Dynamics of Bird Communities, Populations, and Individuals

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PREVIEW

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ABSTRACT

Dynamics of Bird Communities, Populations, and Individuals

Gonçalo Ferraz

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

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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.

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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

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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

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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

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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.

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Do birds of a feather flock together? An experimental study of hetero-specific flocking

INTRODUCTION

Animals of different species occasionally form groups that move and forage together. Examples span a variety of taxonomic groups, including ungulates (Fitzgibbon 1990), primates (Cords 1987, Terborgh 1990), fish (Allan and Pitcher 1986), and birds. Mixed-species flocks of birds occur on all continents in a wide variety of habitats (Moynihan 1962, Buskirk 1976, Morse 1977, Powell 1979, Diamond 1981, Munn 1985, Diamond 1987, Zamora et al. 1992, Latta and Wunderlee 1996, Jullien and Thiollay 1998, Hino

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2000). 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

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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 anwers 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

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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.

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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

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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 21°C, with a mean of 0°C.

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

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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

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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 loosing 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.

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Table 1.1. Experimental Calendar.

Season	Experiment	Period	Dates	Treatment			
				Site 1: Stone House		Site 2: Alleck Meadow	
				Food	Predator	Food	Predator
1	1	1	Nov 27 – Dec 1	–*	–	–	–
		2	Dec 2-6	Full feeders†	–	Full feeders	–
		3	Dec 7-12	–	–	Full feeders	–
	2	1	Jan 9-15	–	–	–	–
		2	Jan 17-22	Full feeders	Merlin‡	Full feeders	–
	3	1	Feb 11-17	–	–	–	–
		2	Feb 18-21	Full feeders	Merlin	Full feeders	–
2	1	1	Nov 27 – Dec 1	Low§	–	Low	–
		2	Dec 2-6	Full feeders	–	Full feeders	–
		3	Dec 7-11	Low	–	Full feeders	–
	2	1	Jan 7-11	Low	–	Low	–
		2	Jan 12-16	Full feeders	–	Full feeders	–
		3	Jan 17-22	Low	–	Full feeders	–
	3	1	Feb 5-9	Low	–	Low	–
		2	Feb 10-14	Low	Kestrel‖	Full feeders	–
		3	Feb 15-19	Low	–	Full feeders	Kestrel
3	1	1	Nov 28 – Dec 3	–	–	–	–
		2	Dec 4-7	Full feeders	–	Full feeders	–
		3	Dec 8-12	Random low¶	–	Full feeders	–
	2	1	Jan 4-12	–	–	–	–
		2	Jan 13-21	Random low	–	Full feeders	–
	3	1	Feb 5-10	–	–	–	–
		2	Feb 11-19	Full feeders	–	Random low	–

* 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.

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