

# BEHAVIOR MATTERS: NARRATING SPECIES LOSS IN THE ECOLOGICAL AND BIBLICAL TRADITIONS

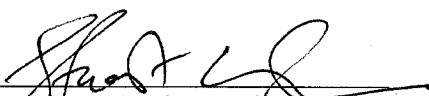
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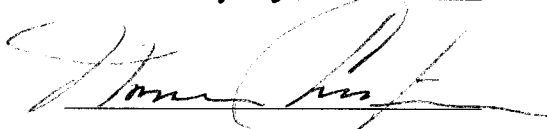
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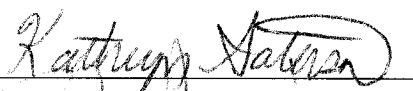
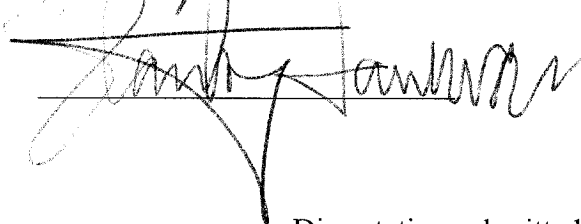
University Program in Ecology  
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Date: 5<sup>th</sup> Oct 2006

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Dissertation submitted in partial fulfillment of  
the requirements for the degree of Doctor  
of Philosophy in the University Program  
in Ecology in the Graduate School  
at Duke University

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## ABSTRACT

# BEHAVIOR MATTERS: NARRATING SPECIES LOSS IN THE ECOLOGICAL AND BIBLICAL TRADITIONS


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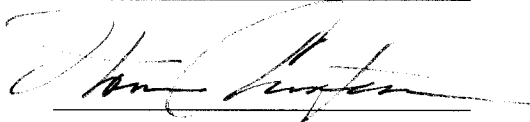
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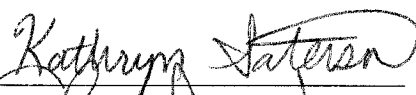
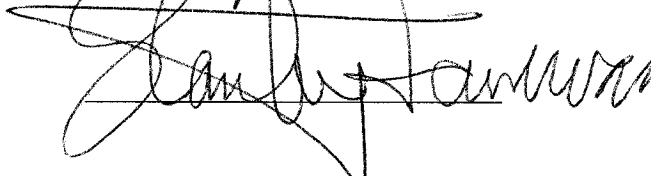
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2006

## Abstract

Species are going extinct at a rate a hundred times faster than expected, with future rates likely to rise to one thousand times faster. But individual species differ in their susceptibility to extinction. In the fragmented habitats that now dominate the planet, some species go extinct rapidly, while others persist. Behavioral differences between species are considered important, but empirical demonstrations are few. The studies that exist tend to be at spatial and temporal scales that are too confined or consider too few species – limiting their broad interpretation. I analyze a 14-year database of bird captures in forest plots from the Biological Dynamics of Forest Fragments Project near Manaus, Brazil to analyze the relationship of behavior to extinction susceptibility. I test how social and ranging behavior influence species loss, and find that species that always forage in groups tend to range widely and disappear from forest fragments. Species differ considerably in how far they disperse before and after fragmentation. Birds that are sensitive to fragmentation tend to move long distances and avoid the clearings between fragments. Species conservation is challenged by more than gaps in ecological knowledge, however. How scientists and religious groups conceive of ethics may limit popular support for conservation. I examine the ethics of two popular scientists, Stephen Jay Gould and E. O. Wilson, as they represent an ongoing debate in the sciences. The foundations of conservation biology – studying biodiversity for its preservation – question Gould’s language of “facts” and “values.” Martin Luther King Jr.’s remarkable social and political success seem to challenge Wilson’s strictly empirical ethics. Unlike Gould or Wilson, Alasdair

MacIntyre and Stanley Hauerwas describe an ethics that affirms both scientific inquiry and social traditions. Focusing on one social tradition – American Christianity – I examine the various approaches by different Christian groups towards species conservation. Some groups affirm conservation; others cast doubt on scientific evidence, claim species are not important, or do not engage the issue whatsoever. I argue ethics are neither strictly empirical nor strictly a matter of an irrational faith. Rather, any ethic requires a determinative will that is formed through membership in one's tradition. Far from offering pat answers, this provides a description of ethics that is currently estranged from conservation science.



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Every beginning is beginning again

Jean-Luc Marion

## Introduction

This dissertation represents four chapters devoted to the ecological and ethical dimensions of species extinction. The first two chapters are concerned with the ethics of extinction, or how humans view their own behavior relative to biodiversity conservation. Here I address how scientists, philosophers, and biblical thinkers consider ethical practice and how this may influence the state of conservation – as an ethical practice – today. The final two chapters deal with the ecological dimensions of extinction, and in particular how a species behavior influences its ability to persist in fragmented habitat. Here I present novel analyses from bird populations in the Brazilian Amazon. Conservation scientists deal with scientific, social, and cultural issues to study and effect conservation. Though the subjects I address are inexorably linked, conservation science, as an academic enterprise, has only scratched the surface of this interface. This dissertation attempts to treat openly these key issues.

In the first chapter, I focus on the hypothesis that how scientists conceive of ethics may limit popular support for conservation. Most scientists take ethical arguments for conservation as given and focus on scientific or economic questions. Though nature conservation is often considered a just cause, there is little further consideration. A lack of attention to ethical theory raises serious concerns for how conservation scientists conceive and practice ethics. I contrast two common ways scientists approach ethics, as demonstrated in the writings of Stephen Jay Gould and E. O. Wilson. Gould casts severe doubt as to whether any ethics are possible from science, whereas Wilson proposes science as the only path to ethics. I argue these two

methods ultimately limit popular support for conservation and I offer Alasdair MacIntyre's "virtue ethics" as an alternative. Unlike Gould and Wilson, MacIntyre provides an ethical theory that reconciles scientific inquiry and social traditions. Recent studies of the Civil Rights Movement in the United States affirm MacIntyre's claims and provide important insights for conservation today. These accounts argue that social solidarity and political success against segregation were possible only as rooted in the particular language, logic, and practices of a robust cultural tradition. If correct, conservation science should attend to several questions. On what basis can conservation achieve widespread cultural legitimacy? What are the particular social currencies for a conservation ethic? What role does science play in such a scheme?

Following MacIntyre, in the second chapter I analyze how one tradition in one setting – Christianity in the United States – addresses species conservation. This chapter reviews the substantial body of scientific research of current ecological trends and surveys the dominant worldviews of Christian ethics towards biodiversity conservation. The Christian worldviews represent unique types of ethics. Each worldview offers a different response to the scientific community advocating biodiversity conservation. My research suggests that the Christian Church in the United States either: encourages biodiversity conservation as an ethical issue with a biblical origin, disagrees with the scientific community that there is a biodiversity crisis, maintains there are more pressing moral concerns, or avoids the issue entirely. I argue that an environmental ethic that is faithful to the Christian tradition is "intratextual," or casts itself into the biblical narrative.

In the third chapter, I switch gears to examine questions of ecological importance. Identifying traits that predispose species to extinction remains a central topic in conservation ecology. Behavioral differences are likely to matter, but empirical evidence is scarce. In one study, social carnivores were more prone to local extinction in fragmented landscapes than solitary carnivores. The posited mechanism is that because social groups range widely, they more often encounter threats in and beyond the edges of their habitat than do solitary species. Here I test the generality of this idea, examining evidence from a different ecosystem and taxon. Using a 14-year bird capture database from forest plots near Manaus, Brazil, I examine how sociality affects bird species' persistence in forest fragments. Flocking species typically range over larger areas than solitary ones. Thus, I hypothesize that flocking species are less likely to persist in small forest patches than non-flocking species. From the literature, I identify 30 species that join mixed flocks or follow ant swarms. I quantify these social frequencies in both continuous and isolated forest plots from mist-net data, which correlates well with an observer-based method. Using analyses of covariance techniques, I find bird species that typically forage in flocks before plot isolation persist for shorter times than those that infrequently join flocks. Species that drop out of flocks after fragmentation persist longer than those that remain in flocks. The model I develop outperforms a nested analysis of variance that treats each species as a variable, inherently testing for life history idiosyncrasies and phylogeny. Recapture rate, calculated using MARK, did not explain the remaining variation from my model.

Flocking behavior, and its plasticity, influences species persistence and so is an important criterion in understanding local extinction.

Lastly, I extend the ideas from chapter 3, examining the spatial behavior of tropical forest birds explicitly. Many ecologists believe birds disappear from tropical forest fragments because they are poor dispersers. I test this idea using a spatially explicit capture database from the Biological Dynamics of Forest Fragments Project near Manaus, Brazil. I measure bird movements directly, over relatively large scales of space and time, both before and after landscape fragmentation. I find that species which disappear from fragments move extensively between plots before isolation, but not after, and often disperse to longer distances in continuous forest than in fragmented forest. Such species also preferentially emigrate from smaller to larger fragments, showing no preference in continuous forest. In contrast, species that persist in fragments are generally less mobile, do not cross gaps as often, yet disperse further after fragmentation than before. “Heavy tailed” probability models usually explain dispersal kernels better than exponential or Gaussian models, suggesting tropical forest birds may be better dispersers than assumed with some individuals moving very long distances.





– One –

## Conservation as virtue: a scientific and social process for conservation ethics<sup>1</sup>

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<sup>1</sup> This chapter also appeared as the cover article for the October 2006 issue of Conservation Biology: Van Houtan, K. S. 2006. "Conservation as virtue: a scientific and social process for conservation ethics." Conservation Biology. 20 (5): 1367-1372. For cover art see Figure 1.1.

## **Introduction – Ethics in conservation science**

Since the discipline of conservation biology began in the late 1970s, scores of university departments, academic journals, and professional societies have emerged. These bodies form an academic collective of conservation science whose goals are to study and preserve nature. Toward this end, conservation science is often said to divide its efforts between scientific research and the application of research to affect policy (Soulé and Wilcox 1980, Soulé 1986, Meffe and Carroll 1997).

In spite of the increasing attention on the science of environmental conservation, conservationists are said to defend nature preservation for distinct reasons. That is, scientists attribute three kinds of “value” to nature: aesthetic, economic, and ethical (Ehrlich and Ehrlich 1981, National Research Council 1999). Biodiversity may inspire, provide resources and information, or have inherent value, respectively. Conservation scientists most often restrict themselves to scientific and economic theory, allowing others to scrutinize ethics and philosophy.

From the perspective of formal education and training, perhaps this theoretical focus is to be expected. But should it remain acceptable? Although avoiding the theory of ethics poses obvious intellectual gaps, it may also cause problems in conservation practice. For instance, overlooking ethical theory may avoid the necessary logic and terms to achieve greater cultural relevance through constructive dialogue with those who do not endorse a conservation ethic. As an example, not all religious groups in the United States affirm a robust form of conservation. Many do, of course, but some

contend with the science, others deem conservation a minor concern, and still others neglect the issue completely (see Chapter 2). How may conservation scientists engage such groups if they only know scientific theory? Perhaps scientists, and especially conservation scientists, should not take ethical theory for granted.

### **Strictly empirical ethics**

Essential to this discussion is conservation science's immersion in ethical language (e.g., Barry and Oelschlaeger 1996, Meine and Meffe 1996, Roebuck and Phifer 1999, Wilson 2000, Soulé et al. 2005). Conservation, even if conceived on scientific grounds, is a framework for a specific "right" outcome. Protecting species, designing nature preserves, restoring degraded ecosystems, promoting sustainable use – these are thought of as "good" undertakings (Marx 1970, Soulé 1985, Roebuck and Phifer 1999, Ludwig et al. 2001). When Pimm says he has "a moral responsibility as a citizen to make people aware of what science means" (Kaiser 2000) he shows that conservation science takes a moral stance and weighs judgments to specific decisions. For some scientists wedding ethics and science is taboo (Wiens 1996, Norton 1998, Kaiser 2000, Nielsen 2001). For others, the opposite may be true and one may necessarily flow from the other (Bazzaz et al. 1998, Lubchenco 1998, Ehrlich 2002). But whether the two are separate or joined how conservation scientists "do" ethics deserves careful theoretical attention. If there is a lack of consensus on nature's value, there may be even less consensus on how ethics are done (Callicott 2006).

According to many conservation scientists, however, empirical science seems the key ingredient in the recipe to save nature. Furthering science, promoting its appropriate use, protecting the Earth's systems – these phrases appear successively in the mission statements of countless conservation organizations. The Society for Conservation Biology, for example, was formed to “develop the scientific and technical means for the protection, maintenance, and restoration of life on Earth.” The Ecological Society of America founded its Sustainable Biosphere Initiative more outspokenly. “Unless the science of applied ecology is based on a sound foundation, attempts to manage the environment are bound to fail” (Mooney and Levin 1991). As Lubchenco alluded in her presidential address to the American Association for the Advancement of Science, ecological preservation “can be only obtained through basic scientific research” (1998). Meffe, the current editor of this journal previously wrote that, “In an ideal world, biologists would experiment, observe, tell policy makers what to do, and it would be done” (Meffe and Viederman 1995).

A trust in strictly empirical conservation ethics is widespread. That is, some scientific inquiry is the necessary means to determine the right measures for conservation (e.g., Lubchenco et al. 1991, Lubchenco 1998, Wilson 1998). Prominent ecologists encourage environmental scientists to demonstrate the broader societal significance of their research (Bazzaz et al. 1998, Ehrlich 2002). For to Bazzaz et al. (1998) ecological science ought to consist of “(i) doing first-rate research and (ii) publishing it in the technical literature for the benefit of scientific colleagues” and “(iii) informing the general public (and, especially, taxpayers) of the relevance and

importance of our work.” Ehrlich is more emphatic: “environmental scientists can be advocates, but also that they ethically must be advocates” (2002). Journal articles therefore, not surprisingly, frequently offer broad policy or management implications (Meffe and Viederman 1995). Armed with scientific research, conservation organizations advocate policies and seek influence with political decision makers. Do these practices falsely restrict conservation to the domain of science? What would be the harm in viewing ethics as being strictly derived from experimental science?

This ethos of science dominance is not without its critics in the conservation community (Barry and Oelschlaeger 1996, Orr 1999, Butler 2000, Ludwig et al. 2001). Such critiques typically argue that “pure science” is a fiction, that no scientific observation is value free, and that scientific decisions can serve political and economic agendas. In essence, scientists are people too. Some then contend that giving science too much responsibility for a greater social welfare (like conservation) is like asking wolves to guard sheep (Butler 2000). Such criticisms are often well-conceived, but seldom address a glaring issue: Can what is problematic – and consequently what is “just” – somehow be understood strictly scientifically or apart from a particular human social tradition? Furthermore, recalling the pastoral metaphor, if biodiversity conservation is sheep, maybe an important question to ask is who plays the shepherd. Prominent scientists provide different answers.

## **Ethics from two influential scientists**

Many scientists are wary of a strong link between science and ethics. The late Stephen Jay Gould is the exemplar in the natural sciences. Gould proposed a theory of “nonoverlapping magisteria” to distinguish facts from morals (Gould 1997, 1999). Gould’s repeated argument was that the two areas are essential – yet completely separate – in the human existence. There is no hope of finding any moral lesson from scientific facts, trying only makes matters worse. Gould later refined his theory but never backed away from its central claim: “Each of the domains or magisteria embodies, inside its own being, so many different methods, concerns, and styles of explanation that no knee-jerk united front could be conceived” (2003: 156). As many know, the backdrop for Gould’s arguments is the frequently hostile science and religion debates over Darwinian evolution. Gould’s experience in this context led him to be extremely cautious with ethical statements. In the end Gould’s caution prevents him from producing any ethic from scientific observation – a concept that is difficult to reconcile with conservation science. Mingling what Gould separates seems appropriate (indeed, even Gould [1990] does not strictly adhere to his theory). But how?

In his strictly empirical or mechanistic notion of ethics, E. O. Wilson’s thinking is a distinct alternative to Gould’s. Like Aldo Leopold before him, Wilson defends the ethical premises of conservation biology, arguing that a scientific understanding of life’s variety increases the ethical significance of protecting it (Wilson 1984, 1998).

The more one knows, the more just a decision one may make. Here, unlike with Gould, facts and morals are not discrete; rather they are purposefully aligned. Wilson contends that ethics are derived from scientific research – an idea widely affirmed in scientific practice. In Wilson’s words: “An enduring code of ethics is not created whole from absolute premises but inductively... through an expansion of knowledge and experience” (Wilson 1984: 124). Later Wilson is more explicit and defends a “purely material origin of ethics” (1998: 263). Gould’s exclusive sets are Wilson’s flow chart.

Although many scientists may be sympathetic to Gould’s position, they seem to practice Wilson’s ideas more often. What is interesting about Gould and Wilson is how their views reveal an ongoing division in the sciences. For Gould, science and ethics are inherently separate and ethics are, at best, a murky process for each person to navigate individually (and perhaps privately). For Wilson, ethics spring from the academic community through a process of observation, logic, and scholarly argument. Perhaps the very real differences between Gould and Wilson flow from their respective undertakings. Thinkers directly faced with immediate and tangible problems – species loss, for example – are understandably inclined toward concepts of justice. Those defending the scientific method from ideology or religious fideism are understandably shy toward ethical commitments. Nevertheless, how ethics are done, who does them, and the particular social context for ethical reasoning, are all relevant and urgent topics for conservation science, the so-called “crisis discipline with a deadline” (e.g., Lovejoy 1980, Soulé 1986, Ehrlich 2002).

Whoever carries the responsibility for doing ethics, though, a stark reality confronts them. The ecological crisis is ever increasing and the voting public does not actually seem to care (Orr 2002, Ehrlich and Ehrlich 2004, Shellenberger and Nordhaus 2005, Kristof 2005). No environmental ethic is articulating and motivating lifestyle changes that are both significant and widespread. Is something therefore lacking with the ethical systems represented in Gould and Wilson? Alasdair MacIntyre's virtue ethics may provide hope.

### **MacIntyrean Virtue Ethics**

An important figure in modern philosophy, Alasdair MacIntyre has contributed broadly to ethics, politics, metaphysics, and the social sciences (Murphy 2003). His work is in large part a critical response to his renowned instructors, the philosophers of science A. J. Ayer and Karl Popper. Like Gould, MacIntyre carefully scrutinizes the link between scientific observation and ethics. Like Wilson, MacIntyre finds a place for scientific experience in ethics. Unlike Gould, MacIntyre argues that any scientific inquiry already has an ethics in tow and that all ethics require a particular sociology. Unlike Wilson, MacIntyre contends that ethics require traditions constituted by practices sustained in particular communities over generations by scientific argument and ritual. Although similar in several respects, MacIntyre is wholly different from Gould and Wilson.



Drawing from Aristotle, MacIntyre argues for an inexorable link between scientific inquiry and ethics. In After Virtue (1981:82) he states, “The modern contrast between the sphere of morality on one hand and the sphere of human sciences on the other is quite alien to Aristotelianism because... the modern fact–value distinction is also alien to it.” Here MacIntyre helps us see that Gould’s language of “facts” and “values” is misleading. Similar to the linguistic argument that language makes thought possible (e.g., Wittgenstein 1953) MacIntyre asserts that observers require concepts to comprehend what they see (MacIntyre 1981, 1999). Referencing Shakespeare’s Hamlet, MacIntyre points to the catch–22 of scientific observation – until one knows what theories to adopt one does not know what is evidence, but unless one knows what is evidence one cannot tell which theories to employ. As a result, Hamlet’s quest to understand his father’s death and how he should act, are not seen as successive actions but the same action (MacIntyre 1977). One does not first perform one then the other; they are both done with the other immediately in mind. Namely, understanding is impossible without prior concepts and just action cannot be extricated from understanding. The ancient Greeks taught these ideas with the aphorism “to know is to do.” In MacIntyre’s view, any attempt to separate “knowing” from “doing” is a misconception.

Science–studies philosophers, especially Thomas Kuhn and John Ziman, treat science as socially embedded and socially constructed activity, as does MacIntyre. In *The Structure of Scientific Revolutions*, Kuhn casts science as a community of persons firmly set in historical contexts (1962). In *An Introduction to Science Studies*, Ziman

claims that social norms render scientific inquiry and cast doubt on the existence of “pure science” (1984). According to MacIntyre, Immanuel Kant, the father of the Enlightenment, even flirts with Ziman’s idea (1981). If scientific observation is not free from historical and social influences then Gould’s fact–value barrier seems porous. Conservation biologists acknowledge this (Barry and Oelschlaeger 1996, Ludwig et al. 2001). What makes MacIntyre interesting is how he extends the argument of science studies philosophy by focusing on the particular social context for ethical practice. In doing so, MacIntyre locates a void in most versions of ethics as practiced by conservation scientists.

For MacIntyre, observing, understanding, and acting intelligibly require the particular place of a social tradition. That is, both science and ethics require a particular place in human society. Although the context may vary it remains essential to their very nature. How an observation, or an ethical judgment, is framed is contextual: “There is no standing ground, no place for inquiry, no way to engage in the practices of advancing, evaluating, accepting, and rejecting reasoned argument apart from that which is provided by some particular tradition or other” (MacIntyre 1988: 350).

Scientific concepts therefore are of a social dimension and dependent on membership to some particular social or biological community (MacIntyre 1999). Therefore, ethics ultimately depend on how people doing them view themselves and the community to which they belong (MacIntyre 1988: 393). Such a view challenges how scientists conceive ethics and contributes something new to conservation ethics (e.g., Callicott 2006) and conservation science.

## **Practical consequences for conservation**

The implications of MacIntyre's argument mean it is a fateful mistake to think one can first determine moral rules abstractly or inductively and later apply them to specific cultural contexts. Yet what MacIntyre names a mistake seems to dominate conservation science. For Hauerwas (2001), determining ethics wholly within science falsely discards the role of nonscientific social traditions in moral practice. A sustainable form of justice then is constituted by and maintained through social practices and traditions within local communities. Essentially, MacIntyre's argument does not invalidate science as a means or type of rational inquiry. However, it does check such inquiry from being a sole, asocial method in forming concepts of justice. Ethics are neither strictly empirical nor strictly a matter of an irrational faith. Rather, in MacIntyre's terms, any ethic requires a determinative will that is formed through membership in one's tradition (something that is often complex). An ethics without these relationships is empty formalism (MacIntyre 1977). Fundamental aspects of conservation biology – identifying ecological problems and solutions – tend to assume a general, inalienable, or universal account of justice. MacIntyre argues this approach is a philosophical mistake: no such thing exists.

The Civil Rights Movement in the United States is evidence to MacIntyre's claims. Two recent independent studies show that the practice of the biblical tradition, in particular, named racism a problem and fanned the movement into flame (Chappell 2004, Marsh 2005). Enthusiasm and solidarity did not come from a theoretical or

academic “common sense” but were legitimized through the language and practices of Christianity (Orr 2001, Brooks 2004). Smart, socially abstract maxims, like those of then-prominent intellectuals John Dewey and Gunnar Myrdal, achieved nothing substantial for African American rights (Chappell 2004). To the contrary, segregation and disenfranchisement were overthrown dialectically – in the particular language, logic, and practices of a particular tradition. In this case, the dialectic was biblical, taking the form of a prophetic story, a pessimism in human institutions (this includes churches), corporate prayer, and – most notably – nonviolence. As for MacIntyre, these studies see the social tradition as the place where ethical reasoning takes place. Viewed this way, the Civil Rights Movement was a religious cause with political implications, not the reverse. Conservation as envisioned in the sciences seems to have this backward.

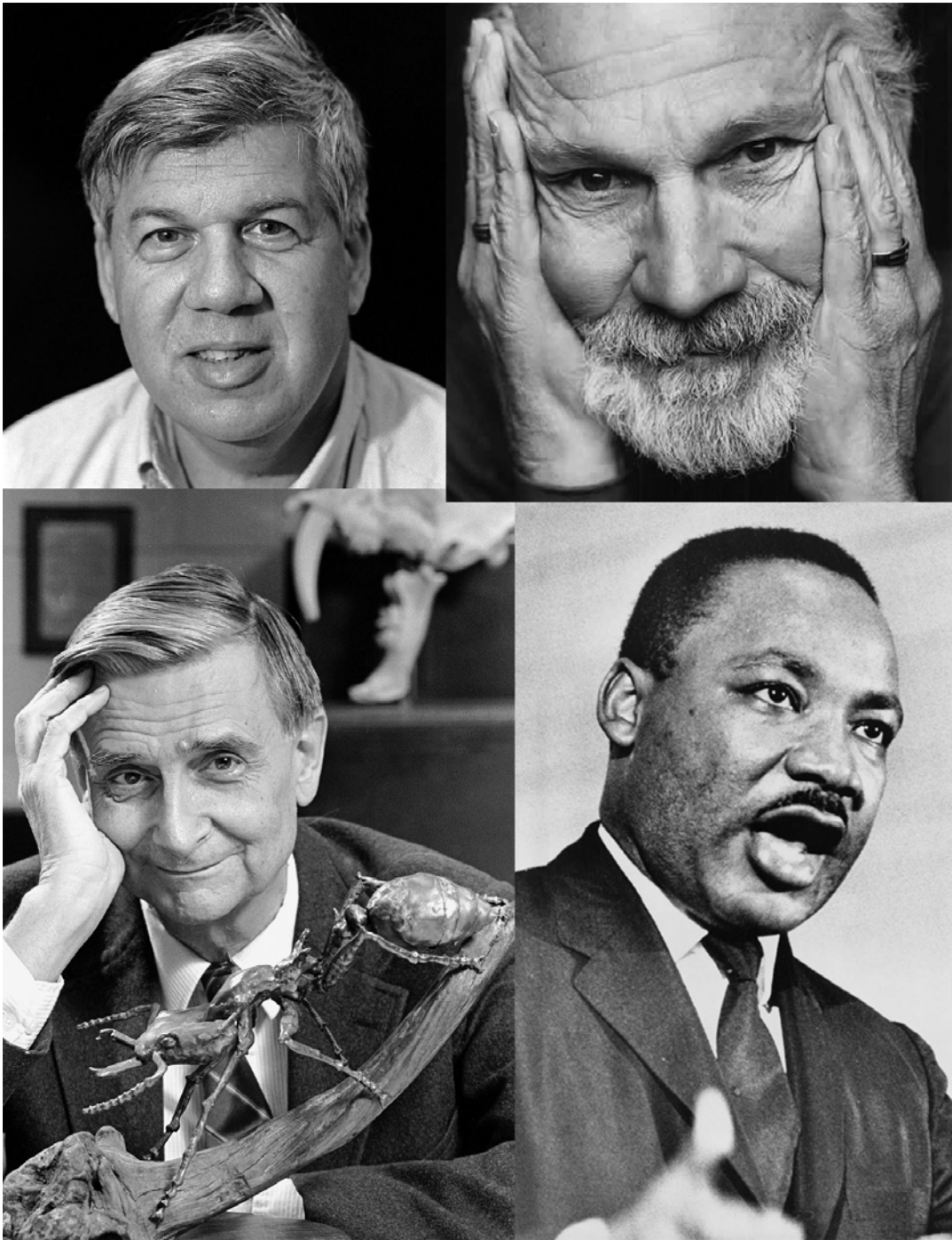
The dominant conceptions of ethics in conservation science may explain conservation’s remarkable unpopularity. What ethical currency do socially generic recommendations carry? What is the social basis for sacrifice or allegiance to the cause of conservation? Conservation science – as an ethic – is no different from other forms of ethical practice. In MacIntyre’s terms, ethics requires a particular communal framework for intelligibility. Conservation arguments, then, require expression in the language of social traditions if they are to be authentic and realized. The resulting goal is not practically intellectual but involves something akin to virtue. The problem with the current ethics in conservation science is that science alone is hard-pressed to name virtues. Perhaps the immediate challenge facing conservation science is to

identify the dialect within particular traditions that names nature conservation a virtue, and subsequently, to work a description of what form virtue takes from within the tradition. Yes, scientific research is crucial in articulating ecological failings. But science itself cannot form socially sustainable ethics. Ethics are in some sense empirical, just not strictly so.

My argument here can be summarized with the following question: Is nature conservation a virtue or is it just good science? If it is plainly a scientific matter, then strict empiricism reigns and the environmentalists' battle is one of scientific research, political savvy, and power (Gill 2001). Nature – which includes human communities – likely loses a battle of this kind. On the other hand, if conservation is a virtue then scientific arguments alone are insufficient and the battle visibly involves ethics, social traditions, as well as science. Strict empiricism is then called into question or is, according to Wendell Berry, “pathological” (2000). On the other hand, the view I describe does not prefer insipid ideology over science, as has been the repeated example of the Bush administration (e.g., Lee 2003, Luntz 2003, Mooney 2005). Rather, my argument elevates science from simply purveying information to a sort of social prophecy; where prophets are not experimenting fortune tellers but professors of a hoped-for future. Then, as for MacIntyre, asking, why should we care about conservation? is not the right question. The social tradition names it a virtue; those doing conservation are just practicing their tradition. “Does the tradition regard conservation?” is a better question. The reason many Americans are thus not outraged at environmental destruction is likely that the tradition most determinative

of their lives – individualism, consumerism, nationalism – does not practice a conservation ethic.

During his stirring “I have a dream” address Martin Luther King Jr. revealed the crux of his vision (Chappell 2004). He saw “out of the mountain of despair a stone of hope.” King’s metaphor is an apt paradox: hope lies amidst despair. Certainly conservation has its own “mountain of despair,” as study after study demonstrates. Spinning despair into optimism for the sake of gaining popular support, as some suggest, seems an unwise distraction and avoids the larger issue. There is no robust hope in the dominant versions of ethics as practiced in the conservation sciences. To succeed as a social cause, conservation needs a hope that academic science itself cannot provide. Conservation needs a cultural legitimacy that inspires enthusiasm, allegiance, and personal sacrifice – in other words, actual changes in human behavior. Such a vision does not provide a straight path to easy answers, rather; it offers a description of ethics currently estranged from conservation science.



**Figure 1.1**

**Figure 1.1:** How scientists consider ethics may limit popular support for conservation. The foundations of conservation biology – studying biodiversity for its preservation – call into question Stephen Jay Gould’s language of “facts” and “values.” Martin Luther King Jr.’s remarkable social and political success challenges Edward O. Wilson’s strictly empirical ethics. Unlike Gould or Wilson, Alasdair MacIntyre (not pictured by request) and Stanley Hauerwas describe an ethics that affirms both scientific inquiry and social traditions, giving new hope for conservation today. Clockwise from upper left: Stephen Jay Gould (photo by Jon Chase, Harvard News Office), Stanley Hauerwas (photo by Chris Hildreth, Duke University Photography), E. O. Wilson (photo by Jon Chase, Harvard News Office), Martin Luther King Jr. (photo by United Press International, United States Library of Congress). Image design by K. S. Van Houtan. This image was the cover image for the journal article version of this chapter.





– Two –

## The various Christian ethics of species conservation<sup>1</sup>

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<sup>1</sup> This chapter has been published elsewhere: Van Houtan, K. S. and S. L. Pimm. 2006. "The various Christian ethics of species conservation." In Religion and the new ecology: environmental prudence in a world in flux. D. M. Lodge and C. Hamlin, Eds. South Bend, IN: University of Notre Dame Press: 116-147.

We tend to take a connection between religion and ethics for granted; one's faith ought to help shape one's moral values. For much of human history, however, worship meant making the proper sacrifices and following the proper ritual; it might have very little to do with morality.

William Placher (1983, 22)

Typology does not make scriptural contents into metaphors for extra-scriptural realities, but the other way around ... It is the text, so to speak, which absorbs the world, rather than the world the text.

George Lindbeck (1984, 118)

## **Introduction: Tensions and Barriers**

The setting is High Table at Balliol College, Oxford University, early in the last century. The characters are the cleric and Master of the college, Benjamin Jowett, and renowned Darwinist and atheist J. B. S. Haldane. The set up is Jowett's question: "What could one conclude as to the nature of the Creator from a study of His creation?" "An inordinate fondness for beetles," is Haldane's reply. Since there are more kinds of insects than anything else, and almost half of all insects are beetles, Haldane's quip is apt. As it turns out, however, this tale is a fabrication (May 1989, Williamson 1989). Nonetheless, it was a popular story at Oxford thirty-five years ago when my advisor, Stuart L. Pimm, was an undergraduate there. To scientists who study biodiversity – the variety of life on Earth – and its evolution, the temptation to cock a snoot at Christians is sometimes hard to resist.

The story has the feel of gallows humor though for it reveals the sometimes strain between science and religion. While Stoll (2006) and Cittadino (2006) address the close historical and ideological ties between Christianity, ecology, and conservation, the tension today in the United States between some sciences and conservative Christians is pronounced (Miller 1999, Eldredge 2000, Mooney 2005:164–185). The threat of Christian-inspired litigation against the teaching of evolution is particularly significant here. In this battle, both sides expend considerable resources with the result being a remarkable cultural stalemate. As an example, a recent USA

TODAY/CNN/Gallup poll shows that 53 percent of Americans reject the Darwinian notion of evolution (2005).

Maybe it is presumptuous in light of the current political climate to ask ecologists and Christians to find common ground in conservation. Yet, that is exactly what I propose. I recognize that some, mostly politically conservative, Christians in the United States likely put “environmentalism” and evolution in the same box. Of course, this association is legitimate. Evolution is an important aspect of ecology. Scientists studying extinction owe large debts to Wallace and Darwin – the founders of evolutionary theory. While the birth of species aids an understanding of the death of species, origins and demises are in many ways different topics. Some Christians may still view this affiliation suspiciously and therefore disregard ecologists and their science.

Even with different positions about evolution, common ground between ecologists and Christians seems possible, if not straightforward. If a biblical basis exists for environmental stewardship, and ecologists have shown ecological peril, then the two groups seem destined coworkers in conservation. However, this consensus is not as common as one may think. As I show in this chapter, for various reasons many Christians in the United States do not support environmental protection. In some ways this situation recalls the role the Church played in the Civil Rights movement of the 1960’s. Martin Luther King then observed that, “the contemporary church is a weak, ineffectual voice with an uncertain sound” (King 1999, 359). King’s remarks could also be said of the role Christians play in the United States today with

environmental protection. Although disagreements between Christians and ecologists regarding evolution are common, tension also exists over the ethics of conservation.

For ecologists, there are three basic ways that biodiversity has value. This is called the three “e’s,” for ethics, esthetics, and economics (Ehrlich and Ehrlich 1981, NRC 1999). That is, biodiversity has an inherent value, is the currency of science, and provides for our practical human needs, respectively. Although each criterion provides its own case for preserving biodiversity, economic arguments are the most common. This comes as little surprise, and the numbers are astronomic. In one estimate, the environment and the services it provides were valued at twice the global GNP, or US\$ 33 trillion annually (Constanza et al. 1997). This figure includes tangible goods (like food and medicines) but also “ecosystem services” such as crop pollination, clean water, and climate stability (Daily 1997). Despite their figures, however, Constanza et al. (1997) do not believe economic arguments are enough for environmental protection. If this is true, then the other forms of valuation – esthetic and ethical – deserve further exploration.

For many Christians economic arguments, like those Constanza and his colleagues present, may miss the mark. A strictly logical approach to Church doctrine or ethics has received much insightful criticism from theological scholars in the past decades (MacIntyre 1981, Lindbeck 1984, Northcott 1996, Placher 1996). Logical reasoning plays a role in religious faith for certain, but it is a more complicated matter. Such scholars pay attention to the scriptures, the church, ritual practices, and the linguistic nature of thought – in addition to rationality. Along this line, Stanley Hauerwas

(1983: 19) adds that, “if what is said theologically is but a confirmation of what can be known on other grounds or can be said more clearly in non–theological language, then why bother saying it theologically?” Here Hauerwas identifies that ethics in non–theological language will be worse than unattractive to Christians – such ethics will be incoherent. Theological language is what gives Christian ethics intelligibility to Christians. As a result, casually using “nature” or “biodiversity” in place of “creation” is incredibly significant when considering Christian environmental ethics.

On the other side of the aisle, ecologists are increasingly seeing conservation as an ethical issue (Wilson and Perlman 2000). Scientists are allowed moral convictions too. At times this places ecologists in the ironic position of expressing their ethical concerns to the Church. “Scientists are bad enough when they promote science” one imagines some churchgoers thinking. “Now they are trying to define our moral agendas!” Indeed, I agree. The conviction for environmental conservation ought to come from the Church – through its inspiration and leadership<sup>2</sup>. As I mention, the problem seems that the Church does not have a coherent vision of environmental ethics (Haught 2006).

Although we can debate how species are born for another century we do not have that long to contemplate extinctions. There is nothing normal with our current planet. The trends of ecological degradation that I discuss are singular in the Earth’s history. They are the direct result of human mismanagement and negligence. For those who

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<sup>2</sup> As both Chappell (2004) and Marsh (2005) argue, Martin Luther King Jr.’s Christian vision propelled the Civil Rights movement to successfully overthrow Jim Crow.

prefer using “creation” in the place of “biodiversity,” perhaps the ethical position ought to be even clearer. Creation is God’s gift to humanity; poor stewardship of this blessing is an explicit sin (Patriarch Bartholomew I 1997). Unless we change our current actions, we will likely commit a third of all creation to an inevitable path to extinction during this century (Pimm 2002: 201–216). Common ground between ecologists and Christians is urgent.

The rest of this chapter is divided into three sections. In the first section, I report on the ecological state of the planet. Science is crucial to a proper conservation ethic; what I present is the consensus of ecologists. I focus on the evidence for massive ecological change to forests, drylands, and oceans, and discuss their impacts to biodiversity. In the section that follows, I propose a typology of Christian environment ethics. Christian groups do not agree on what a “Christian” environmental ethic is. There are deep expressions of concern, certainly. However, many doubt the problem exists. Others deem the problem irrelevant. Some are even indifferent to the issue. The final section is an assessment of the various worldviews.

## **Science’s Worldview: The Planetary Audit**

At the start of the new century, there are 6 billion humans. Some models predict this number to be 9 billion by 2050, but most projections consider that estimate optimistically low (United Nations 2003, 9). Currently, roughly one and a half billion



people live comfortable lives, while another billion are on the verge of starvation. Of the remaining four billion, a quarter will become major consumers (owning cars and refrigerators) within a few decades (Myers and Kent 2003). Population statistics are well known. Their environmental consequences are not.

Land covers roughly a third of the Earth's surface but generates 97 percent of our food (Pimm 2002). Our diverse uses of the land are easily visible where we convert natural systems to agriculture and cities. One all-encompassing single measure to summarize human impacts on the Earth is to weigh the material plants produce each year, and then ask how much of it we consume. The answer is "not much." About 4 percent of the annual plant production is used for our food, for our domestic animals; and by the wood we use for building, paper, cooking, and heating (Pimm 2002: 27–31). That answer is misleading. It does not include how much green stuff we waste while we directly consume the other parts. Add those numbers in and the total human use of plant production comes to almost 40 percent of the global production (Vitousek et al. 1986, Rojstaczer et al. 2001). In other words, humans appropriate almost half of what plants produce every year, and 90 percent of what we consume is wasted.

Most of the stuff we use is from the warmer, wetter half of the planet where plants grow best. What remains in dry or cold areas is much less suitable for our use. The warm wet places are where forests grow most easily. The warmest and wettest of those are the tropical forests. These forests once covered 15 percent of the Earth's land surface, yet they contain an astounding 80 percent of the world's tree species

(Vitousek et al. 1986). Despite this great ecological importance, we do not use tropical forests sustainably. To the contrary, we are continuously harvesting them and reducing their total area. The result is that tropical forests shrink by 10 percent of their original area every decade (Myers 1992, Skole and Tucker 1993). Tropical forests do not regenerate nearly as easily as temperate forests (Pimm and Askins 1995).

The drier half of the land surface offers less plant production. It is harder to grow crops there. Yet, paradoxically, we use these areas in less efficient ways. Drylands are harder to use, they provide less food, and they are easier to abuse. Because they contain few resources, those resources are easier to exhaust. Dryland misuse has led to wind and water erosion and has depleted the fertility of the soils on over half of these areas. As an example, massive plumes of eroded African soil stretch across the Atlantic Ocean. Not only does this demonstrate dryland abuse, the effect to the oceans is significant. These dust plumes destroy corals throughout the Caribbean (Garrison et al. 2003). Grazing animals (mostly cows and sheep) are largely to blame for this mismanagement (Pimm 2002). Grazing has changed the vegetation of these areas often irreversibly (Dregne 1983, Dregne 1986, Dregne and Chou 1992). The effects of dryland abuse are serious and far-reaching.

Next to vegetation and soils, freshwater is another universal currency that we spend freely, and without much consideration for the future. Of the rain that falls over land surfaces, the land soaks up two-thirds. The remaining third runs off the land into

rivers, mostly in remote places, or as floodwater. We consume a remarkable 60 percent of the accessible runoff each year (Postel et al. 1996).

Despite its vastness, about 90 percent of the ocean is a biological desert. We use a third of the ocean's annual production in the remaining area – from which comes 99 percent of the global fish catch. Surprisingly, however, our increasing ability to harvest these fisheries is not yielding a larger catch. In spite of advances in harvesting technologies, overwhelming evidence points to the opposite. Fisheries are declining, and dramatically so. Our activities are destroying the ocean's ability to supply even what we take today (FAO 1995, Pauly et al. 1998, NMFS 1999).

Now, to my focus: biodiversity. Probably 10 million types of animals and plants inhabit this Earth. Their loss poses the greatest environmental concern, as species extinction is irreversible. The scientific position asks, is there anything special about the present loss of species, compared to half a billion years of change? Haven't species always gone extinct? Isn't nature always in flux? Isn't humanity a part of natural ecosystems? If so, are our impacts allowable? The overwhelming scientific consensus is that human impacts are driving species to extinction hundreds to thousands of times faster than is expected from the natural, or background, rate (Pimm et al. 1995, Pimm 2002: 201–216).

A relevant question then is to ask how often life has disappeared at the rate we project? The answer is only five times in life's history. This is potentially the sixth great extinction. For a measuring stick, the last comparable event in the Earth's

history (65 million years ago) eliminated the dinosaurs. We know from the last major extinction that it took about 5 million years to regain the variety of species diversity and an additional 15 million years to restore the variety of families to their previous values (Raup and Sepkoski 1984). To place these numbers in perspective, consider that five million years is twenty times longer than the entirety of human existence. Based on stable population growth, 500 trillion people will be affected during this period, which is 10,000 times all the humans that have ever lived (Myers and Knoll 2001)! Clearly, even if just for anthropocentric reasons, our present course of action deserves consideration.

Scientists use the term “biodiversity” to represent the entire variety of life – ecosystems, species, populations, and genes. Human actions toward land, freshwater, and oceans have already caused biodiversity to decline. Even greater losses will occur if humanity continues its present unsustainable use of natural resources. In documenting this decline scientifically, there has been a focus on species extinctions. Species losses are also the aspect of biodiversity loss most often considered, for example, by the United Nations Convention on Biological Diversity. This chapter too focuses on species extinctions, as species are a proven and effective unit to measure conservation<sup>3</sup>.

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<sup>3</sup> Naturally, the subject is broader and more complex than our simplification. For example, a species may survive in a given area yet lose much of its genetic diversity (Hughes et al. 1997, Hughes et al. 1998). Furthermore, an ecosystem may survive yet shrink enough in area and thus lose its historical function, or even most of its constituent species.

Within our own species, one can apply language as a measure of biological diversity and distinctiveness. All totaled, there are roughly 6,500 distinct languages. An ecologist's first question might be to ask, "What is the minimum number of speakers required to ensure its survival?" That is to say, how many speakers are required so that the language passes onto the next generation, in the face of challenges from the major international languages? History suggests that the cut off is somewhere between 100,000 and a million speakers (Pimm 2000). Above this threshold, languages are resilient to even determined efforts to eliminate them. Below it, and few languages survive. Only about 500 languages are spoken by more than a million people. This suggests that about 90 percent of the linguistic – and so likely cultural – diversity will disappear within a generation. While this may be narrated in some circles as the advancement of modern civilization, the reality of this loss is stark.

The greater part of biodiversity is in the world's tropical wilderness forests. These forests are distributed in three major regions: the Amazon, the Congo, and in and around New Guinea. When these forests disappear, the indigenous peoples inhabiting them do as well. This formula for genocide has culled languages and peoples throughout history. In recent history, the lessons from destroying the prairies and forests in North America, South America, and Australia are clear. The fate of ecosystems and native peoples are linked. When the ecosystems disappear, so do the indigenous cultures.

Finally, there is the concomitant threat of global climate change. The planet has already warmed and done so at a geologically unprecedented rate. This is a direct

result of increasing greenhouse gases from human activity.<sup>4</sup> The projections are that the Earth will warm more, and perhaps much more, in the next 50 years. The ecological consequences of these changes are not easy to predict, but they are already frightening. Other things being equal, species with small geographical ranges will suffer proportionately greater than species with larger ranges (Thomas et al. 2004). Species with small ranges are already disproportionately vulnerable to extinction (Pimm and Lawton 1998). These species simply do not have as many places to survive.

## **The Christian Worldviews**

An interesting tension arises when people sharing the same religion disagree on ethical issues. Even though common traditions unite Christian groups, theological unity is regrettably infrequent. This is certainly true in the case of environmental issues, especially those associated with biodiversity conservation. The remainder of this chapter asks how the major Christian groups in the United States approach the conservation of species. How do they respond to what scientists say about the state of biodiversity? What are the different positions and patterns of thinking? In addition, on what bases do these views disagree? For right now, I focus on dissecting the different positions and not on adjudicating them.

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<sup>4</sup> National Research Council (2001). Additionally, a good summary of the causes and effects of global warming is available at [yosemite.epa.gov/oar/globalwarming.nsf/content/Climate.html](http://yosemite.epa.gov/oar/globalwarming.nsf/content/Climate.html).

To answer these questions, I conducted a survey of Christian ethics on the environment. I researched the official policies of different Christian groups toward biodiversity conservation and extinction. I investigated the resolutions, publications, and public statements of various Christian groups – and their leaders – to see how Christians are responding to this environmental issue. Having discovered several interesting paradigms at the organizational level, I recognize that a truly comprehensive survey is beyond this study. Certainly, the environment–religion connection has received much scholarly attention, even within the context of Judeo–Christian theology. Where previous works focus on theological interpretation, I provide a typology of the most common Christian responses to the call for environmental conservation.

The attitudes that I discuss comprise powerfully held worldviews, offering insight to forging a more faithful and unified Christian ethic among Christians. Such worldviews are not unique to the Christian community (secular groups may hold such views). Yet, they reveal interesting disagreements among Christian groups. I recognize that the everyday practice of Christians may not correspond to the official teachings of their organizations. Such disagreements are not without historical precedent (the abolition of slavery and the Civil Rights movement are other examples).<sup>5</sup> Nevertheless, I surveyed official statements and group leaders to gauge

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<sup>5</sup> Comparing the current discussion with the role Christianity played in the abolition of slavery and Civil rights movement in the United States is illuminating. Dew (2002) provides a worthy account of pro-slavery, secessionist dialogue among white Christians before the Civil War. Chappell (2004) gives a particularly thoughtful counter-example of the role of prophetic Christianity with southern black activists against Jim Crow.

their views, acknowledging that churchgoers do not always do what their leaders teach.

My first hypothesis was that there would be a clear acceptance or rejection of environmental concerns. I assumed that Christians would either support some sort of species conservation or flat-out dismiss it. Rather than finding a simple dichotomy of positions, I encountered a more nuanced scheme of worldviews. I document four unique worldviews that reflect the dominant teachings in the Christian Church toward biodiversity: Earthkeeping, Skeptic, Priority, and Indifferent (Table 2.1).

The Earthkeeping worldview engages biodiversity conservation and embraces it as an ethical issue with a biblical origin. The Skeptic worldview recognizes biodiversity issues, but disagrees with the scientific community that there is a biodiversity crisis. The reasons for this are several and I discuss them below. The Priority worldview focuses not on scientific credibility but on a sort of practical urgency. Simply put, other moral issues trump conservation. The Indifferent worldview does not address biodiversity, endangered species, or extinction whatsoever. Either consciously or unconsciously, the topic is unattended.

I limited my research to three different categories of Christian entities to provide a proper cross-section of Christianity. This study focuses on official denominations, non-profit organizations, and prominent individuals. I restricted my analyses to exclude smaller groups so this study would represent the major Christian groups in America. I only survey denominations with greater than one million members



nationally, organizations with an annual budget of at least one million dollars, and individuals who play an important role in church polity, politics, or culture.<sup>6</sup>

Some may contend with these methodologies. The decision to survey individuals may seem counterintuitive to accurately representing Christian groups, for example. However, I thought it was important to recognize the significant role of group authority structures and the media in communicating and promoting beliefs. Those who lead their denomination, write books, host radio shows, and appear on television have a loud voice and reach a great audience. Additionally, I do not survey non-denominational churches. The many Church of Christ and “evangelical” congregations, for example, are not centrally organized. Although they are numerous and influential, these groups defy simple characterization, and therefore I cannot survey them as a whole. Additionally, some groups I surveyed may express opinions in more than one worldview. Where this is the case, I categorized the entities by their more dominant ethic. In other words, a worldview may represent a group without encompassing it.

The idea for this section is not to judge the merit of Christian groups based on their ecological theology or their political views. Although I hold strong convictions that the Bible calls for environmental stewardship, I impose no blanket judgments based with these findings. Rather, I discuss the rationale and the theology behind the

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<sup>6</sup> Accounting information for all not-for-profit organizations is available on the Internet through the research database, GuideStar, available at [www.guidestar.org](http://www.guidestar.org). Membership statistics for denominations were taken from Mead et al. (2001).

different environmental ethics. If the ecological evidence is correct, this is both necessary and pressing.

### **Earthkeeping Worldview**

The Earthkeeping worldview recognizes the biodiversity crisis and responds to it from a biblically based ethical conviction. Patriarch Bartholomew I, the spiritual leader of the Orthodox Church, summarizes this worldview well. In compelling tones, he declared, “For humans to cause species to become extinct and to destroy the biological diversity of God's creation ... to degrade the integrity of the Earth by causing changes in its climate, stripping the earth of its natural forests, or destroying its wetlands ...to contaminate the earth's waters, its land, its air, and its life with poisonous substances – these are sins” (Patriarch Bartholomew I 1997).

The United Methodist Church (UMC) expresses similar sentiments, clearly articulating their doctrine in several official statements. Beginning with a reference to Psalm 24, one UMC statement states, “All creation is the Lord's, and we are responsible for the ways we use and abuse it. Water, air, soil, minerals, energy resources, plants, animal life, and space are to be valued and conserved because they are God's creation and not solely because they are useful to human beings ... Therefore, let us recognize the responsibility of the church and its members to place a high priority on changes in economic, political, social, and technological lifestyles to

support a more ecologically equitable and sustainable world leading to a higher quality of life for all of God's creation” (UMC 1992).<sup>7</sup>

From the Jewish tradition, Rabbi David Saperstein offers us insight from the book of Genesis. In a lecture to the National Press Club in May 2001, Saperstein equated our current situation with that of the Old Testament patriarch, Noah. He cited Noah’s faithfulness as what saved species on the verge of extinction from the Great Flood. This resulted in a covenant that God gave all of creation. Saperstein declared, “For we are experiencing an extinction crisis. During the time of this press conference, at least three plant and animal species will be lost forever – species that might have produced medicines to save lives, or species that work to purify our air and water, creatures that are links in the food chain – all parts of God’s interconnected creation ... So now we must ask ourselves: Will we, at this moment when so many species are vulnerable, be partners in God’s covenant with creation?” (Saperstein 2001).

The Christian conservation writer Wendell Berry captures this worldview well when he wrote, “to live we must daily break the body and shed the blood of Creation. When we do this lovingly, knowingly, skillfully, reverently, it is a sacrament. When we do it greedily, clumsily, ignorantly, destructively, it is a desecration” (Berry 1979, 272). Paraphrasing Berry: a proper Christian environmental stewardship is the biblically informed interaction of man’s authority and creation’s worth. Here the intent of creation is realized through humility, protection, and use. This intricate

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<sup>7</sup> [www.umc.org](http://www.umc.org), for a link to their environmental resolutions, click “About the UMC,” “Policy Statements,” then “Natural World.”

balance forms a responsibility that comes together in the biblical teachings of environmental stewardship.

To those in the Earthkeeping worldview preserving biodiversity may have several rationales, but all are from the Bible.

### **Skeptic Worldview**

The Skeptic worldview enters the dialogue by disagreeing with the scientists who claim that serious environmental problems exist. This worldview may acknowledge that extinction is occurring, but it asserts that it is not at rates that warrant alarm.

Attention here is primarily on the validity of conservation science. By this worldview, I mean something far more pointed than the guarded language of the United States Conference of Catholic Bishops. The italics are mine. “Opinions vary about the causes and seriousness of environmental problems. Still, we can experience their effects in polluted air and water; in oil and wastes on our beaches; in the loss of farmland, wetlands, and forests; and in the decline of rivers and lakes. Scientists identify several other less visible but particularly urgent problems currently being debated by the scientific community, including depletion of the ozone layer, deforestation, the extinction of species, the generation and disposal of toxic and nuclear waste, and global warming” (USCCB 1992, sect. I).

The Catholic bishops are not themselves skeptics, they merely point to the disunity on the nature and extent of threats to the environment. The Skeptic worldview emphasizes such observations and uses them to deny the need for environmental protection. It is clear from many Vatican publications affirming ecology – from both the Roman Catholic leadership and the Pontifical Academy of Sciences (e.g., Raven 2001) – that the Roman Catholic Church does not doubt ecological problems. I use this quotation merely to articulate the Skeptic view.

The Southern Baptist Convention (SBC) gives a prominent example of skepticism in environmental science. One of the most visible denominations on contemporary political issues, the SBC has historically approved denominational resolutions favoring environmental stewardship. In these particular resolutions, Southern Baptists agreed that a) God has called humans to be environmental stewards, b) environmental crises abound, and c) action to abate these crises is ethical (SBC 1970, 1974, 1990). Recent actions have strayed from this message, however. The Ethics and Religious Liberty Commission (ERLC) – the public policy arm for Southern Baptists – claims that environmentalists often mount “unfounded” campaigns of gloom and doom (2004b). In a message disseminated nationally to Southern Baptists as church bulletin inserts, the ERLC emphasized that “The challenge is separating reality from myth when it comes to determining a proper response to environmental issues” (ERLC 2004b, 1). In another ERLC tract, the scientific status of several endangered species and their inherent value was disputed

(2004a). In the view of the ERLC, environmental regulations such as the Endangered Species Act “have been allowed to spiral out of control” (2004a, 4).

Other groups express similar stances. Several articles from the Focus on the Family media group are revealing. In one, catastrophic global warming is referred to as “a grotesque distortion of science” (Shepard 2004). In another, we are warned that, “Too many environmental decisions and practices are based on incomplete or faulty science” (Howden 2001). George Wiegel, a senior fellow at the Ethics and Public Policy Center (a think tank dedicated to Judeo–Christian moral values) added that, “Fears of chemicals poisoning the land are vastly exaggerated. Species aren’t disappearing at a precipitous rate ... Cooking the books so that Chicken Little always wins is, in a word, sinful” (2002). Another example comes from the Institute on Religion and Democracy (IRD). Criticizing the National Council of Churches’ advocacy of energy policy reform, the IRD casts doubts on the link between fossil fuels and global warming (Nelson 2002). In another article, the IRD labeled climate change science as “silly,” “offensive,” and “one more left–wing cause du jour,” (Tooley 2002).

To Skeptics, ecologists are either wrong in their calculations, or far worse, they are deliberately passing off junk science.

## Priority Worldview

The Priority worldview maintains that biodiversity conservation takes the focus away from issues with greater moral importance. In The Christian witness to the state, John Howard Yoder portrayed this worldview as affirming that, “man’s true need is the initial commitment of faith, so that the church should limit herself to this priority concern and not confuse things by speaking to society at large about all sorts of moral issues” ([1964] 2002: 21). Whatever ecology research shows, preserving our species and our activities has greater relevance. Even if the science of ecology is valid, conservation does not warrant the Church's attention. This is a subtle, but likely prevalent, anti-conservation paradigm.

The Assemblies of God (AOG) church illustrates the Priority position. On their website, the AOG presents their beliefs on several popular contemporary issues (a practice becoming common with many denominations).<sup>8</sup> Here, they present a seemingly contradictory stance on biodiversity preservation. While the AOG acknowledges biblical environmental stewardship, their position seems more concerned with combating New Age spirituality, paganism, and other forms of earth worship. The AOG states, “A major concern for Christians is the overemphasis of the environment at the expense of spiritual issues effecting life and eternity. The Bible’s message declares that spiritual matters (those affecting the hearts of humankind) are the priority issues with God. These and not the environment are the reason He sent

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<sup>8</sup> [ag.org/top/beliefs/contemporary\\_issues/issues\\_02\\_environment.cfm](http://ag.org/top/beliefs/contemporary_issues/issues_02_environment.cfm), for a link to their environmental beliefs, click “Beliefs,” “List of topics,” then “Environmental Protection,” last accessed July 30, 2004.

His own Son Jesus as a sacrifice to save people. For God did not send His Son to save the earth in a physical sense but to save the people who inhabit it. We believe this must be the main focus and concern for all Christians today” (AOG 2004).

[italics ours] According to the AOG, because the Earth will be destroyed in the end times, environmental stewardship takes a back seat to concerns directly related to human welfare.

A separate, although prevalent, attitude in the Priority worldview is that environmental protection stymies economic progress and is overly suspicious of technology. For some in this worldview, human ingenuity will evolve and overcome any environmental problems we encounter. Namely, technology will outpace our ability to create environmental hazards. In short, every environmental problem has, or will have, a technological solution. This worldview has become so widespread that theologians began using the phrases Christian humanism and techno-messianism to describe the attitude (Ehrenfeld 1978, Derr 1997, Wingfield 1999).

Gary Bauer, in his unsuccessful runs for the presidency in 1996 and 2000 also championed the Priority worldview. Outlining his environmental platform, Bauer wrote, “The generation that produced the environmental movement and the anti-technology Unabomber is attempting to indoctrinate the next generation in its anti-technological and anti-progressive creed” (1996, 120). For Bauer, economic freedom and individual property rights have been eroded by federal environmental regulations. “What’s missing in today’s radical environmentalism is balance. Book after book and tract after tract [on the environment] ignores the benefits derived from expanding



human dominion over nature” (123). This argument sets up a conflict between human dominion and ecological stewardship.

The Acton Institute for the Study of Religion and Liberty is a strong force on this specific position. This group boasts an impressive collection of academic and religious figures promoting economic and political issues. To summarize a consistent argument: economic growth generates clean environments, environmental regulations stymie growth, property rights promote conservation voluntarily, obviating government interference (Beisner et al. 2000). Much of what the Acton Institute produces advocates that “richer is cleaner.” In other words, properly implemented free market economics produces wealth and stewards creation. Akin to this reasoning, the Acton Institute also implores human subjugation of nature as a moral imperative. “When man does not exercise dominion over nature, nature will exercise dominion over man and cause tremendous suffering for the human family” (Beers et al. 2000). Beers and colleagues argue the Puritanical environmental position that human “creativity can bring nature to a higher degree of perfection.”<sup>9</sup>

Taken wholly, the value of nature is determined through human use. Prioritizing environmental ethics ahead of economics is avoiding our God-given responsibilities. At the core, however, this worldview emphasizes humanity’s place above all other species. Our concerns should not be pointed at creation, but at concerns directly affecting human beings. Any impediment of economic activity prevents this because

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<sup>9</sup> Full text of this book chapter is available online at [www.acton.org/ppolicy/environment/theology/m\\_catholic.html](http://www.acton.org/ppolicy/environment/theology/m_catholic.html)

it “ignores the full scale of human values that a free economy otherwise allows” (Beisner et al. 2000).

### **Indifferent Worldview**

For various reasons, the Indifferent worldview does not address biodiversity, endangered species, or extinction whatsoever. Biodiversity is simply not a topic that registers in these groups’ resolutions, policies, or publications.

Several groups in this worldview have a self-identified “pro-family” agenda. Pro-family Christian political action groups are common in Washington D. C. Their purpose is to remind legislators of the issues that are important to Christian families. The Family Research Council (FRC) is among the most active and notable of these lobbying groups. According to their mission, the “FRC shapes public debate and formulates public policy that values human life and ... promotes the Judeo-Christian worldview as the basis for a just, free, and stable society.”<sup>10</sup> Not surprisingly therefore, the FRC focuses on legislative issues related to abortion, marriage, pornography, and education. In addition, engaging issues less directly related to families – gambling, foreign affairs, or even tattoos (Parshall 2002) – the FRC does not address environmental policies whatsoever. This is curious considering the clear remarks from the FRC’s former president who said, “conservation and stewardship of the environment are profoundly pro-family concepts” (Bauer 1996).

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<sup>10</sup> [www.frc.org](http://www.frc.org), to see the legislative concerns of the FRC, click “FRC’s issues”

The American Center for Law and Justice (ALCJ) and the influential James Dobson also represent this view. Dedicated to preserving religious and constitutional freedoms<sup>11</sup>, the ALCJ is a frequent litigator of high profile cases in the federal courts. In these activities, the ALCJ argues a definitive political philosophy on specific issues. To date, however, the ALCJ has not taken any stance on issues or cases related to the environment. Dobson, Director of the Christian media giant Focus on the Family – and founding board member of the FRC – represents this worldview. While the organization Dobson now runs is associated with statements I classify elsewhere, Dobson himself avoids issues directly related to the environment. In spite of making daily radio broadcasts that address national political issues, Dobson does not consider biodiversity.<sup>12</sup>

Several historically African–American denominations also maintain this worldview. The African Methodist Episcopal Church, the African Methodist Episcopal Zion Church, the National Baptist Convention U.S.A., Inc., and the National Baptist Convention of America, Inc. all do not engage environmental issues. The lack of official policies, teachings, or published material addressing environmental stewardship here reveals broader organizational and doctrinal issues that go beyond the scope of this essay (Washington 1986, Lincoln and Mamiya 1990).

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<sup>11</sup> Full mission of the ALCJ is available at [www.aclj.org](http://www.aclj.org)

<sup>12</sup> Dr. Dobson's radio broadcasts are archived, and available on his organization's Internet web site, at [www.family.org/fmedia/broadcast](http://www.family.org/fmedia/broadcast)

## **Discussion: Assessing the Scientific and Christian Positions**

### **The Earthkeeping Hermeneutic**

Experience teaches that when participants in two different fields of knowledge meet that they will have simplistic views of one another. For example, when economists meet ecologists, the former have a detailed drawing of the economy and a single, simple box for “ecology” and ecologists have a detailed drawing of environmental processes and a single, simple box for “the economy.” This seems the case for religion and the environment. Those concerned with the practical issues of protecting the environment are likely to see the multifaceted problems of their trade, but view religion, ethics, and the Church, as single and monolithic. The reverse is also common.

Lynn White, Jr. did this in a Science article, citing Christians and their theology as “bearing a great burden” of responsibility for the current ecological crisis (1967). Because White linked Christianity with negative environmental attitudes, his paper had a significant impact with ecologists. By and large, ecologists – and the scientific community in general – received White’s thesis with open arms and the Ecological Society of America responded by awarding him their prestigious Mercer prize. Not everyone was as enthusiastic, however. His ideas raised concern with many Christians who saw the Bible as advocating a distinct environmental ethic (Whitney 2006).

The select ecologists who dig deeper than White may read eco-theology or inspirational writers like Wendell Berry. They might feel reassured that Christians view extinction as an ethical problem. More often, it seems, they will summarily dismiss Christians, either pointing to White's thesis or citing Genesis as a charter for dominion. As this chapter documents, White's position is a simplistic abstraction. Christian environmental worldviews cannot be placed in one simple box. Rather, they represent a multitude of sometimes conflicting ideas. As Christians may have different opinions on the environment, I ask, what does the Bible say? As an ecologist, I recognize the work of theologians who interpret Genesis as a guide to protect the Earth.

A central issue in the theology of ecology is the relative position of humanity with the rest of creation. This has been a flashpoint for disagreement. In the Priority worldview, opinions often stem from a theology that humans, as a species, have a unique relationship with God. This privileged relationship leads to a belief that only humans are redeemable. This view focuses on humanity being set apart from the rest of creation, having a special likeness and future with God. The first chapter of Genesis supports this: "Let us make man in our image, in our likeness... So God created man in his own image, in the image of God he created him." (Genesis 1:26–27). However, significant portions of Christians have taken this passage as the basis to subjugate creation. However, as Richard Hays reminds us of the slogan "God said it, I believe it, that settles it," "bumper-sticker hermeneutics will not do" (Hays 1996, 3).

Calvin DeWitt (1998) sheds light on the dominion issue. In Caring for Creation: Responsible Stewardship of God's Handiwork, DeWitt recognizes three essential biblical principles for conservation. Paradoxically, it is Genesis – the same text often used to confront ecologists – that provides DeWitt inspiration. DeWitt outlines a biblical concept for stewardship in three ways: a) earthkeeping, b) fruitfulness, and c) the Sabbath.<sup>13</sup>

Earthkeeping comes from Genesis 2:15 where God instructs Adam about what he is to do with the Garden of Eden. Looking at the Genesis text in its original Hebrew language, DeWitt translates two crucial words, referencing how they are used elsewhere in the Old Testament. DeWitt reads two important Hebrew words abad and shamar to mean, “to serve and keep nature in dynamic integrity.” Expanding the notion of environmental stewardship, DeWitt derives the fruitfulness principle from Genesis 1. Here God speaks to Adam – as well as to all the birds and fish – instructing them to, “be fruitful, increase in number and fill [the earth].” DeWitt points out that God gives this charge to both humanity and creation. Humans are not alone with the inherent right to be bountiful and fill his habitat. Lastly, DeWitt points to the Sabbath principle as a significant “means of assuring fruitfulness.”

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<sup>13</sup> De Witt's description of biblical environmental stewardship—earthkeeping, fruitfulness, Sabbath—bears remarkable similarity to H. Nouwen's description of the Christian life. Citing a passage in the epistle of John, Nouwen argues that intimacy, fecundity, and ecstasy are vital elements of the Christian who takes the Gospel seriously (1986). A Roman Catholic priest, Nouwen wrote his book from the experiences gained from a year spent at L'arch—a community of handicapped Christians.

As it is generically known, the Sabbath is where people rest from their work one day each week. However, it is a profound rule with deep spiritual implications. As a Hebrew tradition in the Old Testament scriptures, the Sabbath informed agriculture practices (e.g., Exodus 23, Leviticus 25–26). At all times one-seventh of all the farmed land was kept fallow, and every seven years all the land was to rest from cultivation. Every seventh Sabbath year, or the 50th year, was the Jubilee. During the Jubilee, monetary debts were forgiven and all slaves were freed (Lev 25). From the New Testament scriptures, the Christian tradition teaches that Jesus Christ, Himself, embodies the Sabbath and the Jubilee. The fourth chapter of Luke chronicles Jesus recitation of the prophet Isaiah: “The Spirit of the Lord is on me, because he has anointed me to bring good news to the poor. He has sent me to proclaim release to the captives and recovery of sight to the blind, to the oppressed go free, to proclaim the year of the Lord’s favor” (New Revised Standard Version). Therefore, in both the Hebrew and Christian traditions, the Sabbath represents the rejuvenation and restoration of life. As DeWitt mentions, this is integral to earthkeeping.

Earthkeeping, fruitfulness, and Sabbath form a rich theological tapestry that defines biblical environmental stewardship. Those few scientists who got past Lynn White might well ask where such Christian teachings of stewardship today are. Those Christians who consider DeWitt might ask, how does the Christian understanding of Sabbath inform an environmental ethic today? Answers are not always easy to find.

## **Baptizing Secular Conservatism**

Despite well-reasoned arguments like DeWitt's, a strong and organized force interprets the Bible towards a decidedly different environmental ethic. A prominent example is The Cornwall Declaration published by the Interfaith Council for Environmental Stewardship and signed by a broad selection of Christian and Jewish figures<sup>(ICES 1999)</sup>. Underlying The Cornwall Declaration is an acute optimism in human reason and economic progress, complemented by pessimism in government-mediated science. Oddly, The Cornwall Declaration resembles conservative political rhetoric more than it does biblical language.

The signers of The Cornwall Declaration believe that God calls humankind to a “serious commitment” to free-market capitalism, where individual liberty is valued above government interference. Wary of government, the document hails private property rights and widespread economic freedom as the means to “sound environmental stewardship.” As a result, science becomes the path to realize economic prosperity, not a way to assay economic activity itself. Consider three key common environmental issues: human population growth, resource exploitation, and biodiversity extinction. In The Cornwall Declaration, each of these predicaments has a technological solution. For example, overpopulation is not a serious problem as agricultural engineering continues to generate greater crop yields. Overexploitation is not a concern as the ability to extract natural resources increases with technological advances. One assumes that even biodiversity loss can be mitigated through biotechnology. If species drift close to extinction, surely their populations can be



bolstered through Jurassic Park–like efforts (Taggart 2002). Are we to believe these arguments? More important, is there a biblical cause to do so?

Aside from The Cornwall Declaration, the collusion of the political right and the religious right is more than linguistic. For Christians who are skeptical that environmental problems exist, Michael Sanera’s Facts, Not Fear (1999) is a frequent reference (ERLC 2004b). Sanera is neither a theologian nor a scientist of any repute but the former Director of Environmental Education Research of the politically conservative Claremont Institute. However, Sanera is not the only secular conservative cited by anti–environmental Christians. The Southern Baptist church quoted a writer for The Brookings Institution to dismiss ecological science as a false and “assiduous” liberal campaign (ERLC 2004a). In another example, a recent article published by Focus on the Family cites a senior fellow at the reactionary Lexington Institute to debunk climate change science (Howden 2001). Probably, one expects some liaison between such groups, but how much is too much? Where do we draw the line between theology and secular politics?

An examination of the financial reports of several of the groups I surveyed revealed deeper connections between Christian and politically conservative think–tanks. In many cases, the ties were financial as well as ideological. Such nominally distinct groups were not merely promoting similar environmental agendas; the same politically conservative foundations funded them. Some religious organizations I surveyed – The Ethics and Public Policy Center, the Acton Institute for Study of Religion and Liberty, The Institute on Religion and Democracy, and the Institute on

Religion and Public Life, for example – all received major contributions from powerful right-wing political foundations – the Lynde and Harry Bradley, the John M. Olin, and the Sarah Scaife foundations, for example (Goodstein and Kirkpatrick 2004, Philanthropic Research Inc. 2005). This finding is revealing in itself, but even more so given that these same grant foundations also funded extremely conservative political organizations such as The American Enterprise Institute for Public Policy Research, the Claremont Institute, the Heritage Foundation, and The Pacific Research Institute for Public Policy, among others (Philanthropic Research Inc. 2005). Liaisons of this nature are the rule and not the exception.

Although one expects some cooperation between faith-based and political think tanks, these relationships should not transform the meaning of the biblical scriptures. As George Lindbeck reminds us, the Bible does not present us with a “figurative representation” of how life should be, subject to our own political leanings or preferred interpretations (1984, 118). Rather, a faithful theology is “intratextual” as it redescribes the world to fit the scriptural story. Applying Lindbeck to our situation, an environmental ethic that is faithful to the scriptures does not consist of a secular political ideology baptized with certain biblical passages. Rather, it is an inherently biblical ethic, of course, having political ramifications – not the reverse. The collusion of the political and religious conservatism casts doubt on the ethics these partnerships produce.

## **Conclusion: A Better Way**

Tertullian observed that, in first century Rome, conventional wisdom blamed early Christians for society's perils. He wrote, "If the Tiber floods or the Nile fails to flood, if the skies darken, if the earth trembles, if famine, war or plague occurs, then immediately the shout goes up: 'The Christians to the lions'" (Bainton 1964: 44). Although accusing Christianity for our ecological crisis may have appealed to Roman senators, or Lynn White, the view that the Christian faith is summarily anti-environmental is a misconception.

As this chapter demonstrates, Christian worldviews differ greatly in reference to the value of biodiversity and its conservation. Here, I noted four distinct worldviews that encompass typical Christian responses to biodiversity preservation. The patterns I observed were more complex than a straightforward acceptance or rejection of environmental stewardship. Indeed, expressions of support for species preservation were the most enduring worldview I surveyed. This worldview had a strong tradition that frequently employed biblical teachings for its justification. Also represented in my study was a strong attitude of distrust in the scientific community that sounds the alarm for conservation. Largely separate from debates over scriptural meaning, this view calls scientific research into question and recommends conservation efforts be postponed until there is more convincing evidence. Another response I discovered was a prioritization of other issues ahead of environmental concerns. This worldview provided a sort of conservation "lip service" without any demonstrated effect. Amidst

passionate beliefs, there was still ample room for indifference. The remaining worldview I identified did not give significant attention to biodiversity issues or conservation whatsoever.

While the majority of Christian groups officially support conservation, Christians ought not to gloat on their group's environmental theology. A large confusion remains in churches on how to mesh theology and ecology. Concerns over economic prosperity, New Age spirituality, scientism, and liberal ideologies abound. As a result, many Christians may believe the Bible commands some sort of environmental protection, they just will never do anything about it. A 2004 survey by Christianity Today is revealing. According to their poll, over half of those "uncomfortable with environmentalism" are so because there are concerns that are more important. Among these concerns, a strong economy and preventing earth-worship were prominent. Of the remaining, a quarter did not think there were any environmental problems; the rest doubted the Bible's call for stewardship.

Certainly, there are paths of environmental ethics that are secular, some of which are certainly unfaithful to both the Hebrew and Christian portions of the Bible. For those of faith though the primary concern is not nature itself nor humanity, but obedience to the scriptures. The remaining challenge then, requires theologians to teach the scriptures, ecologists to measure the state of the environment, and both to work in concert.

This sort of vision requires both the work of ecologists and the work of the Church – the secular and the Christian. I conclude with another remark for the Conference of Catholic Bishops: “These important issues are being explored by scientists, and they require urgent attention and action.” They continue: “We are not scientists, but as pastors I call on experts, citizens, and policy makers to continue to explore the serious environmental, ethical, and human dimensions of these ecological challenges” (USCCB 1992). I do not call for a baptizing of secular agendas – either liberal or conservative – but rather obedience to God’s word.

	Earthkeeping	Skeptic	Priority	Indifferent
Denominations (106 members)	Roman Catholic Church (59.2)			
	United Methodist Church (8.7)			
	Evangelical Lutheran Church in America (5.2)			
	Presbyterian Church, U.S.A. (3.2)			
	Lutheran Church, The Missouri Synod (2.6)			
	Greek Orthodox Archdiocese of America (2.5)			
	Episcopal Church (2.5)			
	United Church of Christ (1.6)			
	American Baptist Churches U.S.A. (1.6)			
	Russian Orthodox Church (1.1)			
	Christian Church, Disciples of Christ (1.0)			
Organizations	Au Sable Institute	Ethics and Public Policy Center	Action Inst. for Study of Religion and Liberty	Family Research Council
	Christianity Today International	Focus on the Family		
	Nat. Council of Churches of Christ in the U.S.A.	Inst. on Religion and Democracy		
	Nat. Religious Partnership for the Environment	Inst. on Religion and Public Life		
	Sojourners			
	Target Earth International	Toward Tradition		
Individuals	Patriarch Bartholomew I	Richard Baer, Jr.	Gary Bauer	James Dobson
	Tony Campolo	Charles Colson	Jerry Falwell	
	Cal DeWitt	Thomas Sieger Derr	Robert A. Sirico	
	Ted Haggard	Richard Land		
	Pope John Paul II	Richard John Neuhaus		
	Francis Schaeffer	Pat Robertson		
	Ron Sider			
	Archbishop Rowan Williams			

## **Table 2.1**

Worldviews of Major Denominations, Organizations, and Individuals according to their published record on biodiversity conservation. See text for descriptions and methods. Denomination membership in parentheses (in millions).





– Three –

Local extinctions of flocking birds in  
Amazonian forest fragments<sup>1</sup>

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<sup>1</sup> This chapter also appeared as the cover article for the January 2006 issue of Evolutionary Ecology Research: Van Houtan, K. S., S. L. Pimm, R. O. Bierregaard Jr., T. E. Lovejoy, and P. C. Stouffer 2006. "Local extinctions in flocking birds in Amazonian forest fragments." Evolutionary Ecology Research. 8: 129-148. For cover art see Figure 3.8.

## **Introduction**

The risk of extinction varies widely among species (Diamond 1984, Pimm et al. 1995). At large spatial scales, the size of the species' geographical range and the species' local abundance are major factors in determining whether a species survives human impacts (Manne et al. 1999, Manne and Pimm 2001). At smaller scales, differences in local extinction among species can unfold as a naturally occurring phenomenon – such as on birds on small islands (Pimm et al. 1988). These differences are especially striking, however, in the newly fragmented landscapes (Diamond et al. 1987, Rozenzweig 1995) that now cover large areas of the planet (Jenkins and Pimm 2003). Several factors explain why certain species are less susceptible to local extinction than are others. Again, local abundance is one of them (Pimm et al. 1988, Pimm 1991, Rozenzweig 1995).

Gosling and Sutherland (2000) asked what are the effects of “behavior” on extinction – broadly defined. Their synthesis was rich in ideas, but contained few empirical studies. In one of them, Woodroffe and Ginsberg (1998, 2000) demonstrated the importance of how wide-ranging is an individual. Other things being equal, large bodied species range more widely and have lower local abundances than smaller species. Importantly, how far an individual ranges also depends on the species' behavior, here defined narrowly as its sociality. For a given body size, social carnivores have substantially larger ranges as individuals (because their social groups range widely) than individuals of solitary carnivore species. Consequently,

individuals of wide-ranging species had greater contact with edges and other unsuitable habitat. Such contacts increased conflicts with humans and human modified landscapes, increasing mortality, and so the chance of local extinction.

I explore this idea in a different context. Birds of the forest understory that are more likely to move to, or beyond, the edges of their newly fragmented habitat should disappear from forest fragments more quickly. Typically, species that join interspecific flocks range more widely than do solitary species (Stouffer and Bierregaard 1995). The latter should persist longer than the former after forest fragments become isolated. I also predict that flocking species demonstrating a flexibility to forage outside of flocks after forest isolation will persist longer than those that remain in flocks. (Parenthetically, I distinguish flocking as a measure of sociality from mechanisms involving the vulnerabilities of colonial species. For example, the Passenger Pigeon, Ectopistes migratorius, notoriously required vast nesting colonies to persist.)

Insectivorous forest birds often disappear from forest patches quickly after their isolation (Willis 1974, Willis 1979, Karr 1982, Thiollay 1992, Stouffer and Bierregaard 1995, Canaday 1997). There are several explanatory hypotheses, but the underlying mechanisms remain uncertain (Sekercioglu et al. 2002). Among insectivores, many that join mixed-species flocks or follow army ant swarms are highly sensitive to forest fragmentation (Willis 1974, Leck 1979, Lovejoy et al. 1986, Stouffer and Bierregaard 1995), though there are exceptions (Willis 1974, Karr 1982, Stouffer and Bierregaard 1995). These two foraging strategies are distinct and

specialized. (For army ants see: Oniki and Willis 1972, Willis and Oniki 1978, Harper 1987; for mixed-species flocks: Powell 1979, Munn 1985, Stotz 1993, Jullien and Thiollay 1998). Here I consider them collectively because of their general susceptibility to local extinction in fragments.

I show that species that join flocks do so to different degrees and I quantify the differences using data from captures in mist-nets. My extensive experience teaches that the regular checks of mist-nets in humid, tropical forests are generally unrewarded. Occasionally, a check reveals many individuals. These are typically of species known to forage in flocks or follow ant swarms. This experience of contagious captures may be familiar, but does it generate the quantitatively useful information needed to predict the persistence of species in forest fragments? It does so in several important ways.

First, if I assume that captures are not contagious, but random, the frequency of capturing 0, 1, 2, ... individuals should follow a Poisson distribution. I can estimate the single parameter of that distribution from frequencies of captures of 1 and 2 individuals. (I lack the records of how many net checks returned empty-handed, and show that this is not necessary.) There is an excess of captures involving three or more individuals, compared to the assumption of independent capture. In other words, the simultaneous capture of three or more individuals is unexpected – suggesting the birds are traveling together, most likely in a flock. This is exactly the criterion employed by other observational studies of species' flocks (see below).

Second, I show that species that flock according to this criterion are overwhelmingly those determined to flock by observational studies. The exceptions are easily understood and I eliminate them. Third, I show that my numerical measure of propensity to flock – the fraction of individuals captured in flocks over the total number of individuals captured – closely correlates with the comparable measure from independent field observations. (I can do this for most, but not all the species in this study.) Fourth, I show that the species that withdraw the most from flocks after fragmentation are those known to be facultative in their flocking behavior. Finally, my quantitative measure significantly predicts two features of how long species persist in isolated forest fragments.

I demonstrate that, after forest fragmentation, the more often a species was present in a flock, the more quickly it is lost from a given fragment. Species depend on flocking to varying degrees. Those that rely on flocking strategies in continuous forests – and retain that preference in forest fragments – persist for shorter times than those that tend not to flock in fragmented habitats.

## **Methods**

### **Study Site**

The forest bird populations of the Biological Dynamics of Forest Fragments Project (BDFFP) in the central Amazon present an unrivalled context to measure differences

in vulnerability to local extinction. This ecosystem has been studied for 25 years through extensive mist-net surveys conducted both in continuous and fragmented forests (Lovejoy et al. 1986, Bierregaard et al. 2001, Laurance et al. 2001). I analyzed 36,657 mist-net captures from both continuous and fragmented forests at Fazendas Dimona, Esteio, and Porto Alegre at the BDFFP ~ 80 km north of Manaus, Brazil. Mist-nets caught birds in 27 forest plots of 1, 10, 100, and 1000 ha from 1979 through 1993. Eleven plots were isolated from the surrounding continuous forest after sampling began (five 1 ha, four 10 ha, and two 100 ha). The remaining 16 study areas were never isolated (nine 1 ha, six 10 ha, three 100 ha, and two 1000 ha). Lovejoy et al. (1986) and Bierregaard and Stouffer (1997) provide further experimental details.

### **Flocks and Flocking Behavior**

To characterize different species' social tendencies, I examined the literature and mist-net captures. I employ mutually reinforcing measures to define flocking species, flocks, and flocking tendencies.

Relying on field experience, I referenced the authoritative monograph of central Amazonian birds (Cohn-Haft et al. 1997). I include a species in my study only if Cohn-Haft et al. considered it to join mixed-species flocks or follow ant swarms to any degree (see Table 3.1 for descriptions).

Having identified flocking species, I then quantified their tendencies to flock.

Thiollay (1999) defined a mixed-flock as three or more birds of two or more species observed within 10 m of each other. Others' definitions are quite similar (Stotz 1993, Jullien and Thiollay 1998, Develey and Stouffer 2001). Nets were checked every 30 minutes and considered groups of three or more birds of two or more species captured during the same check, within two mist-nets' proximity ( $< 36$  m), as tentatively being a "flock". I characterized army ant flocks similarly, except I allowed for monospecific groups, as is characteristic of these flocks (Willis and Oniki 1978, Harper 1987). This allowed me to calculate the empirical frequencies for capturing single birds, pairs, triplets – and so forth – for both mixed-species and ant-following flocks.

I then addressed whether it is appropriate to consider three or more netted birds to constitute a flock. The number "three" is an arbitrary minimum flock size; except that it encapsulates the considerable field experience of tropical mixed flocks (see above). If there were no flocks, individual birds would enter nets independently of one another and the frequency of group captures would follow a Poisson distribution. I do not have the full statistical distribution, as empty nets were not recorded. Nonetheless, I can estimate,  $\lambda$ , the parameter of a Poisson distribution, from the ratio of the frequencies of captures of one ( $e^{-\lambda} \cdot \lambda$ ) and two ( $e^{-\lambda} \cdot \lambda^2 \cdot \frac{1}{2}$ ) individuals. This parameter estimate allows the prediction of the full distribution of net captures under the Poisson assumption of independent captures. Using the data from continuous forest plots, my results confirm that group captures of three or more birds occurred

more often than predicted. Corroborating previous flock definitions, I deem such captures to be flocks.

Once I defined flocks, I quantified the frequency of species joining flocks. Jullien and Thiollay (1998) and Jullien and Clobert (2000) defined a species' flocking "propensity" as the proportion of individuals observed foraging in flocks to the total observations. Similarly, I created a flocking index for each species from the frequency of in-flock captures divided by total captures for that species. This index was initially derived in continuous forest conditions (using data from all 27 plots) for all species with more than 25 total captures. Fig. 3.1 correlates my measure of flocking behavior to the flocking propensities of Jullien and Thiollay (1998) for species common to the two sites. Jullien and Thiollay did not consider ant followers.

I considered several factors that could potentially invalidate applying mist-net data to these ends. The possibility exists that distress calls from netted birds could attract other birds into nets – thereby confounding my estimate of flocking behavior. From my experience, this only occurred in one species, the Musician's Wren, Cyphorhinus aradus, which is not a flocking species (Cohn-Haft et al. 1997).

I also considered the effect of varying recapture rates between species (Lebreton et al. 1992). Species are active at different heights and in different ways, affecting how often mist-nets detect them (Remsen and Parker 1983, Remsen and Good 1996). Recapture rate cancels out in my flocking index (in-flock captures divided by total



captures). I do evaluate the effects of different recapture rates, when estimating how long species persist.

### **Persistence and Behavior in Fragments**

Post-fragmentation captures document each species' survival in fragments. I defined "persistence" as the length of time that a species was recorded after the fragment's isolation. Low values indicate rapid local extinction. I averaged persistence values across similar-sized fragments (five 1 ha, four 10 ha, one 100 ha) to gather a single measure for each species in each fragment size. If a species was not present in a fragment before isolation, I could not calculate its persistence. If a species was detected before, but never after isolation, I gave it a value of "0." I used data from only one 100 ha fragment, Porto Alegre #3304, as the second 100 ha fragment, Dimona #2303, was isolated too late in the study to provide comparable measures of persistence. The 1000 ha plot, Gavião #1401, was never isolated.

Occasionally the barriers isolating the fragments were poorly maintained (the cattle ranches were abandoned) enabling some species to re-colonize fragments through corridors of Cecropia sp. and Vismia sp. regrowth (Bierregaard and Stouffer 1997, Stratford and Stouffer 2001). Concordantly, I assume that absences of greater than four years in the capture record to be local extinctions followed by re-colonizations, as opposed to continual persistence.

I compared flocking indices for each species before and after plot isolation. Using the previous method, I recorded additional flocks after the plots were fragmented, calculating an additional measure of flocking propensity from captures in the 11 plots that were isolated. I did not characterize flocks in the first three months after fragmentation to avoid the “crowding effect” Lovejoy et al. (1986) observed. I tested the statistical independence of these different values and derived their difference by subtracting the flocking index after fragmentation from the one before. This value served as a measure of change in flocking between continuous and isolated plot conditions.

### **Statistical Analyses**

To test the effect of flocking behavior on persistence I used an analysis of covariance (ANCOVA) model with pre-fragmentation capture frequency, pre-fragmentation flocking index, and change in flocking (after fragmentation) as continuous variables and fragment size as a discrete variable. I developed the model iteratively, or sequentially, to represent the individual effects of the separate behavioral factors graphically.

Captures from all continuous forest plots were used to gauge species' rarity. While capture frequencies alone are biased measures of actual species abundance (Williams et al. 2002) to the extent that they do measure relative abundance I retain them as a statistical correction. Rare species are likely to be lost before common ones (Pimm et

al. 1988, Pimm et al. 1991). Moreover, species with low population densities might seem to “disappear” more often from fragments simply as an artifact of being hard to detect.

Additionally, I calculated the recapture rate,  $p(t)$ , for each species using the program MARK (White and Burnham 1999). I used eight years of captures in adjacent, similarly sampled, continuous forest plots (Florestal, Gavião, and km 34). As individuals moved between these three areas, I pooled the data to attain accurate individual capture series. The best estimate of  $p(t)$  in MARK allowed it to vary annually, according to netting effort. I reconstituted the values for  $p(t)$  for each species, based on an annual effort of 10,000 net hours, to see if these explained the residuals from the full model.

I averaged persistence values in the model within each fragment size treatment, thereby eliminating any differences between individual fragments of the same size. By inspection, I noticed that persistence times within a species, within a given fragment size, were quite similar. To formalize this assumption, I compared my initial covariance model (where persistence is pooled by fragment size) to a similar model that treated each fragment as a class variable. The alternative model posits that how long a species persists depends on the particular fragment in which it is found – that is, not the fragment’s size, but its identity. These differences could arise if, for example, fragments in close proximity to continuous forest held species longer than more spatially isolated fragments. The original model assumes that, among the possible patch metrics, area exerts the dominant effect on species persistence.

Additionally, I checked if flocking behavior affects persistence to varying extents in fragments of different sizes. I ran a more complex covariance model (using the factors: capture frequency, fragment size, flocking index) adding the crossed effect of flocking index and fragment size. This effectively tested for significant differences in the degree that flocking behavior affects persistence (or differences in the slopes) in the three fragment size classes.

Finally, I asked whether there are phylogenetic differences in persistence over and above the effects of capture frequency, fragment size, and flocking behavior. I performed a two-way analysis of variance (ANOVA) involving fragment size and each species as class variables. The resulting residual sum of squares is a pure error term (within species, within fragment) and its reduction over the model with species (represented by capture frequency, flocking index, and change in flocking index) serves as an F test for lack of fit for that model. While the ANOVA inherently tests for significant phylogenetic differences, I plot the residuals from the full ANCOVA model according to phylogeny to check for potential confounding factors. There are multiple factors I exclude that might correlate with extinction risk, though perhaps not directly (clutch size or nest type are examples). These variables tend to correlate with body size, which was not a significant predictor of species persistence when fragment size is considered (ANCOVA,  $df = 1, 85$ ,  $P = .06$ ).

I tested all the models using the general linear models procedure (PROC GLM) in SAS release 9.1 (The SAS Institute, 2003).

## Results

### What constitutes a flock and which species flock?

From the observed frequency of captures of one and two individuals in continuous plots, I fit the expected distribution of pre-fragmentation captures of 0, 3, 4... n (Fig. 3.2). The observed frequency of birds caught in groups of three or more is greater than expected by the fitted distribution. This result confirms field experience that three or more birds compose a flock. There were no captures of exactly 15, 18, or 21 birds, nor any captures with 23 or more.

I identified 30 flocking species in 1,352 flocks from 26,074 net captures before fragmentation. Table 3.1 organizes these species based on the phylogeny of Sibley and Monroe (1990). Flocking species represent: Tyrannidae (4), Thamnophilidae (12), Furnariidae (12), Vireonidae (1), and Certhiidae (1).

I exclude four species considered to join understory flocks by the literature – Yellow-throated Woodpecker (Piculus flavigula), Olivaceous Woodcreeper (Sittasomus griseicapillus), Black-banded Woodcreeper (Dendrocolaptes picumnus), Curve-billed Scythebill (Campylorhamphus procurvoides) – as I caught them too few times (see Methods). I exclude some species from the analyses that I detected in groups of three or more because they are not listed as joining understory mixed flocks or following ants by Cohn-Haft et al. (1997). By chance alone, there should be such species and most can be explained from the species being drawn to fruiting trees, occurring in family groups, and similar, miscellaneous reasons

Figure 3.1 plots flocking index values for each species (based on net captures) against an independent measure of flocking behavior from field observations by Jullien and Thiollay (1998) in French Guiana (Fig. 3.1). Values from both studies are closely correlated (Pearson correlation = 0.86).

### **Behavior and Persistence**

Table 3.2 lists the results of the full model. I have five major results. (1) The effect of capture frequency (“captures”) is numerically small, but statistically significant. (2) Species detected more often in flocks, both before and after fragmentation, disappear from fragments more quickly than those that are not. (3) Larger fragments hold birds significantly longer than do smaller fragments. (4) Species that withdraw from flocks after fragmentation (“change in flocking index”) persist longer than those that do not. (5) The lack of fit test – factoring fragment size, considering each species a variable – was not significant ( $P = 0.16$ ).

Results 1 – 3. Fig. 3.3 shows the effect of flocking index on persistence. Persistence times are corrected for capture frequency and fragment size. Although there is significant variation, the trend indicates that species predisposed to flock with great frequency disappear from fragments faster. Here, the crossed interaction of flocking behavior and fragment size is not significant ( $F = 1.5$ ,  $df = 2, 81$ ,  $P = .22$ ). Thus, the slopes of the three trend lines between plots of different size are not significantly different. (I do not retain this factor in the model.)

Result 4. From the 10,583 captures after isolation, I derive an independent measure of flocking behavior from an additional 444 flocks. Fig. 3.4 plots flocking indexes before and after fragmentation for each species. Generally, birds join flocks less after fragmentation than before, reflected in the observation that most of the points fall below the 1:1 line (paired t-test:  $t = 3.5$ ,  $df = 30$ ,  $P < .002$ ). This confirms three species known to “drop out” of flocks (Stouffer and Bierregaard 1995) – the White-flanked Antwren (Myrmotherula axillaris), Wedge-billed Woodcreeper (Glyphorhynchus spirurus), and Chestnut-rumped Woodcreeper (Xiphorhynchus pardalotus). I identify two additional species that withdraw from flocks: the Barred Woodcreeper (Dendrocolaptes certhia) and Olivaceous Flatbill (Rhynchocyclus olivaceus). In contrast, several species flocked with slightly greater frequency after fragmentation (Table 3.1). Two notable examples are the White-plumed Antbird (Pithys albifrons) and Long-tailed Woodcreeper (Deconychura longicauda).

A species’ ability to decrease its dependence on flocking, in isolated plots, affects its persistence in fragments (Fig. 3.5). Other things being equal, the species that persist longer are those that flock less after fragmentation than before. I illustrate this by plotting the residuals from the previous model against the change in flocking propensity.

## Results of tests for confounding effects

Including differences in persistence within fragments of the same size was not an improvement upon my model. The F test for lack of fit between these two models was not significant ( $F = 1.5$ ,  $df = 7, 281$ ;  $P > .15$ ). This confirms my assumption that I can pool the data based on fragment size.

Concerns about phylogenetic effects raise the issue of whether a model that considers species as discrete entities would be an improvement. It is not. The F test between these two models is not significant (Table 3.2) indicating that a species-specific model does not perform better than one that characterizes species by the three ecological factors I consider (captures, flocking index, change in flocking index.) Of course, there might be more complex phylogenetic effects between species. For example, species within families may be more similar in their persistence times than those between families. Or, there might be differences between the two flocking guilds that are confounded by phylogenetic effects.

I show the residuals from model for each species in Fig. 3.6; coding species by family and social strategy (ant followers or not). Each species has three data points, one for each of the three fragment sizes. The Royal Flycatcher (Onychorhynchus coronatus) was not caught in the 1 ha plots. By chance alone, some species should appear to persist longer and others shorter than the model predicts. For example, the Olive-backed Foliage gleaner (Automolus infuscatus) consistently persists longer than expected and the Buff-throated Foliage gleaner (A. ochrolaemus) consistently



persists shorter than expected (Fig. 3.6). There are no phylogenetic trends (Fig. 3.6). Indeed, the previous example is of two congeners. Moreover, there is no consistent difference based on foraging strategy.

Recapture rate could also potentially explain differences in the model. Species that are difficult to recapture may not appear to persist in fragments, when in fact they simply avoid nets. Fig. 3.7 plots recapture rate against the residuals from the model. No consistent pattern emerges. Contrary to expectation, the species with the greatest capture probability – the Collared Gnatwren (Microbates collaris) – falls below the model in all three fragment sizes.

## Outliers

To the extent that the model does not fit the data well, two species, *G. spirurus* and the Black-headed Antbird (Pernostola rufifrons) consistently persist longer than the model predicts (Fig. 3.5a, Fig. 3.6). In addition to using mature forest, both of these species tolerate forest edges, gaps, as well as secondary forest. Species with such broad habitat requirements are too few to test whether this is a general effect, however. While most of the species persisted in the 100 ha fragment, two species – D. certhia and A. ochrolaemus – appeared to vanish after less than two years (Table 3.1). Both of these species have low capture probabilities (Fig. 3.7), but that factor does not otherwise predict a species' persistence (Fig 3.5c). The Scale-backed Antbird (Hylophylax poecilinota) persists longer than expected in the 10 ha plots (Fig. 3.5b).

This species is unique in that follows ant swarms, but also maintains small individual territories.

## **Discussion and Conclusions**

While it is known that flocking species are susceptible to habitat loss (Willis 1974, Bierregaard and Lovejoy 1989, Thiollay 1992, Canaday 1997, Thiollay 1999), I show that the process has several subtleties. Those species more likely to be in flocks in continuous habitat persist for less time in isolated fragments (Fig. 3.3). Species withdrawing from flocks after isolation persist longer than do those that remain in flocks (Fig. 3.5). Differences in phylogeny (Fig. 3.6) or detection rates (Fig. 3.7) do not provide better explanations of the variation in the data. These findings add to the general notion that behavior influences species' survival in fragmented landscapes.

Quite how flocking should affect persistence is not self-evident. Persistence in an isolated fragment depends on extinction and immigration. My postulated mechanism first assumes that flocking species require more area (and so perhaps leave the fragments sooner) than non-flocking species. More subtly, my mechanism assumes that flocking species do not return to the fragments more readily than non-flocking species. I consider each assumption in turn.

The literature suggests that understory insectivores that join flocks range more widely than those that do not. Birds that regularly join mixed-species flocks range over a

flock territory of 8–15 ha (Stouffer and Bierregaard 1995, Jullien and Thiollay 1998, Develey and Stouffer 2001). By comparison, citing Terborgh et al. (1990), Stouffer and Bierregaard (1995) argue that small insectivores occupy territories smaller (and sometimes much smaller) than 10 ha. Lacking complete data on all ant followers, I deduce they likely range beyond 100 ha (Harper 1987) although not all such species range as widely (Wilson 2003). Ant followers often require several army ant colonies, each occupying ~30 ha, to ensure that they have at least one swarming ant colony at any given time (Willis and Oniki 1978, Lovejoy et al. 1986). Isolated small forest fragments do not provide enough habitat for such wide-ranging species. The more a species relies on flocking as a foraging strategy the more I expect this pattern to be true.

Regarding the second assumption, one can imagine scenarios where flocking species would be more prevalent in isolated habitats. By analogy to island biogeography, wide-ranging birds may occur in fragments solely because they are more vagile. Isolated forest ‘islands’ should contain vagile species at least some of the time, whereas sedentary species should never be present (Pimm et al. 1988). Additionally, wide-ranging birds encounter forest gaps more often than sedentary birds, perhaps encouraging a greater aptitude to cross them. Such arguments are contrary to my findings.

Differences in species’ willingness to cross forest gaps are not well documented. What the literature does suggest is that all forest understory species are reluctant to cross forest gaps (Karr 1982, Thiollay 1992, Stouffer and Bierregaard 1995, Gascon

et al. 1999, Sekercioglu et al. 2004, Laurance et al. 2004). This pattern seems to hold even when the distance between forest patches is only 30 m (Develey and Stouffer 2001). In contrast to these studies, Harper (1987) observed obligate ant-following species fleeing fragments into surrounding continuous forests, sometimes crossing clearings over 300 m. This suggests that some flocking species have the ability and inclination to leave unsuitable fragments to seek habitats elsewhere. Whether species disperse from fragments or whether they die in them is uncertain. However, because of the reluctance to cross gaps, flocking species should not immigrate to isolated fragments from surrounding forests. To survive, flocking species must either flee small fragments or revise their foraging behavior.

Other explanations for my results require I consider the selective mechanisms underlying flocking. Species likely select flocks in both tropical and temperate forests to avoid predators, increase their foraging efficiency, or both (Powell 1985, Terborgh 1990, Jullien and Clobert 2000). Comparing forests across different continents, Thiollay (1999) found insectivores joined flocks more often when raptor abundance was higher. If predators were less frequent in the BDFFP fragments, then species that usually flocked to avoid predators would likely drop out of flocks, as most species seem to do (Fig. 3.4). As mist-nets sample raptors poorly, I make no comment on raptor abundance in fragments. Although this could potentially explain birds flocking less often in fragments, it would not explain why flocking species disappear from fragments.

Studies at the BDFFP demonstrate that the majority of invertebrate groups decrease inside fragments (Lovejoy et al. 1986, Didham 1997, Didham et al. 1998). If birds join flocks in continuous forests to increase their foraging efficiency, a reduction in forage would increase the selective benefits of flocking. As a result, one would expect flocking propensities to increase in fragments. I observed the opposite (Fig. 3.4). Other mechanisms besides foraging efficiency, then, must be at work. Exploring the factors contributing to joining flocks appears secondary to the reality that small forest fragments do not provide enough habitat for flocking species. Neither changes to resource availability nor risk of predation provide simple explanations for the results I obtain.

I instigated this study because of the overarching need to understand the factors that predict extinction. Such factors clearly vary across spatial scales and I am not surprised that what matters will be more complex and more idiosyncratic at smaller scales. One factor common to all scales is local abundance. For a given geographical range, locally rare species are more prone to be threatened globally than are locally common ones. Locally rare species are lost more quickly from small habitat patches (such as islands) than are locally common ones. The mechanism seems obvious: small numbers make a species particularly vulnerable to the vagaries of nature that cause all populations to fluctuate (Pimm 1991). This is surely the explanation for why broadly similar species differ in their vulnerabilities.

I had also assumed it was the likely explanation for differences in species that differ in body size. Woodroffe and Ginsberg (1998, 2000) challenge that confidence.

Species composed of widely ranging individuals essentially run out of space in the fragmented ecosystems that now dominate most of the planet. Other things being equal, larger-bodied species will roam more widely; have lower local densities, and thus higher extinction risks. Importantly, behavioral differences also affect how widely a species ranges, independently of body size. Thus, Woodroffe and Ginsberg not only provide a fundamental (and thus potentially general) explanation for differences in extinction risk, but an explanation that invokes behavior. The role of behavior was appreciated rather more than it was empirically demonstrated. My aim was to determine if the proposed mechanism was a general one.

This 'wider ranging species are at risk' hypothesis immediately resonated with my experience at Manaus. The project's earliest results suggested that the first species to be lost from the isolated fragments were often those with certain behavioral traits – flocking and ant-following – rather than simply those that were locally rare (Lovejoy et al. 1986). My present results confirm this.

Local abundance certainly plays a significant role in predicting which species are lost. Differences in the number of captures suggest that the most commonly encountered species last less than 2 years longer in the smaller fragments than do the rarest species. (This estimate comes from multiplying the ranges of values, 100 to 2000 days in Table 3.1, with the parameter value, 0.332 in Table 3.2.) Differences in the flocking index are more important for species in the smaller fragments, however. Here species that flock the least last over 3 years longer than species that flock the

most. Those species that withdraw from flocks after fragmentation offset the vulnerability of the species that remain in flocks.

These quantitative estimates show that, at least broadly, the behavioral differences between species are more important at this spatial scale than the ecological differences in abundance. Over the landscape, compared to large forest patches, small fragments will lose more species and lose them more quickly (Ferraz et al. 2003). As shown here, the species small fragments contain will be different not only in terms of a simple species list, but in the behavioral features of those species.

**Table 3.1**

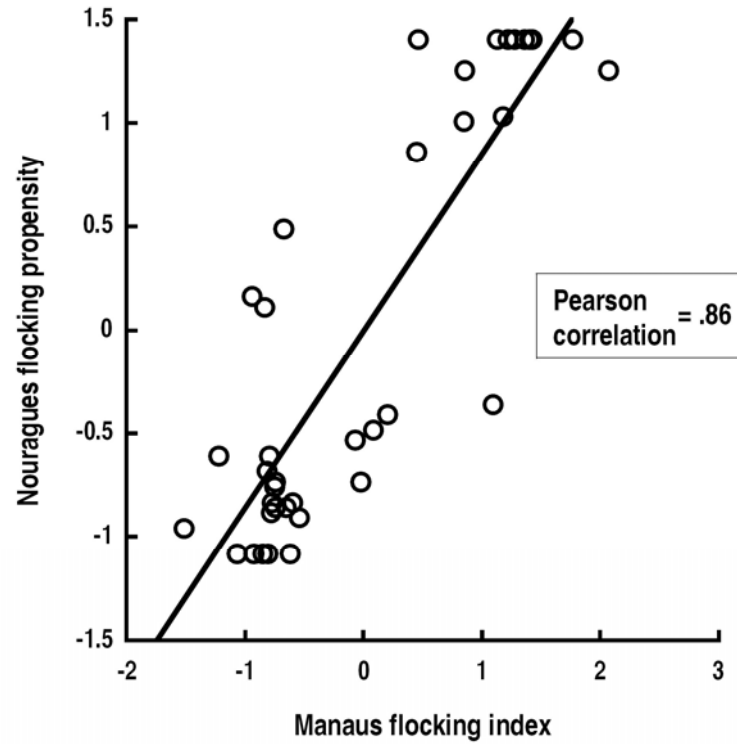
Species	Sociality	Recapture Rate	Pre-fragmentation		Post-fragmentation		Flocking Change	Persistence (days)		
			Captures	Index	Captures	Index		1 ha	10 ha	100 ha
TYRANNIDAE										
<u>Rhynchocyclus olivaceus</u>	u		73	0.32	64	0.19	0.13	851	1192	3063
<u>Terenotriccus erythrurus</u>	su	0.09	68	0.12	58	0.09	0.03	490	1535	3409
<u>Myiobius barbatus</u>	u	0.20	433	0.14	237	0.14	0.00	239	1149	3410
<u>Onychorhynchus coronatus</u>	su	0.27	109	0.17	28	0.18	−0.01	–	462	2989
THAMNOPHILIDAE										
<u>Thamnophilus murinus</u>	su	0.11	79	0.11	59	0.12	−0.01	1427	979	3350
<u>Thamnomanes ardesiacus</u>	u	0.38	973	0.34	376	0.24	0.10	413	1638	3408
<u>Thamnomanes caesi</u>	u	0.07	637	0.32	232	0.27	0.05	329	1915	3350
<u>Myrmotherula guttata</u>	su	0.49	282	0.21	55	0.22	−0.01	116	675	3087
<u>Myrmotherula gutturalis</u>	u	0.33	554	0.34	173	0.29	0.05	381	1888	3408
<u>Myrmotherula axillaris</u>	us	0.19	248	0.28	193	0.22	0.06	1197	2364	3347
<u>Myrmotherula longipennis</u>	u	0.35	480	0.31	228	0.31	0.00	377	1150	3409
<u>Myrmotherula menetriesii</u>	u *	0.13	225	0.25	108	0.23	0.02	493	1202	3408
<u>Pernostola rufifrons</u>	sa *	0.47	515	0.17	344	0.13	0.04	3419	1889	3409
<u>Pithys albifrons</u>	a	0.35	2791	0.27	408	0.30	−0.03	162	142	3410
<u>Gymnopithys rufigula</u>	a	0.30	1538	0.31	263	0.33	−0.02	180	892	3408
<u>Hylophylax poecilinota</u>	sa	0.44	2010	0.18	711	0.14	0.04	753	3552	3410
FURNARIIDAE										
<u>Philydor erythrocerus</u>	u *	0.04	116	0.31	38	0.29	0.02	84	509	3148
<u>Automolus infuscatus</u>	u *	0.46	499	0.34	120	0.33	0.01	327	1056	3281
<u>Automolus ochrolaemus</u>	su	0.05	63	0.32	26	0.31	0.01	0	121	527
<u>Xenops minutus</u>	u	0.28	236	0.28	68	0.31	−0.03	155	662	3198
<u>Dendrocincl</u> <u>a fuliginosa</u>	sua *	0.12	155	0.20	114	0.18	0.02	416	3004	3408
<u>Dendrocincl</u> <u>a merula</u>	a	0.22	660	0.26	57	0.28	−0.02	75	226	3150
<u>Deconychura longicauda</u>	uc *	0.11	87	0.24	40	0.28	−0.04	56	374	3409
<u>Deconychura stictolaema</u>	u	0.34	570	0.24	191	0.20	0.04	80	336	3409
<u>Glyphorhynchus spirurus</u>	us	0.38	1234	0.14	586	0.08	0.06	3492	3552	3410
<u>Hylexetastis perrotii</u>	sa *	0.05	77	0.35	52	0.29	0.06	48	522	1946
<u>Dendrocolaptes certhia</u>	as *	0.07	37	0.16	43	0.07	0.09	1864	1591	374
<u>Xiphorhynchus pardalotus</u>	u *	0.16	545	0.37	467	0.18	0.19	1604	3333	3281
VIREONIDAE										
<u>Hylophilus ochraceiceps</u>	u	0.29	433	0.40	92	0.34	0.06	94	760	3350
CERTHIIDAE										
<u>Microbates collaris</u>	su *	0.63	523	0.23	208	0.17	0.06	408	596	3196



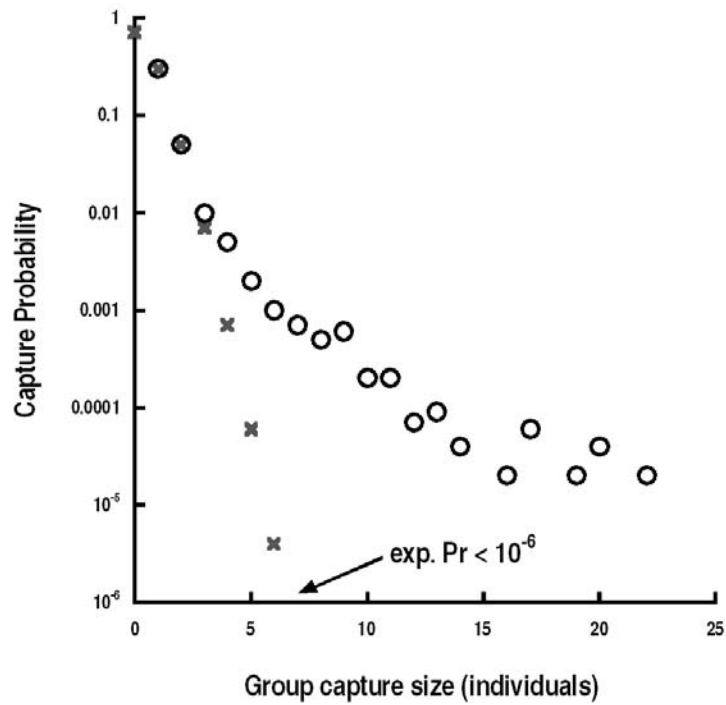
**Table 3.1.** Sociality (in order of prevalence) from Cohn-Haft et al. (1997): “u” – in understory mixed flocks, “s” – solitary or in pairs, “a” – army ant follower, “c” – in canopy mixed flocks, “\*” – described differently in Ridgely and Tudor (1991, 1996). Recapture rate: reconstituted from p(t) parameter in MARK, blank indicates inestimable parameter. Pre- and Post-fragmentation: Captures – total captures during period, Index – proportion of in-flock captures to total captures. Flocking change: decrease in flocking behavior after plot isolation, negative values indicate increases. Persistence: duration species detected in plots after isolation, averaged among similar sized plots (five 1 ha, four 10 ha, one 100 ha), “0” – detected before but not after isolation, “–” – never detected.

Source	df	SS	F	Prob. > F	Parameter	$\beta$ Estimate	SE
Model	5	108491838	33.9	<.0001	Fragment Area		
Fragment size	2	92409893	72.1	<.0001	1 Ha plots	1236	318
Captures	1	3660071	5.7	<.02	10 Ha plots	1876	209
Flocking index	1	7550396	11.8	<.001	100 ha plot	3646	207
Change in flocking index	1	10790001	16.8	<.0001	Captures	0.332	0.139
Residual (error)	83	53184175			Flocking index	-3849	1121
					Change in flock. index	7370	1796
Lack of fit	26	20340669	1.4	0.17			
Pure Error (within species, fragment residual)	57	32843506					

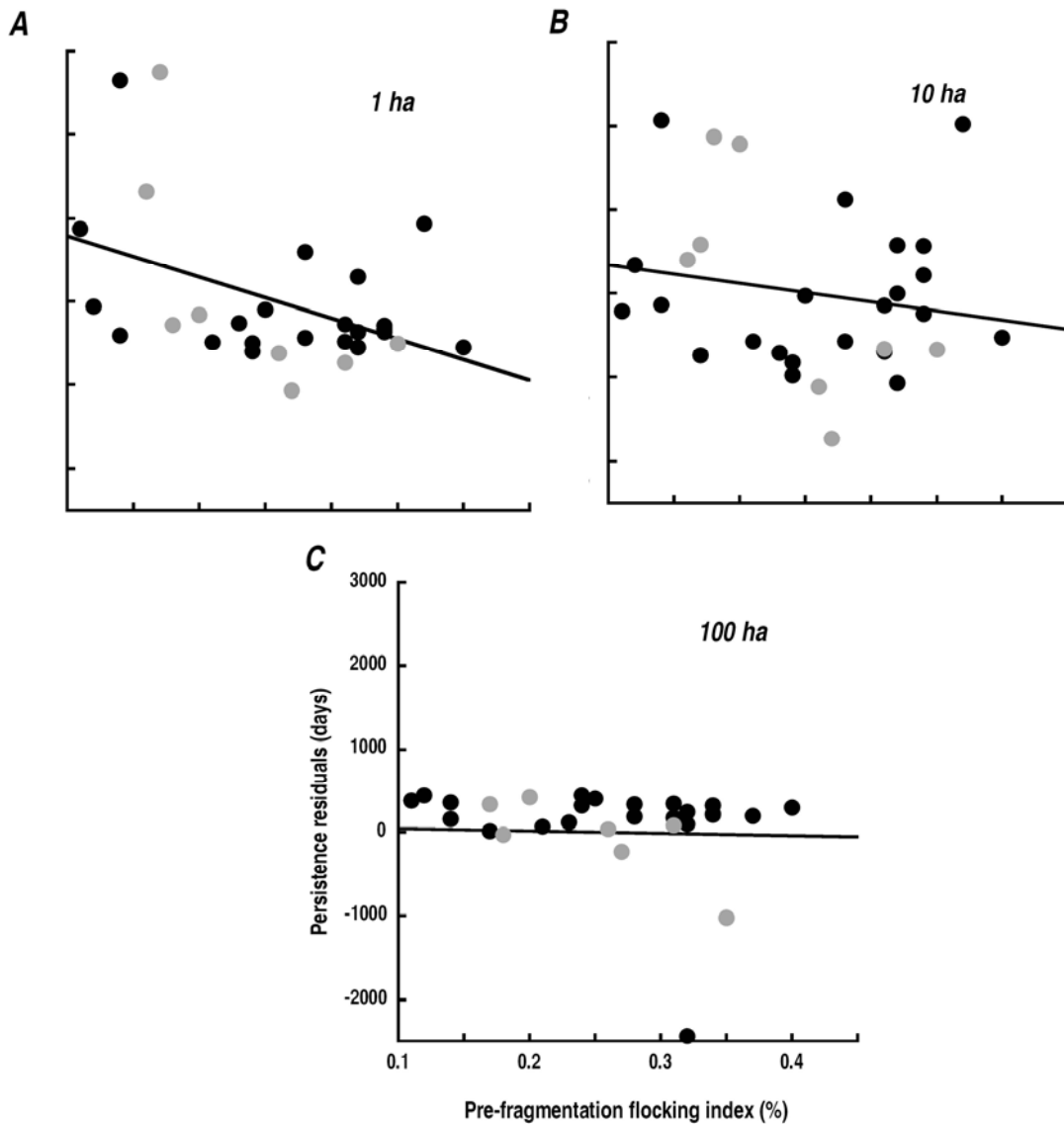
**Table 3.2:** Statistical summary of the full persistence model. Capture frequency, fragment size, flocking behavior in continuous plots, and flock “dropout” after isolation all factor significantly in species persistence. This model outcompeted a model including fragment size and considering each species as a unique variable; serving as a lack of fit test. Model  $R^2 = .67$ .



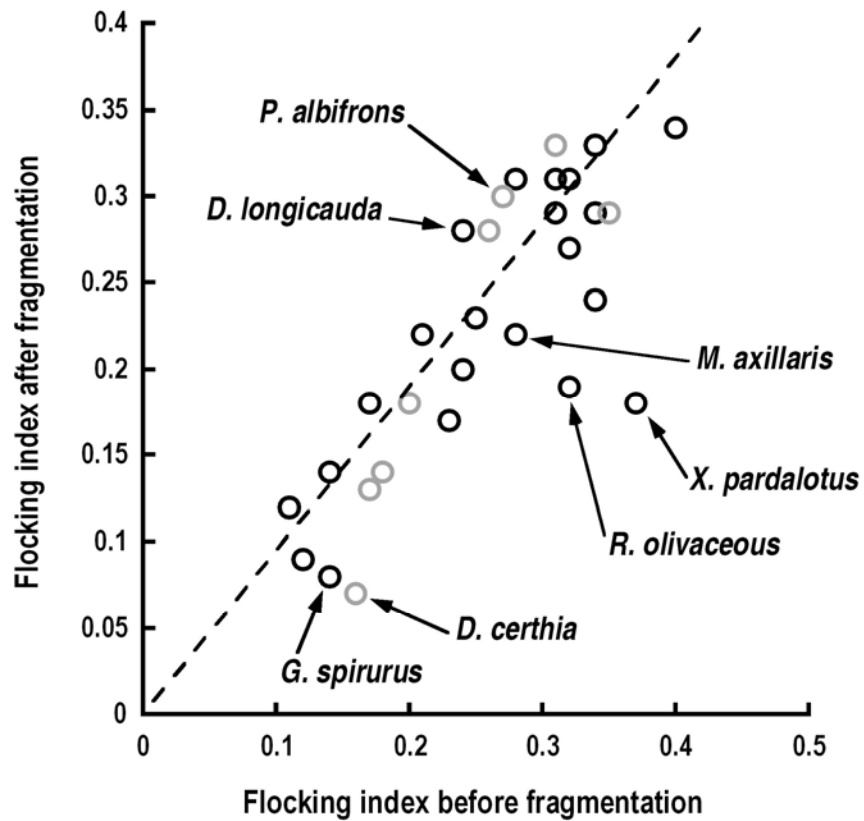
**Figure 3.1:** Flocking tendency measured from mist-net data correlates well with an observer-based method by Jullien and Thiollay (1998). Comparisons are between similar forests in Manaus, Brazil and Nouragues, French Guiana, and are restricted to species in common to both locations. Values shown are standardized.



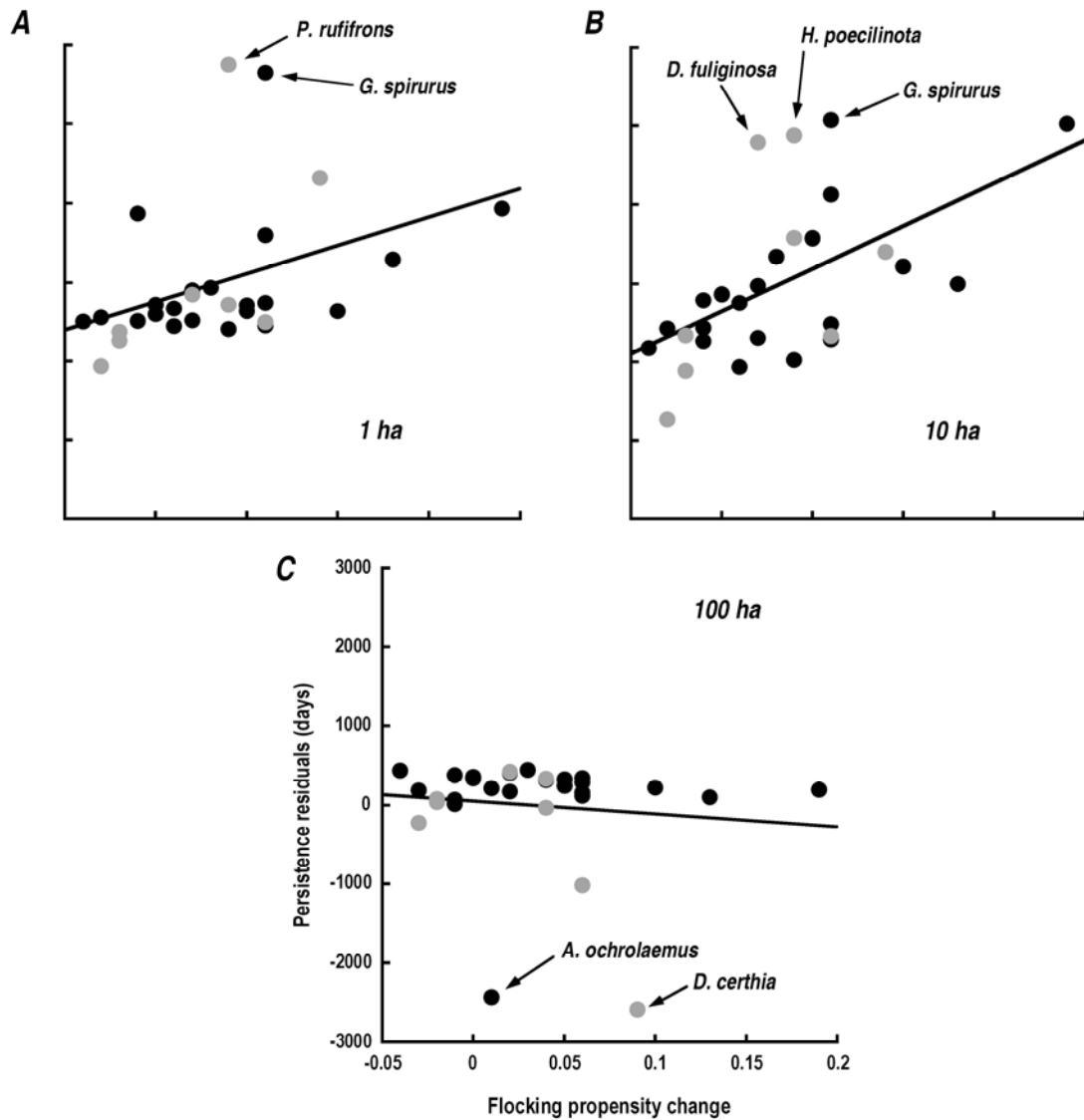
**Figure 3.2:** The frequency of birds caught in groups of three or more is greater than expected by chance alone. Open circles are the observed probabilities of birds netted in different-sized groups. From the numbers of captures of 1 and 2 individuals, I deduce the parameters of a Poisson distribution and so predict the expected probabilities of captures of 0, 1 ... n captures (shown in grey x's). Capture probabilities are log-transformed.



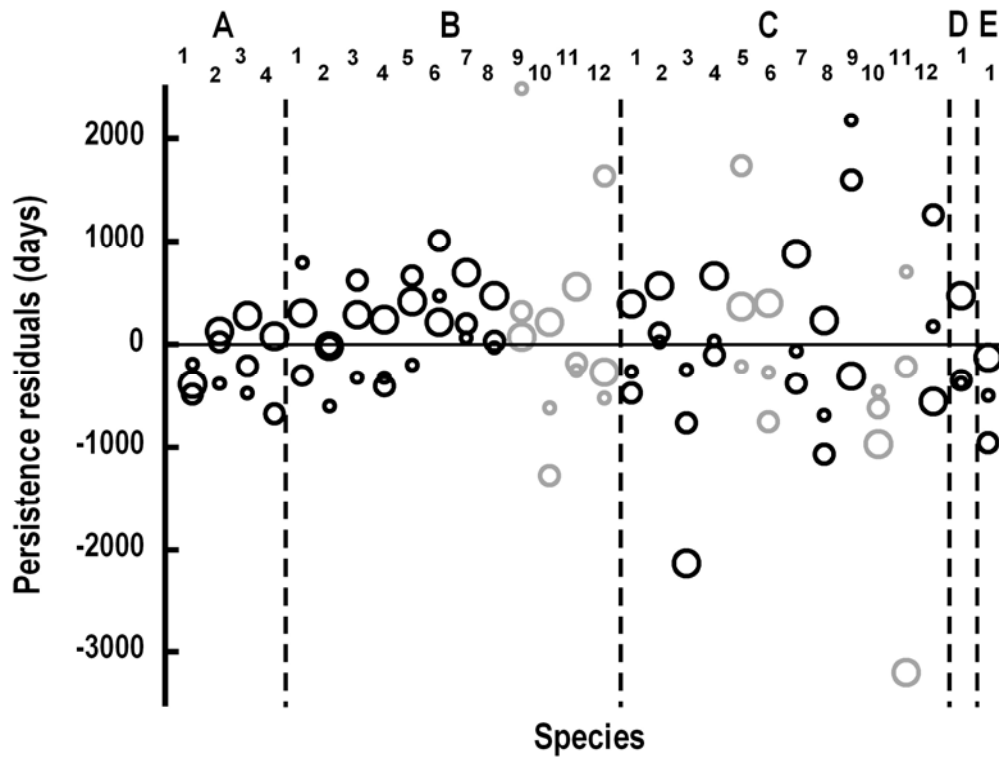
**Figure 3.3:** The more likely a species is found in a flock prior to fragmentation, the shorter the period of time it persists afterwards. Residual values are extracted from a model using capture frequency and fragment size to predict persistence. Data from five 1 ha, four 10 ha, and one 100 ha are shown. Black circles are species joining mixed-flocks, gray circles represent ant followers (this color coding is retained throughout). Trend line represents both guilds.



**Figure 3.4:** Species are generally detected more frequently in flocks before fragmentation (paired t-test:  $t = 3.5$ ,  $df = 30$ ,  $P < .002$ ). The line of equality is dashed. Labeled species are discussed in text.

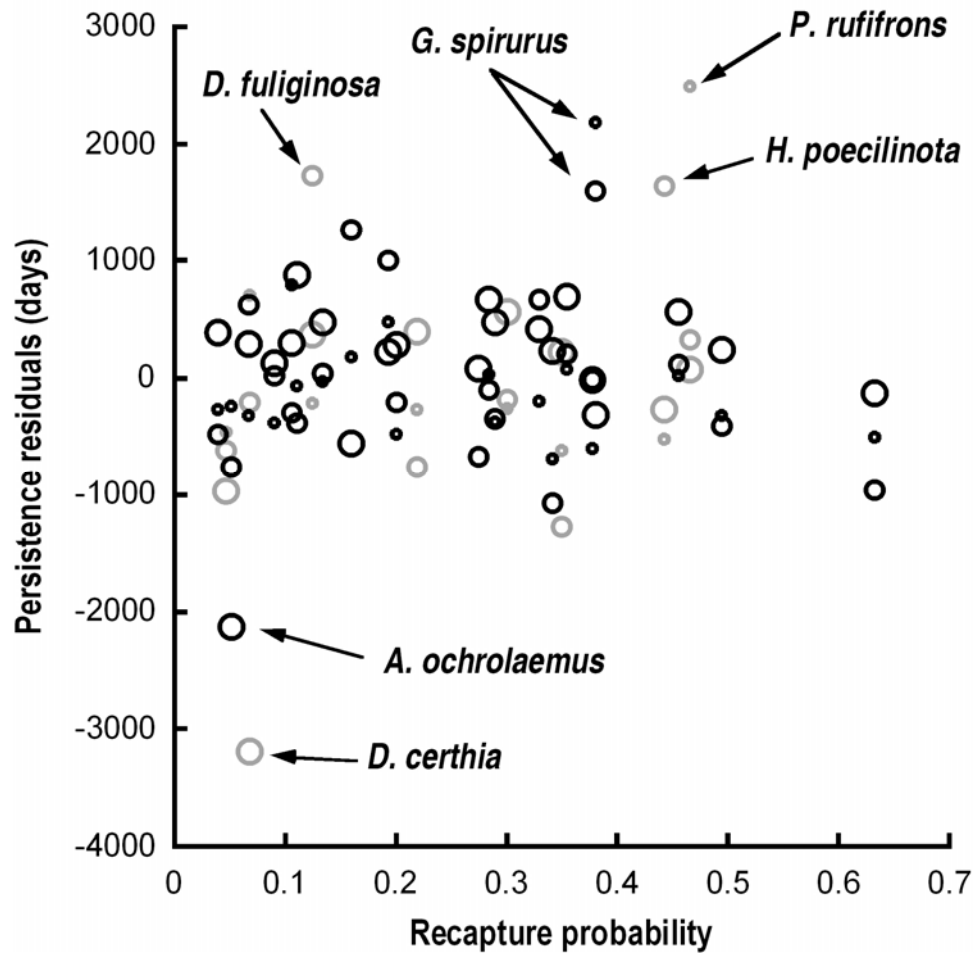


**Figure 3.5:** The more a species decreases its occurrence in flocks as a result of fragmentation, the longer it persists after fragmentation. Residual values are extracted from a persistence model using capture frequency, fragment size, and pre-fragmentation flocking behavior as factors. Labeled outliers detailed in Discussion.

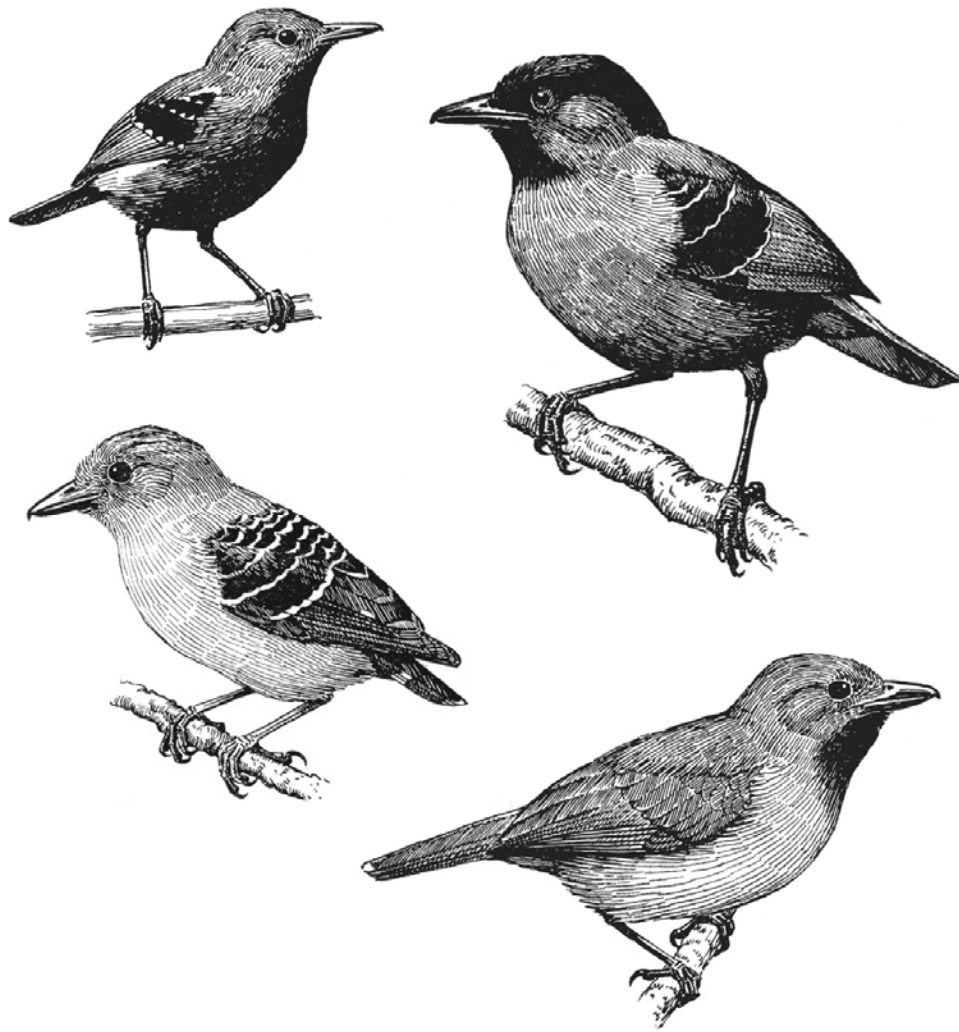


**Figure 3.6:** No clear taxonomic trends explain differences in the model, neither does foraging strategy. Circles increase in size according to fragment area, with small circles representing data from 1 ha plots. A = Tyrannidae: 1) Rhynchocyclus olivaceus, 2) Terenotriccus erythrurus, 3) Myiobius barbatus, 4) Onychorhynchus coronatus; B = Thamnophilidae: 1) Thamnophilus murinus, 2) Thamnomanes ardesiacus, 3) T. caesius, 4) Myrmotherula guttata, 5) M. gutturalis, 6) M. axillaris, 7) M. longipennis, 8) M. menetriesii, 9) Pernostola rufifrons, 10) Pithys albifrons, 11) Gymnopithys rufigula, 12) Hylophylax poecilinota; C = Furnariidae: 1) Philydor erythrocerus, 2) Automolus infuscatus, 3) Automolus ochrolaemus, 4) Xenops minutus, 5) Dendrocincla fuliginosa, 6) D. merula, 7) Deconychura longicauda, 8) Deconychura stictolaema, 9) Glyphorhynchus spirurus, 10) Hylexetastis perrotii, 11) Dendrocolaptes certhia, 12) Xiphorhynchus pardalotus; D: Vireonidae: 1) Hylophilus ochraceiceps; E = Certhiidae: 1) Microbates collaris





**Figure 3.7:** Differences in recapture probability do not explain the model residuals. Recapture rate was calculated in MARK, and allowed to vary annually, with netting effort. Rates shown are reconstituted based on an annual sampling rate of 10,000 net hours. Each species has three points (one for each fragment size). Circles increase in size based on fragment size. The model over-predicts fragment persistence for two species (figure 3.5c) that mist-nets do not detect frequently.



**Figure 3.8:** Clockwise from top: *Myrmotherula axillaris*, *Percnostola rufifrons*, *Thamnomanes ardesiacus*, *Hylophylax poecilinota* (pp 268, 262, 248, and 252 from Haverschmidt, F. 1968. *The Birds of Surinam*, illustrations by P. Barruel, arrangement by K. S. Van Houtan) Images used by permission of the Netherlands Foundation for the Advancement of Tropical Research (<http://www.nwo.nl/wotro>). This image was the cover image for the journal article version of this chapter.



– Four –

Dispersal of Amazonian birds in  
continuous and fragmented forest

## INTRODUCTION

What happens to populations in fragmented habitats compared to naturally continuous ones? The question (Lovejoy et al. 1986) is a pressing practical one, as well as one of intrinsic interest. Species are going extinct at a rate a hundred times faster than expected, with future rates likely to rise to one thousand times faster (Pimm et al. 1995; Pimm et al. 2006). Habitat loss, particularly in tropical moist forests, is the principal driver of these high rates. Human actions do not simply destroy such habitats, for what remains is fragmented and isolated. Our first analyses emerge from the existing literature that supports the idea that tropical understory forest birds are sedentary and avoid gaps. If true, forest clearing should imprison all species in fragments, where the small remnant populations are unsustainable and die out (Pimm et al. 1993). In this study, I directly estimate how far species move using the unique experimental design of the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil. To do so requires a probability model that describes both short distance movement and long distance dispersal. I find that species differ considerably in how far they move before and after fragmentation. Some move unexpectedly long distances and some readily cross gaps between plots. Our second set of analyses stem from knowing most species disappear from fragments rapidly, while some remain (Lovejoy et al. 1986; Ferraz et al. 2003; Van Houtan et al. 2006). I show that dispersal and risk of extinction are linked.

## **The reluctance to emigrate**

In their classic theory of island biogeography, MacArthur and Wilson (1967) start with its application to habitat “islands,” or fragments. Like oceanic islands, fragments gain species through immigration and lose them through extinction. “Extinction” in this context, is not a single process. It could arise from individuals dying locally, but equally, it could be from a lack of immigrants (Brown and Kodric-Brown 1977), or from individuals choosing to leave a fragment (Hanski 1999). For birds on small British islands – a system long considered canonical in island biogeography (e.g., Lack 1969) – smaller islands have higher extinction rates than larger ones, and remote islands gain fewer immigrants than ones near the mainland (Russell et al. 2006). Significantly, by far the largest effect is that species remain on remote islands longer than on near ones, as they are likely reluctant to cross large water barriers.

In tropical forest fragments, are birds reluctant to emigrate through a hazardous matrix? The literature suggests so. The corresponding arguments rely on evolutionary constraints: the birds do not range widely, do not disperse far from their natal territory, and avoid unsuitable habitat due to physical or behavioral limits (e.g., Ehrlich and Raven 1969; Willis 1974; Terborgh et al. 1990; Sodhi et al. 2004). Corroborating these claims, several studies find cattle pasture and agricultural fields a near absolute barrier for tropical forest birds (e.g., Stouffer and Bierregaard 1995; Sieving et al. 1996), while others document these birds avoid roads and forest edges (e.g., Stouffer and Bierregaard 1995; Develey and Stouffer 2001; Laurance et al. 2004). Still other analyses find that the same species which are absent in older

fragments are seldom detected in the deforested matrix between them (Gascon et al. 1997; Şekercioğlu et al. 2002).

However, these arguments suffer from a number of problems. To begin with, studies from temperate and boreal forests do not confirm the idea that forest birds are sedentary and gap-shy. While many agree (e.g., Desrochers and Hannon 1997; Sisk et al. 1997; Haddad et al. 2003; Levey et al. 2005) a significant number do not (Howe 1984; Moore and Dolbeer 1989; Norris and Stutchbury 2001; Fraser and Stutchbury 2004). Evidence from the tropics also varies. Some studies find tropical forest birds cross large gaps often (e.g., Harper 1987; 1989) and even colonize islands isolated by open water (e.g., Wright 1985). Secondly, results from tropical-forest studies should not be extrapolated too far beyond the scope of their experimental designs. For example, many studies either infer gap crossing ability from indirect evidence (e.g., Stouffer and Bierregaard 1995; Gascon et al. 1997; Şekercioğlu et al. 2002), affect behavior by using audio devices (e.g., Sieving et al. 1996; Develey and Stouffer 2001), overlook the different selective pressures for crossing gaps in continuous and fragmented forests (e.g., Develey and Stouffer 2001; Laurance et al. 2004), or are confined to small spatial scales (e.g., Sieving et al. 1996; Develey and Stouffer 2001; Laurance et al. 2004).

In this study I examine avian movement from direct empirical evidence, both before and after the isolation of forest plots, and at spatial and temporal scales that are comparatively extensive. For the first time, I analyze dispersal kernels for tropical forest birds by using a large spatially explicit capture database from the BDFFP. I use

these data to estimate the parameters for a variety of probability distribution models, which correspond to decidedly different types of bird movement. I expect the model that best fits the data will also offer the best conceptual description of how tropical forest birds move in continuous and fragmented forest.

### **Dispersal kernels**

For a given model of bird behavior, there is a probability density function for dispersal distances  $x$  and  $y$  from the starting point, this probability function is called the dispersal kernel. As I compute movement from spatial coordinates, I derive a univariate quantity from two-dimensional data. The distance from the origin to a point  $x, y$  in the plane,  $r = (x^2 + y^2)^{1/2}$ , is called the amplitude. The corresponding amplitude kernel has a distribution of its own which is related to, but distinct from, the distributions of  $x$  and  $y$ . Based on different hypotheses of bird behavior, I select several distributions for  $x$  and  $y$ , and fit their corresponding amplitude kernels to the empirical distributions of  $r$ . All our models are radially symmetric; birds are assumed to move in all directions equally.

The normal, or Gaussian, distribution describes an individual whose movement is shaped by multiple external stochastic forces – a random walk. Such individuals diffuse through space, and as a result, their populations spread rather slowly. For this model the corresponding amplitude kernel is the Rayleigh distribution:



$$f(r) = \left( \frac{r}{\alpha^2} \right) \exp\left( -\frac{r^2}{2\alpha^2} \right), \quad r \geq 0, \quad \alpha > 0 \quad \dots(1)$$

where  $\alpha$  is the scale parameter ( $\alpha > 0$ ), a measure of the average dispersal distance.

Another candidate model, the negative exponential distribution describes individuals that move in one direction with a constant probability of not making it any further than they are. For this model the corresponding amplitude kernel is the Gamma distribution with shape factor two:

$$f(r) = \left( \frac{r}{\alpha^2} \right) \exp\left( -\frac{r}{\alpha} \right), \quad r \geq 0, \quad \alpha > 0 \quad \dots(2)$$

where,  $\alpha$  is again the scale parameter. Note the similarity of form to Eq. (1), except that here the tail of the amplitude kernel has a slower decay than the Rayleigh.

Unlike the Rayleigh or gamma models, “heavy-tailed” or “fat-tailed” probability functions allow movement to greater distances, other factors being equal. Heavy-tailed models assume that some individuals tend towards long-distance movement and the corresponding distributions are typically characterized by power-law tails. Various heavy-tailed models have been used previously in ecological studies, the: Cauchy (e.g., Paradis et al. 2002), log hyperbolic secant (henceforth “log-sech”, e.g., Halley and Inchausti 2002), Lévy-stable (e.g., Brockman et al. 2006), the two-dimensional Student’s t (e.g., Clark et al. 1999), as well as various mixed-models with power-law tails (e.g. Bullock and Clarke 2000; Montoya et al. 2006). Here I

follow Halley and Inchausti (2002), assuming a dispersal kernel such that  $r$  has a log-sech distribution:

$$f(r) = \frac{2/(\pi br)}{(r/\alpha)^{1/b} + (r/\alpha)^{-1/b}}, \quad r \geq 0, \quad \alpha, b > 0 \quad \dots(3)$$

$\alpha$  is the scale parameter as before, and  $b$  is a shape parameter. I define  $\beta$  as the tail index, with  $\beta = 1 + 1/b$  because the probability density function (3) has the form

$f(r) \approx (2/\pi br)(\alpha/r)^\beta$  for large values of  $r$ . The tail index is not fixed but can lie anywhere in the range  $(1, \infty)$ , allowing the rate of decay to vary. When  $\beta = 2$  the distribution reduces to the Cauchy form.

### **Dispersal and extinction risk**

One might expect that species that disperse widely in continuous forest might be those most able to do so after habitat fragmentation. If so, wide-dispersers would be those that persist in the fragments, even only as transient and occasional visitors. I presented the opposite hypothesis elsewhere (Van Houtan et al. 2006). Other things being equal, widely dispersing carnivores are more prone to local extinction than those that readily occupy smaller areas (Woodroffe and Ginsberg 1998). In other words, wide-dispersers run into the hazards associated with meeting or crossing unsuitable habitats. I found a similar effect with the birds in this study site: species that joined flocks or followed army ant swarms quickly disappeared from small

fragments. Species joining flocks only facultatively persisted (Van Houtan et al. 2006). In that study I did not have spatial coordinates for captures and only inferred dispersal behavior. Here I rectify that omission.

## **METHODS**

### **Study Area and Sampling**

The Biological Dynamics of Forest Fragments Project (59°58'11"W, 2°22'25"S) near Manaus, Brazil, is an unrivaled empirical setting to study how populations respond to forest loss and fragmentation. From 1979–1983, eleven forest plots (five 1 ha, four 10 ha, two 100 ha) were established in primary, lowland moist forest at three sites: Dimona, Porto Alegre, and Esteio. At varying times thereafter, the forests immediately surrounding the study plots were clear-cut for cattle pasture, leaving the plots isolated from nearby continuous forest. The resulting fragments were 70–800 m (average = 230 m) from continuous forest after isolation, and separated 250–2450 m (average = 1150 m) from other fragments at the same site. (An additional 17 plots, ranging from 1–1000 ha, located in continuous forest were never isolated.) Linear mist-net transects regularly sampled birds in plots from their establishment until 1993, before and after isolation at each site. Transects consisted of eight 2 x 12 m nets ( $\approx$  100 m) in 1 ha plots and sixteen nets ( $\approx$  200 m) in 10 and 100 ha plots. Transects were typically sampled monthly, and never on consecutive days. Captured birds were described, marked with uniquely numbered leg bands, and released, with

the net location noted. These efforts provide 8,799 recaptures – 3,122 before isolation and 5,677 after – from 106 species. Further experimental details appear elsewhere (Stouffer and Bierregaard 1995, Ferraz et al. 2003).

For this study, I only consider species with >100 recaptures, and grouped according to extinction risk. I consider a species “extinction-prone” if it was not detected in 1 ha fragments one year after their isolation, and not detected in 10 ha fragments three years after isolation (though some returned to fragments after extended absences [Stouffer and Bierregaard 1995]). I consider a species “persistent” if it was detected in 1 ha fragments after a year of isolation, and detected in 10 ha fragments after three years of isolation. In actuality, the majority of extinction-prone species disappeared from fragments in short order and the majority of persistent species remained in fragments for the entire census period. This method netted 13 extinction-prone species and eight persistent species.

## **Data Analysis**

To limit the effect of frequently captured individuals, I exclude same-day recaptures within 200 m, the length of the longest net transect. (If I excluded all same-day recaptures, however, I would miss the five occasions when individuals were netted in different plots, a few hours apart.) Because I document movements from recapture data, the exact date of the movement is often uncertain. For example, when a bird is captured in two separate plots, a year apart, it cannot be determined when the bird

actually made the flight. Knowing the precise dates when plots were isolated (Lovejoy et al. 1986), deducing the state of the matrix between plots in the time between successive captures was often straightforward. As a result, I distinguished movements through continuous forests from those through cattle pasture in most cases. I employ several analyses to understand how isolation affects movements between plots.

First, I quantified movements between plots, relative to the time since a plot's isolation. Time is an important factor as birds were thought to colonize fragments through forest regrowth that occurred after cattle grazing ceased (Stouffer and Bierregaard 1995, Van Houtan et al. 2006). Categorizing time, I consider movements as occurring on the median date between captures and group them in two-year bins relative to the date a plot was isolated. Two-year bins maximized time resolution and maintained sufficient sample sizes. As exceptions, I group all captures after 8 years post-isolation, and pool all pre-isolation captures. Given the data's uncertainty towards gap-crossing dates (see above), this method minimizes date estimation error, yet does not likely skew results (<8% of the capture intervals exceed two years). I represent movements in proportion to a plot's total recaptures for that period, achieving a "movement rate" to account for sampling differences between plots. This rate effectively records the proportion of recaptured birds either coming or leaving a particular plot over a given time period. I make no statistical conclusions from these time-explicit analyses, but use them to show how isolation time affects the flow of birds between fragments and how it interacts with other factors.

Next, I used an analysis of covariance to test the relative importance of fragmentation, species and plot size as determinants of movement rates. For the response variable I used the number of inter-plot dispersals (as a proportion of recaptures) with plot size as a continuous variable, and plot treatment and species type (extinction-prone or persistent) as discrete variables. Though plots are categorized as 1, 10, and 100 ha, I include their slight variations in area here (Ferraz et al. 2003). In this analysis, I exclude plots with <20 recaptures before or after isolation, thus eliminating some plots that were censused minimally. Using this analysis I can test whether the effect of isolation is indeed as great as has been argued and how much it depends on species type.

Following this, I used a contingency table analysis to detect whether emigrations after isolation indicate the selection of certain plots over others. As in the first model, I separated movements into the categories of before and after isolation (resolving time no further), then characterized all emigrations as a movement to a plot that is smaller, larger, or of equal size. For the null model observations, I tallied all such possible permutations at each site (between site movements were uncommon, see below) from the number and size of the plots at that site; a result of the experimental design. Permutations from all sites were totaled, providing the expected observations when movements between plots within each site are of equal probability. Null model observations are then compared against observed emigrations in continuous forest and those between fragments. I tested all statistical models with SAS 9.1 (The SAS Institute 2003).

Finally, for the dispersal kernel analyses, I first determined mist-net coordinates from archived maps of bird censuses, aided by our own GPS surveys. Obtaining spatial coordinates for each capture, I then computed the distance traveled between captures,  $r$ . The probability of observing a movement to any distance from where a bird was first caught,  $\Pr(r_i|c)$ , depends on the probability model,  $\Pr(c|r_i)$ , and the sampling effort at that distance,  $\Pr(w_i)$ . To obtain  $\Pr(w_i)$ , I use ARCGIS (ESRI 2006) to calculate the area censused in 100m annuli radiating from each plot's centroid. I tally the area sampled in each annulus for all 11 plots that were eventually isolated, and divide this by the total area in that annulus, across all plots. This provides a single value,  $\Pr(w_i)$ , for each annulus of the amplitude data. This value is then used to weight the empirical amplitude data, to account for distances that were poorly censused. Lastly, I used maximum likelihood methods to find the parameter estimate(s) most likely given the data, for the Rayleigh, gamma, and log-sech models, using the likelihood function:

$$L = \prod_{i=1}^n \left[ \frac{w(r_i)f(r_i)}{\int_0^{r_{\max}} w(r)f(r)dr} \right] \dots(4)$$

We compare these models using the Akaike Information Criterion (AIC) test that compares models' likelihoods, but penalizes models with more parameters (Halley and Inchausti 2002). To compare models I first minimize the Akaike information associated with the likelihood in (4). The parameters yielding the minimum are found

by using a Monte–Carlo search in parameter space. The model with the lowest Akaike information is the best–fitting model.

## RESULTS

### Rates of movement between plots

For the 21 species I consider, I observe 2,405 individuals and identify 237 movements between plots from 2,437 recaptures before isolation and 189 from 3,996 recaptures after isolation. I excluded 66 plot–to–plot movements from the analyses as I do not know whether they occurred before or after isolation.

Figure 4.1 shows the proportion of plot–to–plot movements divided by the total number of recaptures (both between and within plots). For extinction–prone species, such movements decline after isolation. They later rebound as Cecropia sciadophylla and Vismia spp, colonized the clearings between plots (Fig. 4.1a). This pattern is most pronounced in the 1 ha fragments, but is also observed to some extent in 10 and 100 ha plots. In contrast, persistent species do not move between fragments as often as extinction–prone species, and their movement rates do not change after isolation (Fig. 4.1b).

Figure 4.2 plots the same variable against plot size for the four combinations of continuous versus fragmented forest and extinction–prone versus persistent species. Simple geometry expects that, other things being equal, the proportion of birds



detected in >1 plot will decline as plot area increases. (One leaves one's home daily, one's city occasionally, and one's continent seldomly.) On a log-log scale, the fraction of plot-to-plot movements decreases with increasing plot size ( $F_{1,22} = 93.9$ ,  $P < .0001$ ) at rates statistically similar in the four subsets of the data. For persistent species, (Fig. 4.2b) the fraction does not depend on whether the forest is continuous or fragmented – the species move as if it does not matter. For extinction-prone species however, plot isolation significantly reduces plot-to-plot movements by 61%. For these species, isolation has an imprisoning effect. In continuous forest, however, extinction-prone species make more between plot movements than do species that persist in isolated fragments. (Both species type [ $F_{1,22} = 23.2$ ,  $P < .0001$ ] and plot treatment [ $F_{1,22} = 14.8$ ,  $P < .001$ ] are significant effects.)

Figure 4.3 plots the fraction of movements out of a plot divided by the total number of recaptures within the plot, comparing the results with contingency tables. Considering only movements with each study site – because the distances between them are large – 40% of the possible plot-plot movements involve movements from a smaller to a larger plot. It follows that an equal fraction must be from a larger to a smaller plot. Only 20% of the possible plot-to-plot movements are between different plots of approximately equal size. For extinction-prone species (Fig. 4.3a), in continuous forest, the fraction of movements in these three classes is the same as this null model ( $\chi^2 = 0.84$ ,  $P > 0.65$ ). In contrast, extinction-prone birds in isolated fragments preferentially emigrate from smaller to larger plots, by more than a 3:1 ratio ( $\chi^2 = 10.3$ ,  $P < 0.006$ ). One might expect this result simply from sampling

differences or from plot size alone. If this were the case, however, I would expect these patterns in continuous forest as well. I observe no such pattern (Fig. 4.3a). For persistent species, again there are no differences in emigration when comparing to the null model ( $\chi^2 = 0.09$ ,  $P > 0.95$ ). But nor is there a difference in the fragmented landscape: while there is a slight tendency for there to be more movements from smaller to larger fragments, it is not statistically significant ( $\chi^2 = 1.85$ ,  $P > 0.35$ ).

### **Spatial displacement**

We plot the aggregate percentage of area sampled in 100m annuli radiating from each plot's centroid (Fig. 4.4a). Unsurprisingly, further distances are sampled less often than near distances. As described in the methods, I use these data to correct for the incomplete sampling of the landscape. For example, plots cover <10% of the landscape beyond 600m from the point of capture (Fig. 4.4a). Because poor sampling surely inhibits the chance of observing dispersals to distances >600m, it is a critical factor for modeling dispersal.

To determine which model describes dispersal best, we use the AIC comparisons (Table 4.1). In all the cases examined, the heavy-tailed log-sech model has lower Akaike information than for either the Rayleigh or gamma distributions (associated with Gaussian and exponential dispersal kernels respectively). This indicates that it is a better description of the data. This can be seen visually in Fig. 4.4b. Here, we plot the cumulative distribution for the empirical data, and compare it to the maximum

likelihood model for the Rayleigh, gamma, and log-sech models (Fig. 4.4b). By visual inspection alone, the log-sech appears most similar to the empirical data particularly for far distances. In theory, the Rayleigh model expects most observations to fall close to the original capture, but to accommodate the long distance dispersals present in the data, grossly underestimates the number of dispersals over short distances. Crucially, the Rayleigh model observes all individuals too soon. The two-parameter gamma model similarly describes the empirical observations well in the near regime but poorly in the tail. Only the log-sech distribution achieves a close fit to the data both near the origin and at long distances (Fig. 4.4b). It is obvious that the latter model is a better fit for the data both close to the origin and far from the origin.

That the log-sech distribution provides the best fit is especially significant as it holds no matter how I categorize the data: according to age and sex (Table 1), by pre- and post-isolation categories (Table 4.1), or into species (Fig. 4.5). Juvenile birds disperse further than adults, which I expect as a consequence of observing natal dispersal (Table 1). Males and females show no differences, however (Table 4.1). I might expect males to disperse further than females, perhaps seeking new territories (Krebs and Davies 1993), but the majority of the species I survey do not defend individual territories (Cohn-Haft et al. 1997). When all species are lumped, isolation does not appear to affect the dispersal kernels (Table 4.1), though, I might expect gap avoidance when extinction-prone species are considered singly (Fig. 4.2a).

Finally, I further divide the data by species, organize them by the taxonomy of Sibley and Monroe (1990), and distinguish extinction-prone species from those that persist in fragments (Fig. 4.5). In continuous forests, extinction-prone species generally disperse to greater distances than persistent species. After plot isolation, such species – during the time times they persist – tend to move shorter distances. The wing-banded antbird (Myrmornis torquata) is an extreme example of an extinction-prone species; with an extremely heavy tail before isolation ( $\alpha = 256$ ,  $\beta = 1.7$ ), but withdrawing after isolation ( $\alpha = 67$ ,  $\beta = 2.2$ ). I might expect an extreme reaction to landscape fragmentation in M. torquata as this terrestrial antbird may have difficulty traversing large areas without the cover of forest canopy. This species' terrestrial nature does not prevent long distance displacements before isolation, however. Conversely, persistent species tend to move further after isolation than before. The white-flanked antwren (Myrmotherula axillaris) is an example, with a much heavier tail after isolation ( $\alpha = 174$ ,  $\beta = 1.8$ ) than before ( $\alpha = 63$ ,  $\beta = 2.3$ ). This is perhaps expected as M. axillaris frequents primary forests, secondary forests, edges, and gaps (Cohn-Haft et al. 1997); and even bred in small fragments at the BDFFP (Stouffer and Bierregaard 1995).

## DISCUSSION

Isolation limits the propensity for some birds to move between forest fragments, by 61%, for the species that disappear from small fragments within three years after

isolation. That said, 18% of the recaptures of these species in 1 ha fragments are outside those fragments, falling to 5% for 10 ha, and <2% for 100 ha fragments (Fig. 4.2a). In the time these extinction-prone species remain in fragments, they preferentially disperse from smaller to larger plots, likely selecting forest patches with more area. Importantly, the distances moved for all birds are substantial, particularly for extinction-prone species. For most species shown in Fig. 4.5, we estimate that a small fraction disperse beyond 5 km. This statistic is certainly influenced by the few records at large distances, but these data are compelling precisely because those distances are sampled infrequently. If there were more nets spaced >5 km apart, we would likely have detected more movements there. That the heavy-tailed model is the best fit for all the species we examine makes the result a general one, and confirms Grinnell's (1922) idea that long distance movements by birds are not accidental, even for tropical forest birds.

How do we reconcile our results with the existing literature? Stouffer and Bierregaard (1995) argue that forest fragments “are analogous to true islands,” and Develey and Stouffer (2001) claim that “open pastures are nearly absolute barriers to movement” for many of the species we consider. The frequency and distance of movements we observe did surprise our colleagues (P. C. Stouffer, R. O. Bierregaard pers. comm.). That we found such long dispersals in the data from the BDFFP is in large part a testimony to the experiment and its data. It has large numbers of observations, taken over many years, and over a linear distance of 41 km. The BDFFP's unique experimental design made these analyses possible. We also

documented long distance dispersals as we anticipated their possibility. Laurant et al. (2003), in contrast, exclude all movements  $>300$  m from their analyses. Such movements constitute nearly 20% of the movements we document; excluding them misses data of huge significance.

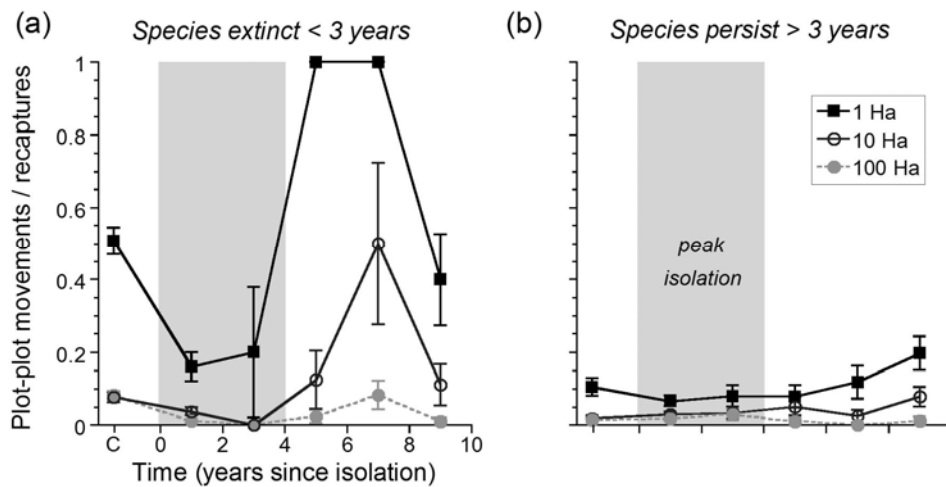
The log-sech AIC value of 106074 was the lowest value of any model and fits the data histogram reasonably well over four orders of magnitude for distance. The choice of the log-sech heavy-tailed model was made for convenience; other heavy-tailed families will not differ significantly in their performance. From our tests, for example, the Lévy-stable series (Nolan 1998) yielded similar AIC values. For one parameter models, the best fitting was the Cauchy model (AIC = 106694). Our choice of the Rayleigh and one-parameter gamma models is based on theoretical model of classical diffusion, where the dispersal kernel tends to have either a two-dimensional Gaussian or exponential form, leading to a density of zero at  $r = 0$ . We can relax these assumptions and use either exponential or Gaussian models directly, the fitting of the model at  $r = 0$  is better but still fits badly in the tail giving values of 107192 and 111864, respectively. A two parameter gamma distribution reduces the AIC value to 106158, but this fits the tail poorly. Thus, the main result of this analysis is the amplitude kernel (distribution of distances between capture and recapture) tends to have an extremely heavy tail, supporting the biological conclusion that while most of any species do not move far, there is always a small number of individuals that move very long distances.

The comparison between extinction-prone and persistent species might also be unexpected. We find that species that range widely are those that disappear from the fragments more rapidly. Generally, the birds that go extinct in fragments are those that forage in groups – following army ant swarms or joining mixed species flocks. Species only facultatively relying on either of these strategies, move to much shorter distances and cross gaps less often, but are more likely to persist within fragments. We documented this general pattern when using social tendencies as a proxy for ranging behavior (Van Houtan et al. 2006). The present movement analyses confirm that social species range more widely than solitary ones, or those that only occasionally forage in groups.

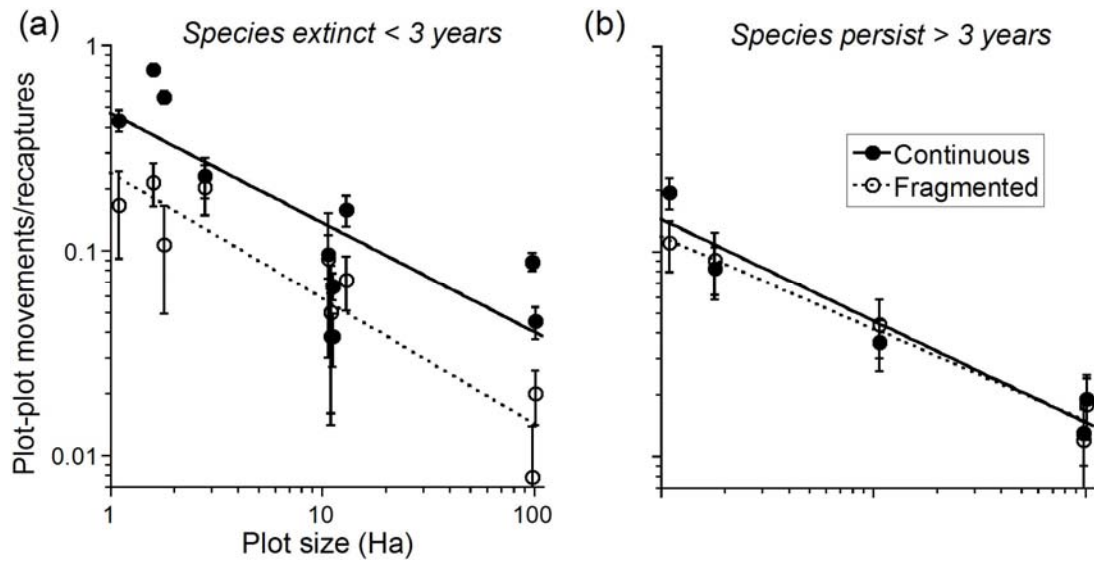
DATA CATEGORY	AIC VALUES			LOG-SECH PARAMETERS	
	Rayleigh	Gamma	Log-Sech	$\alpha$	$\beta$
ALL DATA	135216	117738	<b>106074</b>	315	1.77
DEMOGRAPHY					
Females	27432	22634	<b>19766</b>	174	1.80
Males	36698	31286	<b>28025</b>	186	1.80
Adults	74242	66979	<b>61064</b>	309	1.76
Juveniles	2678	2563	<b>2386</b>	934	1.82
ISOLATION					
Before	46605	41444	<b>37602</b>	310	1.77
After	88450	76284	<b>68476</b>	317	1.77

**Table 4.1:** Comparing Akaike Information Criterion (AIC) for Gaussian, Exponential, and log-sech distributions. The log-sech distribution consistently outperforms the exponentially bounded functions, achieving a good fit both near the origin and at long distances. The log-sech parameters,  $\alpha$  and  $\beta$ , are listed for each subset of the data.

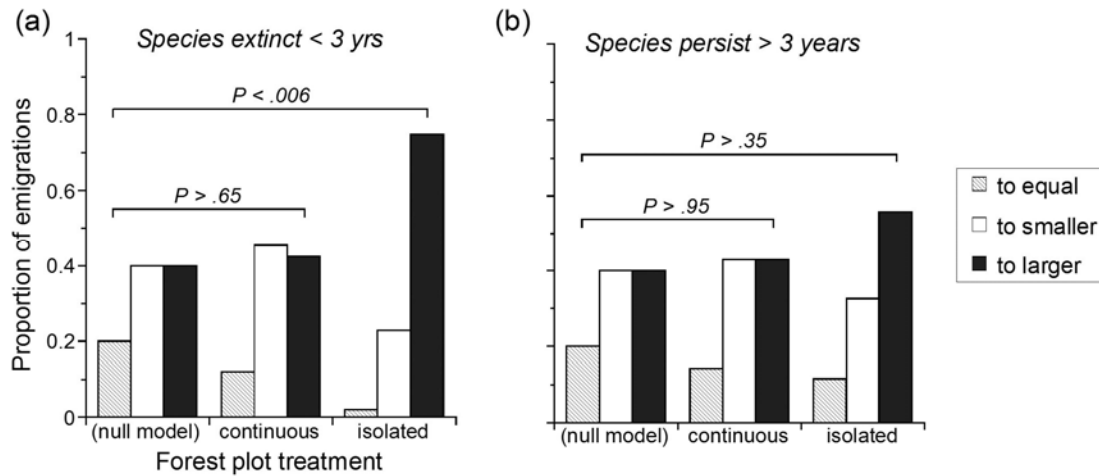




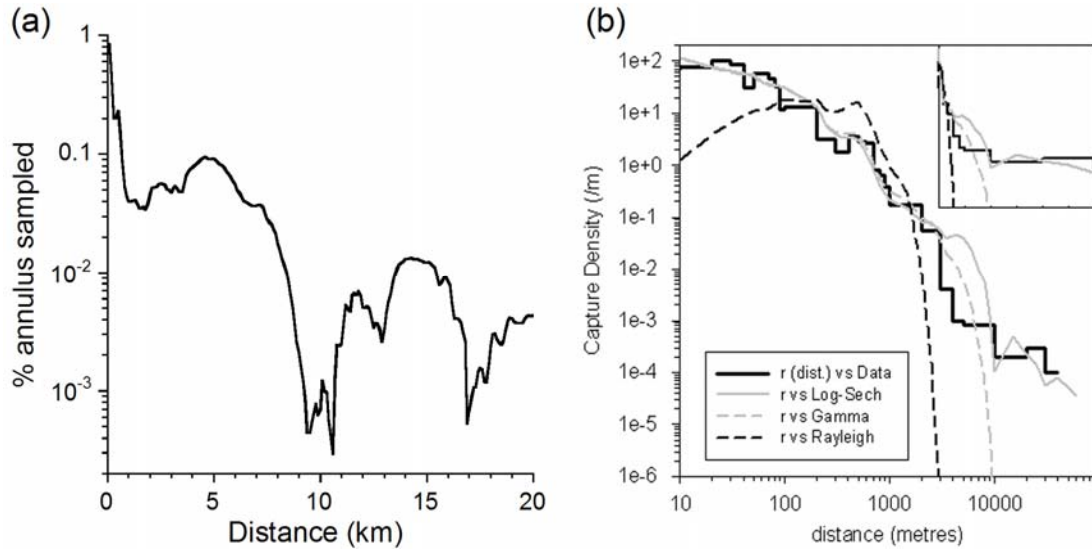
**Figure 4.1:** Extinction-prone species cross deforested gaps between plots more frequently than species that persist in forest fragments, and are adversely affected by plot isolation. (a) In plots of all sizes, extinction-prone species shows decreases in plot-plot movements immediately after a plot's isolation. Movements rebound as margins surrounding plots regenerate forest. (b) Species persisting in forest fragments do not move between plots as frequently as extinction-prone species, and show only minor differences before and after isolation. Paired-year data plotted as median date ("1" represents 1–729 days after isolation). Gray area represents peak isolation before secondary regrowth between fragments. "C" indicates plots in continuous forest.



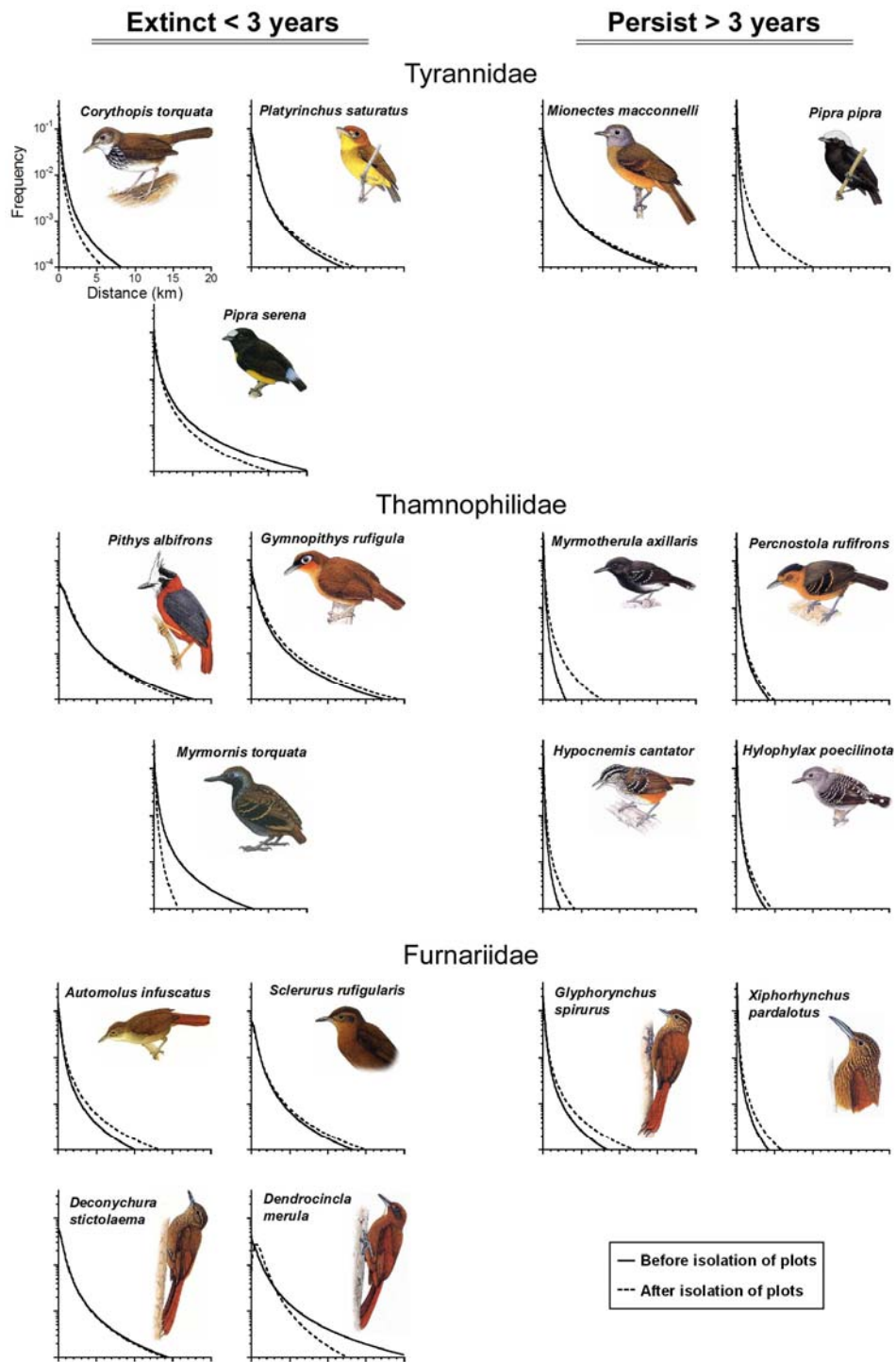
**Figure 4.2:** Movements between plots decrease with increasing plot size, consistent with a power law. (a) For extinction-prone species, movements decrease 61% after isolation. (b) Birds that persist in fragments, however, show no differences before and after isolation of plots. Bars are s. e. for the binomial proportion. For the full covariance model (see text for details),  $R^2 = .85$ ,  $F_{3,22} = 41.5$ ,  $P < .0001$ .



**Figure 4.3:** Extinction-prone birds more often emigrate from smaller to larger fragments, where persistent species show no preferences. (a) Emigrations of extinction-prone birds observed in continuous plots ( $n = 99$ ) conform to null model expectation ( $\chi^2 = 0.84$ ,  $P > 0.65$ ), those observed after isolation ( $n = 48$ ) differ ( $\chi^2 = 10.3$ ,  $P < 0.006$ ). (b) Persistent species show no preferences, either before or after isolation (see text). Null model proportions are the tally of all possible plot-plot movement permutations within the same site.



**Figure 4.4:** (a) Percentage of landscape sampled with mist nets decreases with increasing distance from original capture. We calculate 100 m annuli from the plot centroid, determining the area sampled and total area in each annulus. Data from all 11 isolated plots were added to achieve a single corrective value,  $\Pr(w_i)$ , for fitting distance kernels. (b) Histogram of recapture distances. The  $x$ -axis is the distance of the recapture from the previous capture. The bars represent the empirical data with the area of each bar equal to the number of recaptures for each distance interval. (Thus the height of each bar is the number caught in that interval divided by the interval size width of bar). The total area is therefore 8799, the total number of recaptures. The axes of the histogram are logarithmic for visual clarity. The expected histograms for the three models are shown for comparison: the gamma distribution, the Rayleigh distribution and the log-sech distribution (fitted by MLE). The intervals for the empirical histogram are 10m wide up to 100, then 100m wide up to 1000, then 1km wide up to 5km, and 5–10km. The last three bins are 10km wide. Although this choice is arbitrary, it does not fundamentally alter the shape of the histogram (note also that the fitting procedure does not depend on the choice of intervals). Inset shows the same histogram with only the vertical axis logarithmic.



**Figure 4.5.**

**Figure 4.5:** Forest fragmentation reshapes the dispersal kernels for most species. Extinction-prone birds move further than persistent birds in continuous forest, and show depression in long distance movement after forest fragmentation. Persistent species, conversely, displace further after fragmentation. Displacement kernels are compared between closely related species, based on the taxonomy of Sibley and Monroe (1990). Bird illustrations by Guy Tudor (Ridgely and Tudor 1994).



## Appendix

The following lists the sources from which I have drawn information in order to classify the worldviews of denominations, organizations, and individuals in the table above. The references are self-authored and published unless otherwise noted. All URLs current as of September 2005.

### Denominations

African Methodist Episcopal Church ([www.amecnet.org/](http://www.amecnet.org/), Lincoln and Mamiya 1990)

African Methodist Episcopal Zion Church ([www.theamezionchurch.org/](http://www.theamezionchurch.org/), Lincoln and Mamiya.1990)

American Baptist Churches U.S.A. (ABC USA 1989, [www.abc-usa.org/resources/resol/ecology.htm](http://www.abc-usa.org/resources/resol/ecology.htm))

Assemblies of God  
([ag.org/top/beliefs/contemporary\\_issues/issues\\_02\\_environment.cfm](http://ag.org/top/beliefs/contemporary_issues/issues_02_environment.cfm))

Christian Church, Disciples of Christ (Christian Church 1991, [www.webofcreation.org/education/policystatements/disciples.htm](http://www.webofcreation.org/education/policystatements/disciples.htm))

Episcopal Church ([www.eenonline.org/](http://www.eenonline.org/), Anglican Communion 1999, Golliher 1999, Global Anglican Congress 2002)

Evangelical Lutheran Church in America (ELC 2000)



Greek Orthodox Archdiocese of America (Belopopsky and Oikonomou 1996)

Lutheran Church, The Missouri Synod (LCMS 2000)

National Baptist Convention of America, Inc. ([www.nbcamerica.net/](http://www.nbcamerica.net/), Washington 1986, Lincoln and Mamiya 1990)

National Baptist Convention, USA ([www.nationalbaptist.com/](http://www.nationalbaptist.com/), Washington 1986, Lincoln and Mamiya 1990)

Presbyterian Church, U.S.A. ([pcusa.org/environment](http://pcusa.org/environment), PCUSA 2001)

Roman Catholic Church (Cabibbo and Arber 2001, Pontifical Academy of Sciences 2001)

Russian Orthodox Church (Moscow Patriarch 2004)

Southern Baptist Convention (SBC 1970, SBC 1974, SBC 1990, Ethics and Religious Liberty Commission 2004a, Ethics and Religious Liberty Commission 2004b)

United Methodist Church (UMC 2000, UMC 1992)

United Church of Christ ([www.ucc.org/justice/environment.htm](http://www.ucc.org/justice/environment.htm))

## **Organizations**

Acton Institute for Study of Religion and Liberty

([www.acton.org/ppolicy/environment/](http://www.acton.org/ppolicy/environment/), Beers et al. 2000, Beisner et al. 2000)

Au Sable Institute ([ausable.org/au.ourmission.cfm](http://ausable.org/au.ourmission.cfm))

Christian Coalition of America ([www.cc.org/issues.cfm](http://www.cc.org/issues.cfm))

Christianity Today International (Snyder 2001, Livingstone et al. 2001, Sider 1993, CTI 2004)

Ethics and Public Policy Center (Cromartie 1995, Weigel 2002)

Family Research Council ([www.frc.org](http://www.frc.org))

Focus on the Family (Hartwig 2000, Howden 2001, Melville 2001, Shepard 2004)

Interfaith Coalition for Environmental Stewardship (ICES 1999)

Institute on Religion and Democracy (Tooley 1999, Nelson 2002, Tooley 2002)

Institute on Religion and Public Life

National Council of Churches ([www.ncccojustice.org](http://www.ncccojustice.org), White 2003)

National Religious Partnership for the Environment ([www.nrpe.org/](http://www.nrpe.org/))

Sojourners ([www.sojo.net](http://www.sojo.net), Barnett 2004)

Target Earth International ([www.targetearth.org](http://www.targetearth.org))

Toward Tradition ([www.towardtradition.org](http://www.towardtradition.org), Klinghoffer 2001)

## **Individuals**

Richard Baer, Jr. (Baer Jr. 1998)

Patriarch Bartholomew I (Bartholomew 1997)

Gary Bauer (Bauer 1996)

Tony Campolo (Campolo 1992)

Charles Colson (ICES 1999, ICES 2003)

Thomas Sieger Derr (Derr 1998, ICES 1999)

Calvin DeWitt (DeWitt 1998, Livingstone et al. 2001)

James Dobson ([www.family.org/fmedia/broadcast](http://www.family.org/fmedia/broadcast))

Jerry Falwell (Tooley 1999, Kupelian 2001)

Billy Graham (Greer 1996)

Ted Haggard ([www.nae.net](http://www.nae.net), Sandy Cove 2004, Goodstein 2004)

Pope John Paul II (John Paul II 1998, The Vatican 1991)

Fr. Richard John Neuhaus (Neuhaus 1971, Neuhaus 1997)

Pat Robertson (Robertson 2002)

Francis Schaeffer (Schaeffer 1970)

Ron Sider (Sider 1993)

Fr. Robert Sirico (ICES 1999, Strode 2000)

Archbishop Rowan Williams (Williams 2004)

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### **Education**

Ph.D., Ecology, Duke University, 2002–2006 (S. L. Pimm, advisor)

Ph.D. program, Ecology, Columbia University, 2001–2002 (S. L. Pimm, advisor)

M.S., Biological Sciences, Stanford University, 1998–2000 (P. Ehrlich, advisor)

B.A., Environmental Science, University of Virginia, 1992–1996 (J. Galloway, advisor)

### **Publications**

Van Houtan, K. S., Pimm, S. L., and Colchero, F. (in preparation) Sea turtle recovery plan for the Dry Tortugas and Everglades National Park, 1995-2006. United States Fish and Wildlife Service Report.

Van Houtan, K. S., Pimm, S. L., and van Aarde, R.J. (in preparation) Management lessons from ungulate translocations in South African game reserves, 1930–2000.

Van Houtan, K. S., and Northcott, M. (under contract) The ethics of extinction. Veritas Books, Downers Grove, IL.

Van Houtan, K. S., and Northcott, M., Editors. (in review) God, Darwin, and the destruction of nature: five ethical interventions. Duke University Press, Durham, North Carolina.

Northcott, M., and Van Houtan, K. S. (in review) Saving nature from the nation-state. in Van Houtan, K. S., and Northcott, M., Editors. God, Darwin, and the destruction of nature: five ethical interventions. Duke University Press, Durham, North Carolina.

Van Houtan, K. S., Pimm, S. L., Halley, J., and Lovejoy, T. E. (in review) Dispersal of Amazonian birds in continuous and fragmented forest.

Van Houtan, K. S. (2006) Conservation as virtue: a scientific and social process for ethics. *Conservation Biology*. 20 (5): 1367–1372.

Van Houtan, K. S. and Alvarez–Loayza, P. (2006) Diet of nestling Green–and–gold Tanagers, with a note on breeding behavior. *Ornitologia Neotropical*. 17 (2): 307–312.

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### **Selected Awards, Grants, and Fellowships**

- 2005 Harvey Fellowship (\$45000, Mustard Seed Foundation)
- 2006, 2005 Kenan Colloquium Fellowship in Ethics (\$2000, Kenan Institute for Ethics)
- 2005 Melon Fellowship (\$500, Center for Latin American Studies, Duke University)
- 2004 Preparing Future Faculty Fellow (national initiative, facilitated at Duke University)
- 2003 Foreign Language Area Study scholarship (\$25000, U.S. Dept. Education)
- 2000 Ronald Wessels Award for Teaching Excellence (\$300, Stanford University)
- 2000, 1999 Excellence in Undergraduate Teaching Award (Stanford University)
- 1999 Wohlford Fellowship (\$3000, Morrison Institute for Population Studies)
- 1999 Tambopata Fellowship (\$2000, Latin American Studies, Stanford University)
- 1997 Environmental Research Grant (\$400, The North Face Corporation)

### **Society Memberships**

- American Association for the Advancement of Science, Neotropical Ornithological Society, Sigma Xi, and Society for Conservation Biology.