t_{50}$ estimates would be smaller than those shown.) The Kakamega study, in contrast, assumes non-zero equilibrium numbers of species—a better assumption for larger fragments.

Given these differences, there are interesting similarities. Figure 3.8 suggests a rough scaling: a 1000-fold increase in area leads to a 10-fold increase in the time it takes fragments to lose half the species they will eventually lose. Fragments of ~100 ha (1 km$^2$) lose many species within one or two decades. Fragments with more than 100 ha still lose some species, but do so over a timescale of a few decades to perhaps a century.

This experiment originated in the search for a minimum forest fragment area that would be sensible for conservation. Much work in the intervening two decades has shown that smaller areas simply retain fewer species than do larger ones. But area itself does not set a clear enough constraint on conservation measures. The results we present connect area to time and time does impose such a constraint. Only the largest fragments retain species long enough to offer hope of remedial actions, such as the regeneration of cleared forests. It may take a couple of decades for secondary forest to achieve any structural development (Lucas et al. 2000) and at least 100 years to recover mature biomass levels (Fearnside 1996). Conservation managers would want to have forest fragments large enough to protect species until they can be “rescued” by forest re-growth. Our results relating time to area suggest that “large enough” — for the understory birds considered here — must be measured on a scale of 1000 ha (=10 km$^2$) or more. This is unfortunate when one considers that for some species-rich areas of the planet, a large proportion of remaining forest is in fragments smaller than 1000 ha (Gascon et al. 2000). Such
fragments will have limited conservation value for forest-dependent birds, at least. An even more challenging question is how large fragments should be if there is no hope of forest re-growth rescuing their stranded species. Our scaling results suggest that even fragments as large as 10,000 ha (=100 km$^2$) loose many species — likely the ones of most conservation concern — when isolated for a century.

Minimum size is important in itself, but so is choosing an appropriate scale for assigning conservation priority. A common procedure selects the minimum set of areas that, if protected, would conserve all of some predefined set of species (such as all endemic species, or all threatened species). Such techniques depend on the widely varying resolution of the available data in species ranges. They are susceptible to the “Noah’s Ark effect” (Pimm and Lawton 1998), in which the total area needed to protect all species becomes vanishingly small — and politically tempting — provided one accepts an unreasonably small resolution (the area occupied by a pair, in the case of the Ark). Conversely, too large a spatial resolution results in the selected areas being too large to meet the economic or political constraints on reserve establishment. Without knowing the appropriate spatial resolution that scaling rules provide, priority setting can fall into either ecological irrelevance or practical impossibility. Our results provide a lower bound to the minimum fragment size for birds. Determining the fragment sizes required to slow the losses of other taxa to manageable levels will require more estimates similar to the ones presented here.
The pieces of fragmentation

Dense urban areas and extensive agricultural fields completely replace the pre-existing land cover. Most landscape changes, however, are less thorough. They leave behind isolated fragments of the once continuous cover, limiting habitat availability and the movement of organisms. Fragmentation affects a large fraction of the Earth and threatens its most species-rich areas (Gascon et al. 2000). The concept is relevant and popular, but too abstract – different scientists measure and define fragmentation in different ways. In science, abstract ideas often become reified (Slobodkin 2001), they get a life of their own and become part of jargon as if they had an objective meaning and widely accepted implications. ‘Stability’ (Pimm 1984) and ‘biodiversity’ (Slobodkin 2001, Slobodkin 2003) are two examples, to which I add ‘fragmentation.’
I examine the use of ‘fragmentation’ in the literature, seeking to uncover its various meanings and to select which research questions, from the myriad of possibilities, are likely to be most useful when answered. To structure the argument, I focus on the definition of fragmentation, the assessment of its effects on populations of organisms, and the generalization of results from multiple studies. Having reviewed a selection of journals, I outline broad observations on what is the norm for proceeding through each stage. Each observation highlights major unanswered questions. Finally, I search for unconventional approaches, i.e. studies that differ from the established norm in their treatment of fragmentation. Together, the norm, the unanswered questions, and the innovations, provide a framework for re-defining fragmentation as a small set of tractable research problems.


The first search returned more than 1,000 papers, mostly on astrophysics and cell biology. I narrowed this list to ‘fragmentation’ as landscape change, and ended up with 256 entries. The majority of entries (~88%) are from 1995-2003. My list includes papers
on population-level consequences of landscape change, plus some papers that merely described the change without measuring consequences. A considerable number reported consequences at the community level. I included those papers as well because most community measures imply the presence or absence of individual populations. Nevertheless, there are community measures, such as community ‘nestedness’ and changes in species turnover, which I do not consider.

I catalogued papers according to the measure of fragmentation (cause) and the examined response variable (hypothetical effect). Some papers look at chains of inter-related response variables. They may also look at several response variables independently of each other, or use more than one measure of fragmentation. To sort these differences, I defined a finer unit of analysis: the study. Each paper may have several studies, each with only one measure of fragmentation and one or more inter-related response variables. The database of studies has 375 entries. Interested readers can obtain an electronic copy of the database from the author.

**WHAT IS FRAGMENTATION AND HOW DOES IT MATTER?**

The term ‘fragmentation’ entered ecology in the seventies, through the SLOSS debate. It appears in a paper title for the first time in 1982 (Simberloff and Abele 1982). Since then, it has gained remarkable popularity. According to the ISI database, there were 23 articles about ‘habitat fragmentation’ published in 1992. In 2002, there were 241 – a tenfold increase. Since 1989, the National Science Foundation (USA) allocated almost seventeen
million dollars to fragmentation-related studies. Even the media are starting to use the term, as attested by more than fifty hits in news sources on the LexisNexis database.

All approaches to fragmentation refer to loss of habitat and increased isolation of the remaining habitat patches. This apparent unity breaks down, however, when one looks at how fragmentation is measured in the reviewed studies (Table 4.1). A third of the literature employs a variety of qualitative measures, including such basic ideas as ‘continuous’ versus ‘fragmented’, or ‘isolated’ versus ‘non-isolated’, or with versus without ‘corridors.’ Roughly, 20% of all studies quantify fragment sizes, 10% the distance to a habitat edge, and a further 10% the distance between habitat patches. Prior reviews on fragmentation found a divergence between theoretical and empirical studies (Harrison and Bruna 1999, McGarigal and Cushman 2002); I find a similar pattern. The four fragmentation measures that theoretical studies use most are cover with fixed configuration, configuration with fixed cover, patch removal, and permeability to movement. These are, in turn, the four measures that empirical studies use the least. The first two measures, in particular, emphasize the separation between habitat cover and habitat configuration. Early studies did not discriminate so explicitly. Does this diversity of opinion matter? I argue that it does, because the different measures force different management approaches.

Wilson and Willis (1975) formulated a set of rules of refuge design stating the advantage of single large over several small, short-edge over long-edge, clumped over dispersed, and connected-by-corridors over isolated refuges. These rules had a lasting influence on conservation biology (Hanski and Simberloff 1997); indeed, many fragmentation
Table 4.1. Measures of fragmentation

<table>
<thead>
<tr>
<th>Measure</th>
<th>Description</th>
<th># Studies</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Qualitative</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Blended patch size and isolation</em></td>
<td>Fragmentation increases as patches become increasingly small and isolated, but there is no separate consideration of patch size and isolation</td>
<td>53</td>
</tr>
<tr>
<td><em>Blended patch size and isolation with fixed area</em></td>
<td>Similar to the measure above but keeping total habitat area constant across fragmentation states</td>
<td>12</td>
</tr>
<tr>
<td><em>Binary isolation</em></td>
<td>Compares isolated and non-isolated patches regardless of area</td>
<td>17</td>
</tr>
<tr>
<td><em>Matrix isolation</em></td>
<td>Fragmentation levels correspond to isolation by different types of matrix assumed to have different permeability to movement</td>
<td>7</td>
</tr>
<tr>
<td><em>Corridors</em></td>
<td>Fragmentation distinguishes sets of patches connected by corridors from those</td>
<td>24</td>
</tr>
<tr>
<td><em>Other qualitative</em></td>
<td></td>
<td>15</td>
</tr>
<tr>
<td><strong>Quantitative</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Patch size</em></td>
<td>Size (or mean size) of patches without regard to isolation</td>
<td>77</td>
</tr>
<tr>
<td><em>Patch removal</em></td>
<td>Measures decrease in the number of patches, or number of patches available for colonization</td>
<td>12</td>
</tr>
<tr>
<td><em>Cover</em></td>
<td>Proportion or amount of area with a given type of land cover</td>
<td>30</td>
</tr>
<tr>
<td><em>Cover with fixed configuration</em></td>
<td>Measures changes in habitat amount while holding configuration constant. There are multiple measures of configuration</td>
<td>9</td>
</tr>
<tr>
<td><em>Configuration with fixed cover</em></td>
<td>Measures changes in configuration while controlling for, or fixing, cover. As above, there are multiple measures of configuration</td>
<td>13</td>
</tr>
<tr>
<td><em>Permeability to movement</em></td>
<td>Quantitative version of <em>Matrix isolation</em> above</td>
<td>9</td>
</tr>
<tr>
<td><em>Isolation by distance</em></td>
<td>Any variant of a nearest neighbor distance between patches or between patches and a pre-defined non-fragmented area</td>
<td>35</td>
</tr>
<tr>
<td><em>Distance to edge</em></td>
<td>A variety of measures of distance to a pre-defined edge. Includes those studies that merely distinguish edge from interior.</td>
<td>38</td>
</tr>
<tr>
<td><em>Amount of edge</em></td>
<td>Measures the proportional cover or linear extent of a pre-defined edge.</td>
<td>11</td>
</tr>
<tr>
<td><em>Other quantitative</em></td>
<td></td>
<td>13</td>
</tr>
</tbody>
</table>
measures seem tailored for their empirical test. Note the recurrence of fragment size (Bender et al. 1998, Connor et al. 2000), edge (Paton 1994, Murcia 1995, Fagan et al. 1999), isolation (Tischendorf and Fahrig 2000b), and corridor (Beier and Noss 1998) studies. This trend changed only in the mid-nineties, once landscape and patch-occupancy studies became popular and began to take area and configuration apart (Andrén 1994, With and Crist 1995, Bascompte and Sole 1996). One of these (Andrén 1994), a review of abundance and presence/absence in fragmented landscapes, is the most cited paper in the literature search. Even though many empirical studies still measure edges and corridors, no one challenges the compartments of fragmentation (Villard 2002) – so much so that some scientists use the term ‘fragmentation’ to designate change in configuration, leaving habitat loss aside as a separate issue.

This dichotomy opens the door to an applied question (Kareiva and Wennergren 1995): In a world of limited space, can we minimize the effects of habitat loss with adjustments in habitat configuration? There is an implied management scenario: one may not be able to prevent the loss of x% of the habitat, but may be able to control where the habitat is lost.

In the abstract, ecologists model configuration as the degree of aggregation of habitat cells in a landscape grid. Suppose we start with a continuously covered landscape. As we gradually destroy habitat in randomly located cells, we eventually reach a threshold where the remaining patch ceases to span across the landscape. At this point, if the destroyed area were filled with a liquid, the liquid would flow (or ‘percolate’) through the landscape. Percolation theory (Gardner et al. 1987) predicts this threshold. Early
modeling results suggest that a population subject to a similar loss of habitat will also show an extinction threshold (Bascompte and Sole 1996). At first, with abundant habitat, the population decreases in proportion to habitat loss, but at a certain point, it drops abruptly and eventually goes extinct. Extinction and percolation thresholds do not necessarily match but they are both affected by the pattern of cell removal – this is where configuration comes in. We might identify a tolerable limit to habitat removal and possibly, lower that limit through adjustments in configuration. This prospect however, has not been fulfilled. Empirical evidence of extinction thresholds is scant (Jansson and Angelstam 1999, Lennartsson 2002), and discouragingly hard to assemble (Fahrig 1997, Trzcinski et al. 1999). The early models were not wrong, but they only told part of the story. Lenore Fahrig’s review (2002) of modeling studies sums up the rest: even though different models predict different extinction thresholds, the potential benefit of adjusting configuration is often too small to have any management relevance.

Landscapes with the same habitat area and different configurations provide a valid theoretical scenario but they are difficult to find in the real world. Some studies fabricated artificial landscapes to simulate the scenario – a strategy that imposes obvious limitations of spatial scale and has, therefore, limited applicability (McIntyre and Wiens 1999). The most successful approach has been to measure a variety of landscape configuration indices (number of patches, total edge, etc.) and to statistically eliminate their correlation with habitat area (Trzcinski et al. 1999). This strategy allows the examination of pure configuration effects at scales of hundreds to thousands of square kilometers. The few studies that did this (measuring effects on the presence/absence and abundance of birds) found mixed results (Fahrig 2002). The strongest conclusion is that
effects of area tend to be much stronger than effects of configuration. Most species do not respond to pure configuration. The ones that do, may either suffer or benefit from increased fragmentation (Fahrig 2003).

Should one conclude that configuration does not matter? Clearly not. A road that bisects a protected area and a corridor that connects two reserves are strong examples of configuration changes with strong management implications. The answer, however, draws as much from ecology as it does from the socio-economic constraints of landscape management. The history and practice of conservation shows that roads are usually bad and large connected areas are good. If managers ignore configuration they risk dramatic losses in future area.

For example, analyses of satellite images from the Brazilian Amazon (Oliveira-Filho 2001) reveal distinct patterns of forest fragmentation that can be identified in a variety of geographical locations. The patterns: ‘fish bone’, ‘large properties’, and ‘independent colonization’, result from different histories of settlement. Will they have different biological consequences? There are two parts to the answer. One, ecological, depends on whether the patterns differ with regard to habitat loss, configuration, or both. The other, socio-economic, depends on the future landscape changes that will result from the continued playing of political, social, and economic forces that lead to the present pattern.

There are two lessons. First, we cannot demand that all conservation choices be justified solely on ecological grounds. Socio-economic considerations must be given their role when they matter. Second, while ignoring socio-economic constraints, ecologists should focus energetically on one key question: When does configuration matter? Clearly, it
does matter for some species, but the most fragmented configurations (considered independently of habitat amount) may have positive as well as negative effects on populations (Fahrig 2003). In some cases, there will be so many possible measures of configuration that one may have to focus on the complementary question: When is area not enough to explain the effects of fragmentation? Statistically removing the effect of area from an assortment of landscape indices is one approach, but there may be others. A simple (and rarely used) approach is to examine population densities in habitat patches of different sizes (Tjernberg et al. 1993, Connor et al. 2000). If density remains constant across sizes, organisms may be sampling patches at random (Haila et al. 1993, Andrén 1996) – regardless of their configuration.

ASSESSING THE EFFECTS OF FRAGMENTATION

Landscape change affects a population’s physical environment, its predators, prey, and competitors, the behavior of its individuals, and other immediate factors. These, in turn, may affect demographic parameters, leading to changes in population variables (such as population size, variability, and growth rate) and ultimately determining the population’s presence or absence. In total, the literature identified 21 response variables (Fig. 4.1). The various papers examined 375 ‘links,’ that is, either the effect of fragmentation on one of the 21 variables or the effect of one variable on another. Most studies (66% of the total, 84% of empirical studies) link fragmentation with only one variable; a minority examines ‘chains’ of two or more links. Examining a link does not amount to proving a response.
Fig. 4.1. Diagram of response variables in fragmentation studies. Circle sizes indicate the total number of links to each variable in six classes: [1-6], [7-12], [13-24], [25-48], [49-96], and [96+]. Arrows show frequency of the most common links in four classes of increasing darkness: [7-12], [13-24], [25-48], [49-96]. Links examined fewer than seven times are not illustrated.
In fact, in the face of so many measures of fragmentation, one cannot expect consistent responses. My focus is on the choice of response variables.

Not all variables receive the same attention (Fig. 4.1). Population size and the species’ presence-absence, commonly regarded as endpoints, receive the most. Factors that mediate these outcomes (indicating mechanisms) are less studied. There are very few studies on competitors and parasites. There are some studies of how fragmentation affects dispersal and reproduction but very few focus on the roles of resource availability and survival.

One may argue about the usefulness of studying mechanisms (Haila 1999), but if one measures intermediate factors at all, they should be carefully chosen. One of fragmentation’s most plausible effects is that of locking organisms in small habitat patches with insufficient resources. Yet only a few studies (Burke and Nol 1998, Zanette et al. 2000, Sekercioglu et al. 2002) focus on resource availability. Locked and starved organisms are more likely to die. If not locked, they may die while searching for other patches. Survival is clearly an important variable (Haila 1999, Tischendorf and Fahrig 2000b) but it is the least studied of the demographic parameters. Reproduction has three times as many links mostly due to the popularity of two field techniques – pollination manipulation (Cunningham 2000) and artificial-nest predation (Chalfoun et al. 2002) – that measure impacts on reproductive success. While it is important to explore successful techniques, to understand the most important mechanisms one must focus first on the most important consequences.
Perhaps the most striking aspect of the multiple assessments of fragmentation effects is the almost complete absence of dynamic considerations. Examples of dynamic response variables include population variability, population growth rate, and gene flow. These variables received only eleven, ten, and eight links respectively. To break the standard approach of looking for a fixed response to a fixed landscape, one needs, at least, a temporal dimension on the response variable. This may be done indirectly, by accounting for the age of habitat fragments (Crooks and Soulé 1999, Crooks et al. 2001); or directly, by observing changes in real time (Robinson 1999, Gonzalez and Chaneton 2002, Ferraz et al. 2003). Once having measurements of a response variable through time, the particular description of the dynamic process is a matter of formal choice.

**DRAWING GENERALIZATIONS**

What management strategies can apply to a wide range of landscapes? Most studies conclude that much depends on the species (Robinson et al. 1992). Reviews of species’ responses to corridors (Beier and Noss 1998) and habitat edges (Murcia 1995) illustrate the point. This invites the question: are there general traits that determine a species’ vulnerability to fragmentation?

One approach is to redefine fragmentation by incorporating species traits in the measures of landscape state. The assumption is that a landscape that is fragmented for one species may not be so for another. For example, building a road through a forest patch may subdivide a population of a forest interior bird species, but it may not make any difference for a tree with a long dispersal distance. Species-based landscape indexes can
change according to dispersal range and area-requirements of the focal species (Vos et al. 2001). Functional measures of landscape connectivity (Tischendorf and Fahrig 2000b, a) are species-based landscape indexes as well. They reflect both fragmentation and its effects on organism movement throughout the landscape.

A second approach takes a conventional measure of landscape change (one that is independent of species) and asks what species are more vulnerable to it. By measuring species traits as well as their reactions, these studies identify traits that associate with the response to fragmentation. One approach is to model the spatial distribution of species with varying dispersal abilities and habitat specialization in habitats with different degrees of fragmentation. Modeling and experimental comparisons among species (With and Crist 1995) show that those with higher habitat specialization and longer dispersal ranges shift from random to aggregated distributions at lower levels of habitat destruction. Recent studies elaborate the experimental treatment of movement and dispersal under fragmentation (With et al. 1999, Berggren et al. 2001), but there are still few comparisons among species. The literature on correlates of extinction (McKinney 1997) does draw comparisons among many species, but it rarely refers to a common environmental threat (Owens and Bennett 2000) – much less to a measure of fragmentation.

Three factors play into a species’ response to fragmentation: What does it need (habitat specialization); How much does it need (area requirements); And how far can it move to get it (dispersal range). Sixteen percent of the reviewed studies look at dispersal (or other measures of movement); however, I found only one study that mentions all three factors
in a prediction of vulnerability to fragmentation (Dale et al. 1994). These factors usually appear one or two at a time. Studies look at habitat specialization (Andren et al. 1997), the combination of area requirements and dispersal range (Vos et al. 2001), or the interplay between dispersal range and habitat specialization (With and Crist 1995). The evidence of interaction between pairs of factors (With and Crist 1995) raises the unanswered question of how the three factors interact.

UNCONVENTIONAL STUDIES

A number of rules – widespread approaches and methods – apply in almost all fragmentation studies. Researchers occasionally break these rules. At times, rule breaking reveals unsuspected questions or new solutions to old problems.

Fragmented landscapes are usually represented as habitat patches in a matrix of non-habitat. Even studies that qualify the matrix follow the fundamental habitat/non-habitat dichotomy. With and Crist (With and Crist 1995) broke this rule by defining three types of landscape cover with measurable qualities. Their approach eliminates the need to define one type of cover as perfect or as absolutely hostile. Also according to the conventional representation, patches may interchange organisms among themselves, but rarely with the matrix. Each patch has a boundary (or an edge) dividing it from the matrix. In reality, however, there are many cross-boundary interactions (Janzen 1986). For example, matrix predators can mediate the patch size threshold for prey population persistence (Cantrell et al. 2001). A similar scenario might apply to the propagation of
disease under fragmentation (McCallum and Dobson 2002). Could a matrix-inhabiting pathogen reservoir mediate the effects of disease in a patch-inhabiting population?

A second rule is that fragmenting landscapes change from one static form to another, through loss of habitat. Static landscapes are a major simplification. Landscapes can easily maintain a certain amount of habitat that keeps changing its location. On such dynamic conditions, metapopulation persistence can change with habitat amount, as well as with the rate of change in its location (Keymer et al. 2000). What happens if landscapes gain, rather than loose, habitat? Hale et al (2001) found substantial genetic mixing of English and Scottish squirrel genes following the growth of pine plantations between once-isolated habitat patches. Is there any symmetry between responses to fragmentation and ‘de-fragmentation’?

Finally, species must respond to landscape change within the bounds of their fixed traits. A few studies break this rule by acknowledging intra-specific variability, selective mortality, and adaptation to the new landscape (Van Dyck and Matthysen 1999). The conventional assumption is that evolutionary changes take place at a slower pace than demographic ones (Haila 1999). Fragmentation, however, must impose selective pressures on movement-related traits. For example, a sparser distribution of resources will benefit individuals that can move to find them. On the other hand, individuals trapped in very isolated patches will not benefit from a risky dispersal. Indeed, some populations of butterflies and damselflies show genetically based differences in flight-related traits across locations with different levels of fragmentation (Van Dyck and
Matthysen 1999). One may also track changing ‘traits’ in a non-evolutionary context. Area requirements, for instance, may change with the abundance and spatial distribution of resources (Haskell et al. 2002). Such changes must affect a species’ response to fragmentation.

**CONCLUSION**

The current literature does not reveal one clear and widely used definition of fragmentation. I could not even find one dominant measure of this form of landscape change: We know it when we see it but we do not know what it is. While it may be pointless to attack a popular term, it is relevant to highlight a few of its many faces. Taking apart the multiple approaches to fragmentation, one finds a number of relevant and well-defined problems that will certainly survive the vagueness of the broader term. The most important challenge is to understand when the effects of fragmentation go beyond the effects of loss in habitat area. Meeting this challenge requires a clear measure of fragmentation, as well as an informed choice of response variables. In particular, it is important to compare survival at different levels of fragmentation. A complete understanding of the effects must provide some insight into the mechanisms linking landscape change to the fate of populations. Ideally, studies should look simultaneously at a few interconnected response variables. This is easier in theoretical than in empirical studies, but feasible in both. Generalizations about fragmentation only become possible if we set aside the simplified expectation of all-purpose management rules. Species differ in many traits that may influence their response to landscape change. Among these traits,
area requirements, habitat specialization, and dispersal range seem to hold the greatest explanatory power.
Afterword

The four chapters of this dissertation cover a wide enough variety of topics that it becomes difficult to draw one relevant biological conclusion pertaining to all of them. I will, therefore, summarize the most important conclusions on a chapter-by-chapter basis.

The effect of food supplementation on the formation of mixed-species flocks is mediated by the spatial and temporal distribution of the supplement. Such distribution conditions Black-capped Chickadee movement that, in turn, conditions flock formation. This result suggests that food availability affects the mechanism of flock formation; however, since mixed-flocking may increase or decrease depending on distribution one cannot conclude that birds join flocks for the benefit of a foraging reward. In fact, the results are entirely compatible with an anti-predator benefit. Further research should focus on the experimental effects of predation risk and on the questions of whether flock members
may consistently overestimate risk or lack the behavioral plasticity to adjust flocking behavior to changing levels of predation risk.

The Common Tern study shows that the combination of colony choice, breeding success, and trapping success over the years results in a Markov process with short-term memory. Inter-annual dependence in capture histories of Common Terns is a simple phenomenon. It would be interesting to learn more about the meaning of zeros (non-captures) in those Terns that are known to be alive. What are the relative contributions of trapping failure, breeding failure, and temporary colony change to the observed patterns?

In chapter 3, we showed that patches of forest with up to 100 ha lose one half of their initial number of understory bird species in less than twenty years. This is the case, even when we account for possible species re-colonization following forest regrowth. Smaller fragments lose species faster – under most estimates, 1-ha fragments lose half of their species in up to five years. The question that needs to be answered next is what kinds of species go extinct first. My post-doctoral research proposal outlines procedures for addressing this problem while focusing on a subset of species for which we can obtain reliable estimate of extinction probability.

The review on habitat ‘fragmentation’ illustrates how ecologists are far from converging on one dominant use of the term. The reviewed articles outline (or imply) more than sixteen different measures of fragmentation. The most concerning observation is the extreme rarity of studies that explicitly separate habitat area from habitat configuration. Any progress in the study of fragmentation – and the very usefulness of the term – relies on the distinction between these two landscape aspects.
References


