

**A Consumer-Resource Framework for Evaluating Anthropogenic Effects on
Wildlife and Habitat**

BY

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THESIS

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This thesis is dedicated to my daughter Irene and husband Kevin.

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VMH

CONTRIBUTION OF AUTHORS

Chapter I, my introduction, explains how my dissertation uses a consumer-resource framework to address ecological questions. Chapter II shows a consumer-resource model I developed. Chapter III is published (Hunt, V. M., Magle, S. B., Vargas, C., Brown, A. W., Lonsdorf, E. V., Sacerdote, A. B., Sorley, E. J., Santymire, R. M.: Survival, abundance, and capture rate of eastern cottontail rabbits in an urban park. *Urban Ecosyst.* 17; 546-560: 2013); I designed and performed the experiment and wrote the manuscript. E. Sorley and R. Santymire assisted with lab work. E. Sorley, A. Sacerdote, C. Vargas, S. Magle and A. Brown assisted with fieldwork. E. Lonsdorf supervised. Chapter IV is in press and I am sole contributor (Hunt, V. M.: Reproductive Success and Habitat Selection in Black-crowned Night-Herons (*Nycticorax nycticorax*) in a City Park. *Am. Midl. Nat.*; in press). Chapter V is published (Hunt, V. M., Jacobi, S. K., Knutson, M.G., Lonsdorf, E. V., Papon, S., Zorn, J.: A Data Management System for Long-term Natural Resource Monitoring and Management Projects with Multiple Cooperators. *Wildl. Soc. Bull.* 39; 464-471: 2015.) S. Jacobi and E. Lonsdorf contributed to tool development. M. Knutson conceived the manuscript and provided writing guidance. J. Zorn and S. Papon vetted details. Chapter VI is published (Hunt, V. M., Jacobi, S. K., Gannon, J. J., Zorn, J.E., Moore, C. T., Lonsdorf, E. V.: A Decision Support Tool for Adaptive Management of Native Prairie Ecosystems. *Interfaces Articles in Advance*; 1-11: 2016). S. Jacobi, J. Gannon, J. Zorn, C. Moore and E. Lonsdorf contributed to tool development and provided guidance writing the manuscript. Chapter VII represents unpublished research on an invasive wetland plant species.

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LIST OF ABBREVIATIONS

BCNH	Black-Crowned Night-Heron
DST	Decision Support Tool
EC	Electrical Conductivity
HIREC	Human Induced Rapid Environmental Change
IT	Information Technology
JHE	Joint Hypergeometric Estimator
NPAM	Native Prairie Adaptive Management
RFLP	Restriction Fragment Length Polymorphism
SQL	Structured Query Language
USFWS	United States Fish and Wildlife Service
USGS	United States Geological Survey
VBA	Visual Basic for Applications
XML	Extensible Markup Language
ZNGI	Zero Net Growth Isocline

SUMMARY

I use a consumer-resource framework to narrow the gap between data and theory in the study of competitive coexistence. First, I develop a generalizable consumer-resource model with implications for wildlife populations that are subsidized by humans. The model suggests that improving local conditions of consumers in one habitat may displace consumers from a spatially separate habitat if the consumers require a shared resource. I describe how outcomes from the model could be evaluated empirically. I then present two studies in which I use classical field ecology to investigate population dynamics in urban wildlife consumer species. Eastern cottontail rabbits (*Sylvilagus floridanus*) in an urban park occurred in higher population densities than populations in natural habitats, a potential consequence of subsidization via landscaping. In a study of Black-Crowned Night-Herons (BCNH; *Nycticorax nycticorax*) in Chicago, BCNH showed behavioral flexibility in habitat selection. This flexibility may be facilitated by an overabundance of a resource shared amongst multiple colonies over an expansive area: Lake Michigan's foodshed. In the last three chapters, I describe management efforts to control invasive species, and environmental conditions that may affect success of such efforts to intentionally reassign resources (e.g., physical space and soil nutrients) from invasive consumers to diverse assemblages of native consumers. This work demonstrates the utility of applying a consumer-resource framework in a range of ecological scenarios to achieve conservation objectives. I propose expanding this approach to address the core challenge put forward by reconciliation ecology; increasing biodiversity in habitats that meet both human land-use needs and the needs of non-human species.

I. INTRODUCTION

A. Background

I am a mathematical ecologist interested in explanatory models and simulations that deepen our understanding of the consequences of human activity on other species, and predictive models to inform natural resource management. This work builds on a large body of theory aimed at understanding consumer-resource dynamics in ecological systems, and uses a consumer-resource framework to evaluate outcomes from several empirical studies, bridging the gap between empirical work and theory in the study of competitive coexistence. One way this consumer-resource framework could be applied to increase biodiversity in human-modified landscapes is via reconciliation ecology. To realize the vision proposed by reconciliation ecology, we must understand how anthropogenic manipulation of resources affects non-human species, and use this information to guide management efforts that aim to increase biodiversity and promote the success of diverse assemblages of native species in human-modified landscapes. This thesis takes steps towards addressing these needs for reconciliation ecology.

Herein, I contribute to competition theory by developing a consumer-resource model based on Vincent et al. (1996) in which I simulate dynamics of systems with both spatially mixed and spatially separate resources. I describe how the outcomes from the model could be evaluated empirically in natural systems. On the empirical front, I use classical field ecology to investigate the community context, population dynamics, and abundances of consumer species. I focus on human-modified systems for which reconciliation ecology would be applicable.

The study of competitive coexistence, and the biodiversity that this phenomenon promotes or inhibits, is fundamental in ecology (Tilman, 1980). Competition theory describes mechanisms via which the interactions between consumers and resources, e.g., predators and prey in food webs, influence community structure in heterogeneous ecological systems (Amarasekare, 2003). Empirical investigation of consumer-resource interaction lags behind theory; there is a current need for work that reconciles empirical and theoretical efforts (Amarasekare, 2003).

The research presented in this thesis takes inspiration from and builds on a large body of literature and mathematical models developed around consumer-resource interactions. In systems in which multiple consumer species compete for a single resource, community structure is governed by the principle of competitive exclusion (Gause, 1932; Grinnell, 1904). In such a system, if one consumer species has an advantage over another, no matter how slight the advantage, it will displace its competitors. Therefore, coexistence requires tradeoffs and completely overlapping competitors cannot coexist (Gause, 1932). In 1968, Hardin considered the implications of tradeoffs in a consumer-resource system characterized by anthropogenic depletion of resources. In the scenario Hardin described, humans consume finite resources provided by the planet Earth, including its food, space, air, etc. (Hardin, 1968). Hardin (1968) predicted that unregulated anthropogenic exploitation of Earth's resources, motivated by the shortsighted goal of maximizing individual gain, would ultimately result in universal suffering; "Freedom in a commons brings ruin to all."

In the 1980s, Tilman developed a graphical-mechanistic approach to address theoretical problems posed by exploitative competition in consumer-resource systems. Tilman used zero net growth isoclines (ZNGIs) in the resource state space to represent

all possible combinations of two resource levels at which a consumer species would neither decline nor increase (Tilman, 1982). Tilman's R^* law predicts that in an exploitative system, the consumer species which requires the least amount of a limiting resource to subsist at equilibrium will displace its competitors (Tilman, 1982). When consumer species compete for multiple resources, the resulting community composition is predicted by Tilman's graphical theory (Tilman, 1980, 1982; see also Abrams, 1988). Coinciding with Tilman, Oksanen et al. (1981) developed theories on community structure in exploitative systems with multiple trophic levels, and on the role of primary production.

In a system of two consumer species and one resource, equilibrium resource levels that support both consumers are determined by the intersection of the two ZNGIs pertaining to each of the consumer species. The outcome of competition depends on the orientation and shape of the ZNGIs, which are, in turn, influenced by attributes of consumers and resources. A non-exhaustive list of factors that influence the shape and orientation of ZNGIs includes dietary shifts in the consumer's life cycle (Schellekens et al., 2010), the functional response of consumers to resources (Vincent et al., 1996), consumer dispersal (Haegeman and Loreau, 2015), consumer foraging traits (Holling, 1959; Vincent et al., 1996; Wilson and Richards, 2000), and nutritional qualities of resources (Tilman 1980). Figure 1 illustrates general shapes of ZNGIs for three nutritional types of resources: substitutable, essential, and complementary.

Substitutable^a



Essential^b



Complementary^c



Consumers

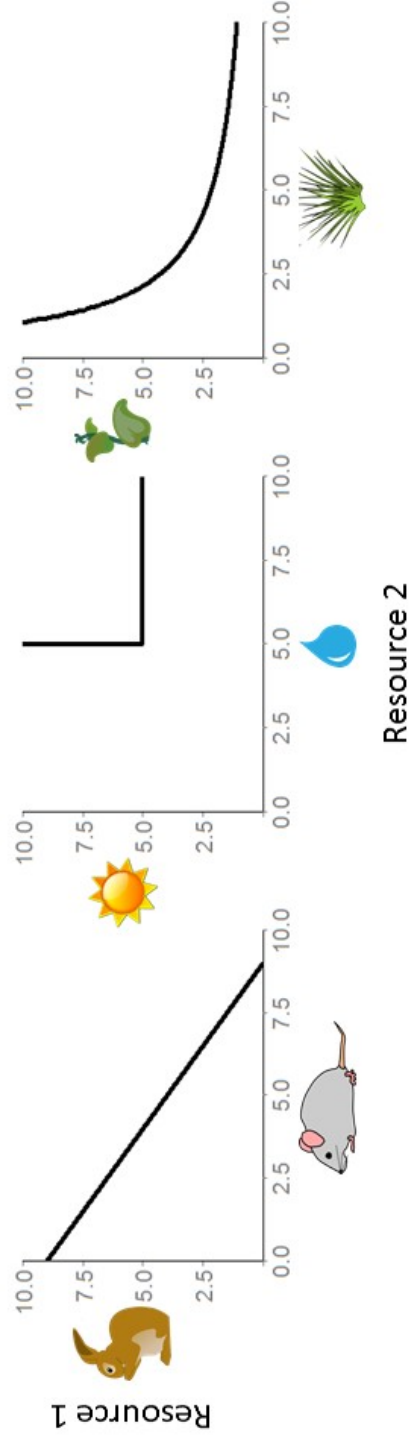


Figure 1. General shapes of zero net growth isoclines (ZNGIs) for different nutritional types of resources.

^a Small mammal prey species are substitutable for a carnivore.

^b Light and water are essential for a plant.

^c Two species of plants are complementary for migratory birds.

In this dissertation, I evaluate anthropogenic effects on ecological communities from the perspective of consumer-resource theory. Anthropogenic effects can be 1) byproducts of ongoing anthropogenic processes such as urbanization or 2) outcomes of intentional management actions. For an example of the former type of anthropogenic effect, urbanization may unintentionally displace bird populations (consumers) when nest trees (resources) are removed. For an example of the latter type of anthropogenic effect, application of herbicides, such as glyphosate, targets invasive plant species (consumers), rendering physical space and soil nutrients (resources) previously monopolized by invasive species available to native consumer species.

Reconciliation ecology provides opportunity for the practical application of consumer-resource and competition theory (Rosenzweig, 2003). Michael Rosenzweig, my "academic grandfather" (advisor of my advisor, Joel Brown), introduced reconciliation ecology in the book Win-Win Ecology in 2003. Reconciliation ecology invites us to consider the opportunities that human-modified landscapes provide for biodiversity, and calls for promotion of biodiversity in human-modified environments by intentionally forging novel ecological niches (Rosenzweig, 2003). Creation of niches entails modification of consumer-resource interactions to promote coexistence of additional consumer species. Rosenzweig (2003) refers to species that opt to live in human-modified landscapes as *kulturfolger*, after the German word meaning culture-follower. *Kulturfolger* species include house sparrows (*Passer domesticus*) and rock doves (*Columba livia*). In contrast, most species are *kulturmeider* (culture-avoiders) to varying degrees. The goal of reconciliation ecology is to transform some *kulturmeider* species to *kulturfolger* species by creating niches for them in human modified

landscapes. For example, nest cavities are a limiting resource for eastern bluebirds (*Sialia sialis*). Suitable cavities are scarce due to the routine removal of snags in human-modified landscapes, and due to competitive invasive cavity-nesters including European starlings (*Sturnus vulgaris*), a definite *kulturfolger*. Reconciliation ecology calls for constructing nest boxes to serve as artificial nest cavities, thereby increasing resource availability and subsequently boosting eastern bluebird populations (Rosenzweig, 2003).

In the research presented here, I use a consumer-resource perspective to address two main needs for reconciliation ecology. The first need is for methods to evaluate how anthropomorphic changes to resource availability in human-modified landscapes affect non-human species. The second need is for tools to improve the success of management efforts which reassign resources from monocultures of invasive consumer species to diverse assemblages of native species.

B. **Chapters**

To bridge the divide between the theory and empirical study of consumer-resource interactions, my dissertation includes chapters that develop theory and chapters describing empirical studies. I discuss how the theory could be tested empirically and how the empirical studies align with theory.

Following my introduction in Chapter I, in Chapter II I develop a consumer-resource model with implications for subsidized wildlife populations such as feral cat colonies. In Chapters III and IV, I use classical field ecology to investigate anthropogenic effects on systems with one consumer and one resource, and compare predictions from spatial competition theory to observed outcomes. In Chapter III, eastern cottontail rabbits (*Sylvilagus floridanus*) are consumers and garden plants provide resources. In Chapter IV, black-crowned night herons (BCNH; *Nycticorax*

nycticorax) are consumers and nest sites are resources. In the final three chapters, I consider multiple consumer-resource interactions and the effects of intentional anthropogenic manipulation of resources in actively managed systems. Chapter V and VI are companion chapters. In Chapter V, I present a generalizable decision support tool (DST) aimed at increasing the diversity of native species in large-scale habitat management efforts conducted by the U.S. Fish and Wildlife Service (USFWS). Chapter VI documents application of the DST in the case of adaptive management of invasive species in native prairie ecosystems. Chapter VII presents novel research on management and implications of resource availability on invasive common reed (*Phragmites australis*).

Chapter II presents a relatively simple consumer-resource model that depicts how changing conditions in one habitat may affect consumers in a spatially separate habitat via indirect effects mediated through a shared resource that crosses both habitats. The model, an expansion of the work of Vincent et al. (1996), suggests that increasing the carrying capacity of a local resource in one habitat may displace consumers from a spatially separate habitat. This outcome has potential implications for animal populations that are subsidized by humans. For example, feeding feral domestic cat (*Felis catus*) colonies, which increases their local resource availability, may displace spatially separate wildlife consumer species that compete for shared small mammal or reptilian prey. These results underscore the importance of appropriate spatial scale of study, and of accounting for all interacting consumers and resources when studying consumer-resource systems.

Chapter III focuses on a ubiquitous mammalian herbivore in urban areas, the eastern cottontail rabbit (hereafter, rabbit). In urban settings, rabbits may be considered

pests because this *kulturfolger* is so successful that they cause extensive vegetative damage by foraging in gardens. In Lincoln Park, Chicago, Illinois, where my study occurred, damaged plants were swiftly replaced. From a consumer-resource standpoint, wherein rabbits are consumers and garden plants provide resources, the rabbits experienced markedly elevated resource availability. In the simplified system, in which I consider only one resource and one consumer, theory predicts that increasing resource carrying capacity or resource renewal rate will increase the population size of consumers at equilibrium. I determined that rabbits occurred in high densities in Lincoln Park compared to rabbits in natural environments (Hunt et al., 2013). Therefore, experimental observations aligned with predictions from consumer-resource theory. However, because predicted outcomes of increasing resource carrying capacity vs. increasing resource renewal rate are similar, as illustrated by Figure 2, further experimentation (e.g., detailed plant surveys in managed vs. unmanaged gardens) would be required to differentiate between these two potential mechanisms. In Figure 2, depletion trajectories represent the outcomes of simulations of consumer-resource dynamics. The depletion trajectories show how resources are depleted by consumers over time, beginning at the resource supply point (at the beginning of the simulation) and ending at the ZNGI if the system reaches equilibrium, or beneath the ZNGI if consumers are displaced.

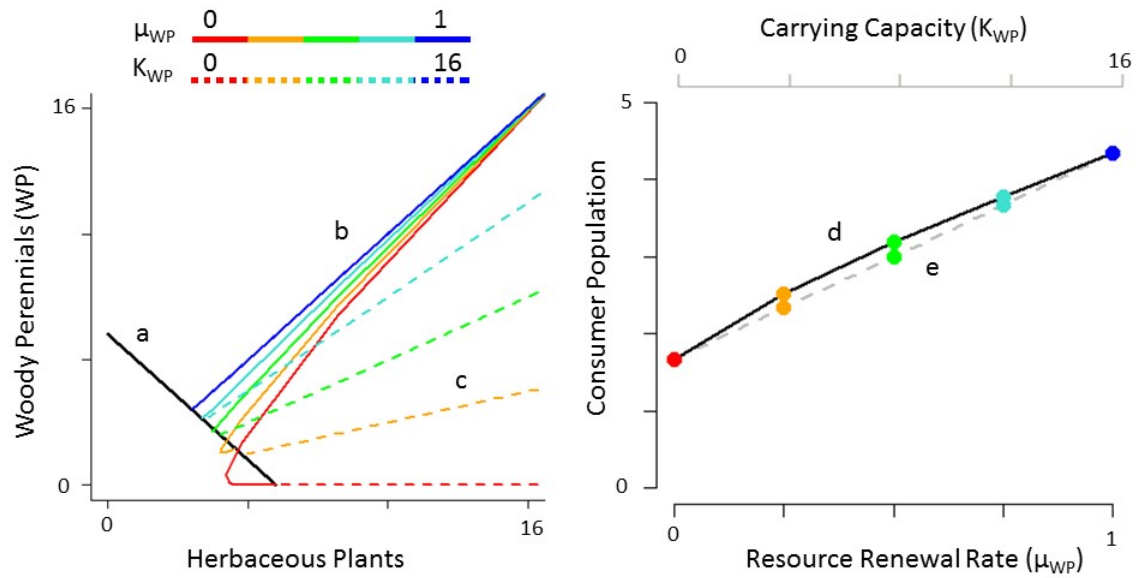


Figure 2. Theoretical effects of increasing carrying capacity or resource renewal rate of woody perennial plants in Lincoln Park on the rabbit population.

- ^a Zero net growth isocline (ZNGI).
- ^b Depletion trajectories varying carrying capacity (K) of woody perennial plants.
- ^c Depletion trajectories varying resource renewal rate (μ) of woody perennial plants.
- ^d Rabbit population sizes varying K .
- ^e Rabbit population sizes varying μ .

In the consumer-resource system in Chapter IV, BCNH are consumers and nest sites are the resources of interest. The BCNH population I studied chose an urban area in Lincoln Park for breeding. I conducted daily BCNH censuses at two discrete habitat patches in the park and used logistic regression to model habitat selection as a function of year and colony size. The logistic regression model supported the idea that BCNH exhibited behavioral flexibility in habitat selection in response to year and colony size. Behavioral flexibility may have facilitated the BCNH colony's success in a human-modified landscape under conditions of human induced rapid environmental change (HIREC; Sih et al., 2012).

One possible explanation for observed behavioral flexibility is that my study design omitted an important resource: food. BCNH can forage over an expansive area encompassing many potential habitat patches suitable for breeding. BNCH in Lake Calumet make daily foraging trips to the Chicago lakefront, an approximately 60 km round-trip (Levengood and Schaeffer, 2010). I record a large influx of BCNH in 2011, coinciding with a colony collapse in Lake Calumet. The Lincoln Park BCNH colony is a newly established population, and as such may not have attained equilibrium population size. I suspect that BCNH in Lincoln Park could select habitat patches as a function of colony size and year because they had not yet depleted resources (food or nest sites) to a limiting level (the ZNGI). Therefore, the BNCH were not yet resource-limited in Lincoln Park (Figure 3). Because food and safety are generally complementary (Brown, 2000), I depict food and nest sites as complementary resources in Figure 3. This study reinforces the importance of including all interacting consumers and resources in a system into one's study design, as concluded from the consumer-resource model in Chapter II.

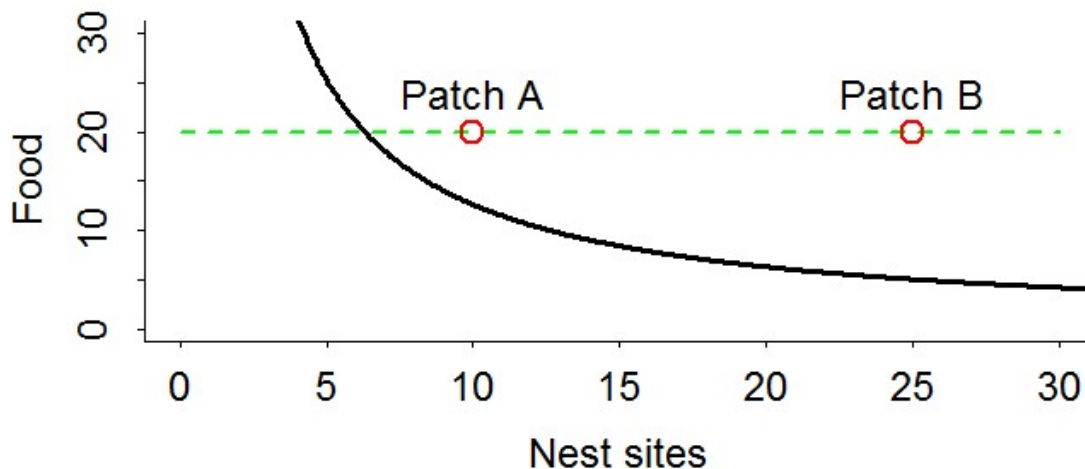


Figure 3. Conceptual graphic of consumer-resource interactions in a colony of Black-Crowned Night-Herons with two habitat patches in one foodshed, where neither resource is at a limiting level. The solid black line represents the zero net growth isocline (ZNGI). The dotted green line represents the system's food supply at the time of colonization. Red circles indicate resource levels at two habitat patches in the same foodshed.

For reconciliation ecology to be a success, we need ways to evaluate how changes to resources in human-modified landscapes affect non-human species (Chapters III and IV). We also need tools to improve the success of management efforts to increase biodiversity in human-modified landscapes. In Chapters V, VI and VII, I investigate intentional management efforts to increase biodiversity by reassigning resources from monocultures of invasive consumer species to diverse assemblages of native species.

Chapter V documents a generalizable DST actively used in six collaborative, large-scale land management efforts conducted by the USFWS. The chapter focuses on the attributes of data management required for successful habitat management. In large-scale efforts, data from many cooperators, often spanning vast spatial areas and multiple administrative regions or organizations, must be efficiently centralized and processed. Data must be consistent in content and quality over the project's lifespan, which may last many years to account for the slow nature of some ecological processes. To overcome these data management challenges, I develop a comparatively inexpensive system that combines the centralization capability of a web-based database with the analytical capacity of a locally housed relational database.

Chapter VI describes a specific implementation of the DST that is broadly outlined in Chapter V. The USFWS uses the DST to reintroduce defoliation techniques into their standard management practices on native prairie lands. In prairies managed by the USFWS, historic exclusion of burning and grazing likely facilitated invasion of introduced species including two aggressive non-native grasses: smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*) (Grant et al., 2009, Gannon et al., 2013). The DST facilitates implementation of an adaptive management approach developed by a joint USFWS-US Geological Survey development team to assess relative efficacies of management techniques in terms of reassigning habitat resources from invasive species to a more diverse assemblage of desirable native species (Gannon et al., 2013).

In Chapter VII, I study non-native common reed, an emerging cryptic invader in wetland habitats in North America (Saltonstall, 2002). An invasive strain of common reed chokes out native plants and create dense stands that reduce bird diversity (Benoit

and Askins, 1999). The ultimate *kulturfolger*, invasive common reed thrives on anthropogenic disturbance (Brisson et al., 2010; Eallonardo and Leopold, 2014; Jodoin et al., 2007). In my study, a network of land managers located across North America collected soil samples from wetlands invaded by common reed, and from approximately 15 m outside of invaded areas. Based on soil nutrient analyses, I provide insights into resource availability in non-native vs. native common reed stands, and into consumer-resource dynamics that may contribute to delimitation of common reed-invaded wetlands.

From a consumer-resource perspective, invasive common reed monopolizes resources and displaces competitors, including many native consumer species, in invaded wetlands. Because common reed outcompetes native species via multiple mechanisms and over large areas, its removal may allow native species to fill several ecological niches (Figure 4). Substituting a different invasive species and terrain type, Figure 4 could also apply to the DST used for native prairie management in Chapter VI; in both instances, the goal of invasive species management from a consumer-resource perspective is identical.

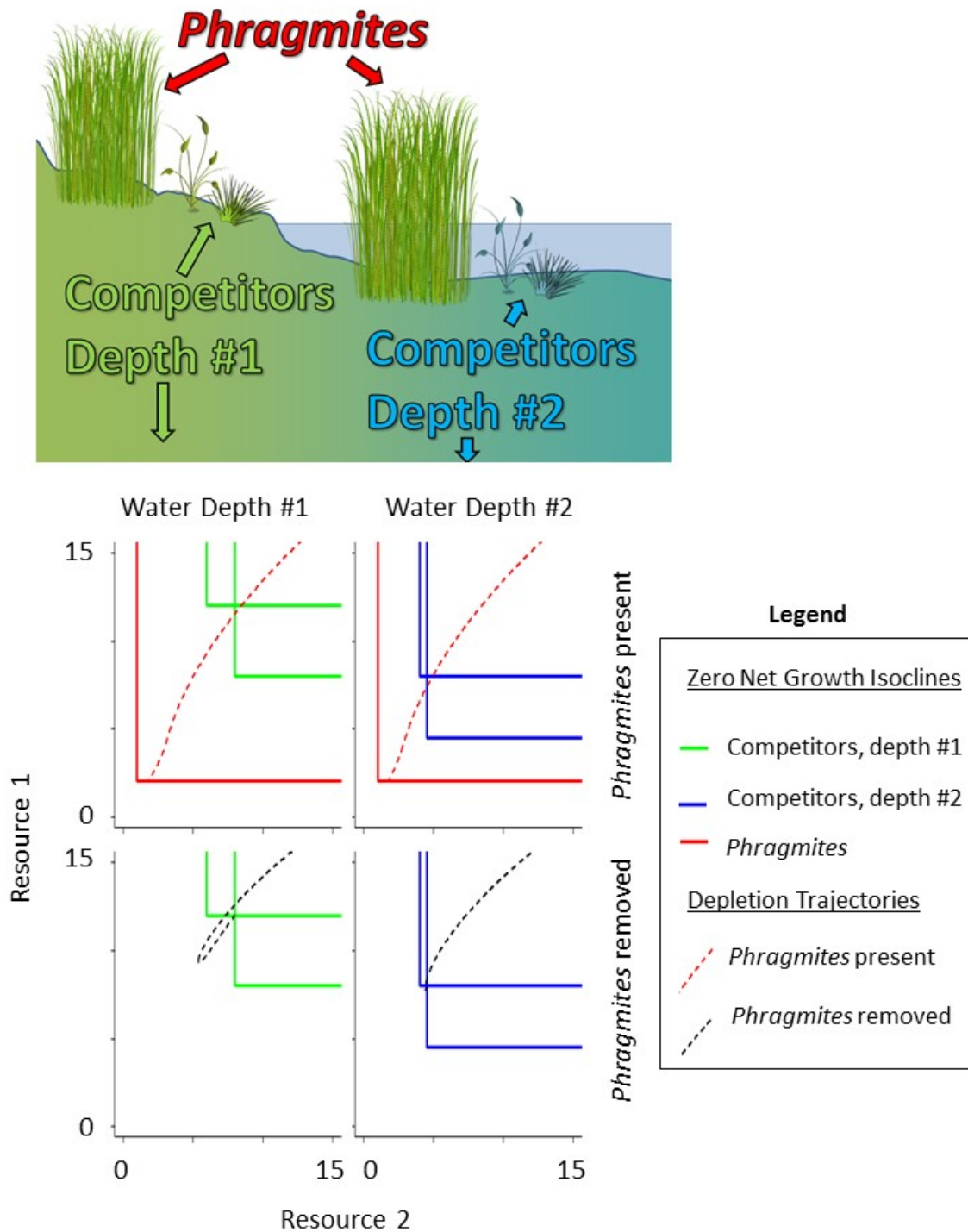


Figure 4. Conceptual illustration of how removal of non-native common reed (*Phragmites australis*) could facilitate coexistence of native competitors.

C. **Prospectus**

Reconciliation ecology appeals to me because of its hopeful message: in many cases, we could modify our habitats in a way that better promotes coexistence with non-human species. Fulfilling the potential of reconciliation ecology requires understanding the complicated consequences of our actions, and rethinking the ways in which we alter the environment. I aspire to contribute to this effort.

The theory of reconciliation ecology focuses on maintaining or increasing biodiversity in general, but specific examples provided in Win-Win Ecology focus on the single species or phylogenetic groups (Rosenzweig, 2003). A very specific metric determines "success," seemingly mismatched with an immensely broad fundamental objective: increasing biodiversity. The small scale of examples provided by Rosenzweig is a core criticism of reconciliation ecology (criticisms are reviewed by Geisler, 2010). This sparked my interest in alternative ways to frame the problem posed by reconciliation ecology – how do our actions affect wildlife and wildlife habitat, and how could we change our actions to better achieve conservation goals? Lundholm and Richardson (2010) propose an approach to reconciliation ecology focusing on habitat analogues. Herein, I propose an approach to reconciliation ecology focusing on consumer-resource interactions. By developing expertise in this area, I will be equipped to seek solutions to complex environmental issues such as mediating effects of climate change and managing invasive species. I hope that others will use this consumer-resource focused approach to reconciliation ecology to inform conservation efforts and ultimately to increase biodiversity in human-modified landscapes.

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II. DISPLACEMENT VS. COEXISTENCE IN CONSUMER-RESOURCE SYSTEMS WITH SHARED AND SEPARATE RESOURCES

A. Abstract

Competition for local and shared resources is widespread, e.g., birds in a colony compete locally for nest sites, and against neighboring colonies for prey. However, there is little understanding of conditions facilitating coexistence vs. displacement in such systems. Extending traditional models based on Type I and Type II functional responses, we simulate consumer-resource systems in which resources are substitutable, essential or complementary. With complementary, and even more so with essential resources, a small increase in carrying capacity or decrease in handling time of a local resource may exclude a spatially separate consumer species, even when the effect on shared resources is small. Two habitats and three limiting resources support at most three consumer species because with four consumers, consumers in the habitat with the lower shared resource requirement drive the shared resource level beneath the intersection of the consumer species' zero net growth isoclines in the other habitat. This work underscores the importance of determining appropriate scale-dependencies when studying metacommunities. Studies must encompass habitats occupied by consumers of any shared resources to illuminate such effects. We discuss model applicability to complex systems, including how urban wildlife consuming natural and anthropogenic resources may displace rural competitors by depleting shared prey.

B. **Introduction**

Competition for resources on multiple scales is widespread in nature (Levin, 1992; Grover, 1997; Denny and Gaines, 2007). For example, in a colony of seabirds, individuals compete against one another for nest sites, and against birds in neighboring colonies for prey. As a second example, in tide pools, filter feeding mussels and barnacles compete locally for space on rocks and compete on a larger scale with organisms in nearby pools for prey such as plankton which are dispersed by tidal flow. Although the study of competitive coexistence is fundamental in ecology (Amarasekare, 2003), our understanding of consequences for coexistence in systems with local and shared resources is hampered by the complexity that is introduced when multiple spatial scales are considered simultaneously (Levin, 1992; Grover, 1997; Haegeman and Loreau, 2015). Herein, we extend Holling's disc equation, which models a predator's response to varying prey densities (Holling, 1959), to simulate consumer-resource dynamics in systems characterized by shared and local resources with non-dispersing consumers occupying separate habitats.

No approach has previously been developed for non-dispersing consumers with shared and local resources. Haegeman and Loreau (2015) developed a graphical-mechanistic approach to predict coexistence in systems with dispersing consumers and immobile resources, e.g., zooplankton consumers and phytoplankton resources in spatially distinct water layers. Amarasekare (2008) developed a consumer-resource dispersal model with three trophic levels: resource, consumer, and predator. In the models developed by Haegeman and Loreau (2015) and Amarasekare (2008), consumers disperse but resources do not. However, we imagine many scenarios in which mobile, waterborne, or airborne resources like carbon dioxide (CO_2) disperse further than consumers and are therefore shared across multiple consumer habitats.

Models herein predict how resource distribution on multiple scales influences population dynamics of consumers, thus providing guidance for study design of metacommunity systems. Guidance regarding appropriate scale for laboratory and field experiments in consumer-resource systems is valuable because observations of coexistence and biodiversity depend on the scale of study (Grover, 1997; Ricklefs and Miller, 2000; Kneitel and Chase, 2004). Some processes like dispersal are more likely to affect smaller scale field experiments (Cooper et al., 1998). Scale dependency can be problematic if the scale of an observed pattern mismatches the scale of the pattern's driver (Levin, 1992; Cooper et al., 1998). Likewise, tradeoffs operating at multiple scales may facilitate coexistence, but tradeoffs are typically studied on only one scale (Kneitel and Chase, 2004).

We consider all combinations of three nutritional resource types (substitutable, essential and complementary) and two functional responses (Types I and II). For substitutable and essential resources, we build on the work of Vincent et al. (1996), who investigated systems with either mixed (shared) or separate (local) resources. We develop a novel approach for complementary resources to expand applicability of our model. Examples of complementary resources include plants consumed by herbivores (Schmidt et al., 1998), fruits consumed by frugivorous birds (Whelan et al., 1998), and food and safety in general (Gilliam and Fraser, 1987; Brown, 1988). We use the multiplicative Cobb-Douglas equation (Cobb and Douglas, 1928) as the basis of our growth function with complementary resources. The Cobb-Douglas equation is widely used in economics and has ecological applications (e.g., Brown and Robinson, 2006; Jorge et al., 2012).

This article provides insight into how changing the parameters that govern the consumption of the local resource in one habitat can displace consumers from a separate habitat. First we illustrate the general manner in which the model functions with a system of

two habitats, two consumers, two local resources, and one shared resource, wherein one habitat is assumed to be of superior quality for consumers relative to the other habitat; this is our system of primary interest, and we refer to it as the primary system throughout this manuscript. We compare the primary system to a system in which there is only one consumer, and all resources in the system are available to that consumer. We also compare the primary system to a system in which there are two habitats, but all parameters of the two habitats are identical. We then demonstrate, using the primary system, how increasing local resource carrying capacity in one habitat can lead to the loss of consumer species from a separate habitat. We compare outcomes from decreasing local resource handling time to increasing carrying capacity, showing how either can result in displacement. In the discussion, we describe implications of the results as they pertain to various complex natural systems and to study design.

C. **Model description**

We extend traditional consumer resource models based on Holling's disc equation to consider consumption of locally available resources and a shared resource mixed across two habitats, A and B. Each habitat is occupied by one local resource and one consumer species. The local resource in habitat A (R_1^A) is only available to consumers in habitat A (N^A), and the local resource in habitat B (R_1^B) is only available to consumers in habitat B (N^B). A shared resource (R_2) is available to N^A and N^B . This is our primary system (Figure 5). We assume resources are valuable and consumer fitness is a function of resource consumption.

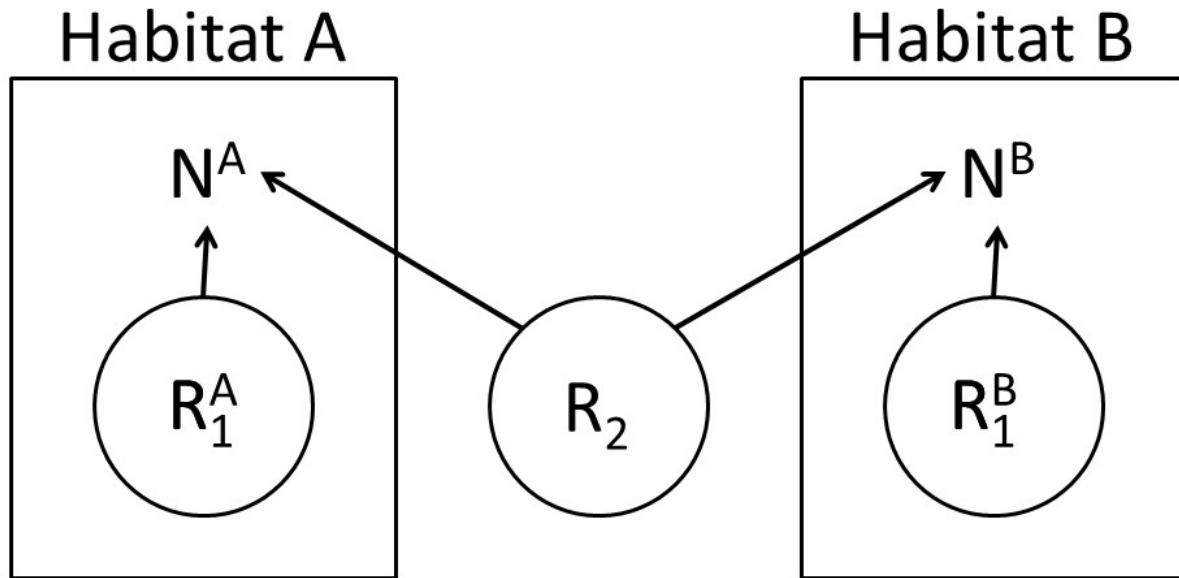


Figure 5. The primary system of interest: a consumer-resource system, where habitats A and B each have a locally available resource, R_1 . A shared resource, R_2 , is available to consumers in both habitats. The consumers do not move between habitats and do not directly interact. However, consumers in each habitat interact indirectly through the shared resource, R_2 .

1. **Nutritional types of resources**

We consider resources of three nutritional types: substitutable, essential, and complementary. Substitutable resources are mutually exchangeable. Consumers compensate for a decrease in one substitutable resource by consuming proportionally more of another resource. For example, glucose and fructose serve as substitutable sources of carbon for bacteria (Ricklefs and Miller, 2000). Conversely, essential resources have the potential to limit consumer population sizes independently. For example, silicon and phosphorous are essential elements for

diatoms. In this case, the value of consuming a mixture of resources is equal to the value provided by the scarcest resource, following Liebig's law of the minimum (Ricklefs and Miller, 2000). We define complementary resources as resources that contribute to fitness multiplicatively, or for which there are diminishing returns from consumption of one resource without consumption of another resource (Brown, 2000).

Community composition and equilibrium resource levels are predicted by zero net growth isoclines (ZNGIs) (Tilman, 1980, 1982; Abrams, 1988). ZNGIs are lines in the resources state space that represent all combinations of resources that maintain constant consumer populations at equilibrium. If resource levels are above the ZNGI, consumer population growth is positive, and consumption drives the resource level down to the ZNGI. If resource levels are below the ZNGI, consumer population growth is negative.

For two substitutable resources, let the growth rate of consumers in habitat $j \in \{A, B\}$ be given by

$$\frac{dN^j}{dt} = (c_1^j b_1^j + c_2^j b_2^j - d^j) N^j. \quad (1)$$

Consumption of the local resource in habitat j is a function of the local resource and is given by c_1^j . Consumption of the shared resource in each habitat is given by c_2^j . Consumption multiplied by b_i^j , conversion efficiency of turning resource $i \in \{1, 2\}$ into consumers in habitat j , yields per capita increase in population size from consumption of the local and shared resources. Consumer population size decreases at per capita mortality rate d^j in habitat j .

For essential resources, growth depends on the resource whose consumption yields lowest per capita growth (the limiting resource). Let consumer growth with essential resources be given by

$$\frac{dN^j}{dt} = (\min\{b_1^j c_1^j, b_2^j c_2^j\} - d^j) N^j \quad (2)$$

where variables are defined following equation (1).

For complementary resources, we use a form based on the Cobb-Douglas function (Cobb and Douglas, 1928). For habitat j , fitness is a function of $C_1^{j\alpha} C_2^{j\beta}$ where $\alpha + \beta = 1$. Let growth with two complementary resources be given by

$$\frac{dN^j}{dt} = (b^j C_1^{j\alpha} C_2^{j\beta} - d^j) N^j \quad (3)$$

where α and β are relative ratios of consumption of the local and shared resources respectively.

For all nutritional types, growth of resources follows a chemostat model (Monod, 1949; Vincent et al., 1996)

$$\frac{dR_1^j}{dt} = \mu_1^j (K_1^j - R_1^j) - N^j C_1^j \text{ and} \quad (4a)$$

$$\frac{dR_2}{dt} = \mu_2 (K_2 - R_2) - \sum_{j \in \{A, B\}} N^j C_2^j \quad (4b)$$

where μ is resource growth rate, K is carrying capacity, and other variables follow equation (1).

2. **Functional responses**

Consumption depends on the functional response of consumers. Note that although consumption and its components are habitat specific, we drop the habitat indicator to simplify notation in this section.

For a Type I functional response, consumption of the local resource C_1 is $a_1 R_1$, where a_1 is encounter rate of the local resource and R_1 is abundance of the local resource. For a Type II functional response, consumer growth is a function of encounter rate and handling time h . Overconsumption of non-limiting resources is non-optimal because time spent searching for and handling non-limiting resources would be better spent obtaining the limiting resource. To represent this, we introduce parameter p , probability of accepting an encountered item of either the local or shared resource. With substitutable resources, the only reason to reject an

encountered food item is if the reward for handling time does not compensate for the mortality costs or if a preferred food is sufficiently abundant. Assuming the local resource is more valuable than the shared resource, $\frac{b_1}{h_1} > \frac{b_2}{h_2}$ and $p_1 = 1$. If $R_1 < \frac{b_2}{a_1(b_1 h_2 - b_2 h_1)}$ then $p_2 = 1$, otherwise $p_2 = 0$. Under these conditions, consumption of resources in a Type II system is given by (Vincent et al., 1996)

$$C_i = \frac{p_i b_i a_i R_i}{1 + \sum_{i \in \{1,2\}} p_i a_i R_i h_i}. \quad (5)$$

With either essential or complementary resources, consumers may exhibit partially selective diet choice. For two essential resources, if $\frac{a_2 R_2}{a_1 R_1} > \frac{b_1}{b_2}$ then R_1 is limiting, $p_1 = 1$ and $p_2 = \frac{a_1 R_1 b_1}{a_2 R_2 b_2}$. If $\frac{a_2 R_2}{a_1 R_1} < \frac{b_1}{b_2}$ then R_2 is limiting, $p_2 = 1$ and $p_1 = \frac{a_2 R_2 b_2}{a_1 R_1 b_1}$ (Vincent et al., 1996).

Therefore, the limiting resource is always consumed and the probability of consuming the non-limiting resource is a function of the relative value of the resource to the consumer.

Consumption with essential resources is given by the following two equations (Vincent et al., 1996):

$$C_1 = \frac{b_1 a_1 R_1 p_1}{1 + a_1 R_1 p_1 \left(h_1 + \frac{b_1}{b_2} h_2 \right)}, \quad (6)$$

$$C_2 = \frac{b_2 a_2 R_2 p_2}{1 + a_2 R_2 p_2 \left(h_2 + \frac{b_2}{b_1} h_1 \right)}. \quad (7)$$

If consumers forage opportunistically for complementary resources, introducing handling time leads to an opportunity cost associated with overabundance of non-limiting resources in the system. The ZNGIs are angled away from the axes rather than being parallel to the axes in such a system. However, if consumers of complementary resources forage optimally and consume a partially selective diet, the shape of the ZNGI is equivalent to that of the system without handling time. Consumption and growth functions for complementary resources with

opportunistic vs. optimal foraging and complementary resources are derived in the following sections.

Under a given level of consumption (C_i where $i \in \{1, 2\}$) the fitness value of consuming more of the local resource (R_1) or shared resource (R_2) is given by:

$$\frac{dN^j/dt}{dC_1} = \frac{\alpha b C_1^\alpha C_2^\beta}{C_1} \quad (8)$$

$$\frac{dN^j/dt}{dC_2} = \frac{\alpha b C_1^\alpha C_2^\beta}{C_2} \quad (9)$$

An encountered item of the shared resource should be rejected if greater fitness can be had by searching for and handling an item of the local resource than by simply handling an item of the shared resource. Therefore, consumers foraging optimally will reject an item of the shared resource if:

$$\frac{a_1 R_1 \frac{dN^j/dt}{dC_1}}{1 + a_1 R_1 h_1} > \frac{\frac{dN^j/dt}{dC_1}}{h_2} \quad (10)$$

Equation (10) can be rewritten as:

$$\frac{\alpha a_1 R_1 C_2}{1 + a_1 R_1 h_1} > \frac{\beta C_1}{h_2} \quad (11)$$

The likelihood of being partially selective increases with α , a_1 , R_1 , h_2 , and C_2 and decreases with β , h_1 , and C_1 . A similar equation can be had for when an encountered item of the local resource should be rejected. In the event that the condition in equation (11) is satisfied, then the forager should modulate its consumption of the shared resource so that the condition is met with equality, which means C_2 should be determined by C_1 according to the following relationship (found by setting the above equation equal and solving for C_2 as a function of C_1):

$$C_2 = \frac{\beta(1 + a_1 R_1 h_1)}{\alpha a_1 R_1 h_2} C_1 \quad (12)$$

Conditions governing consumption in a system with optimal foraging can be visualized as isolegs, lines that divide the resource state space into regions in which consumers use different foraging strategies. Substituting the consumption rates when feeding is opportunistic and rearranging equation (12) yields the isolegs separating when the forager should be an opportunist, and when it should be partially selective (Table I). Between the isolegs, consumers forage opportunistically, consuming resources as encountered. At high values of one resource, consumers reject consumption of some of the more abundant resource to increase consumption on the more limiting resource (Figure 6).

TABLE I**CONSUMPTION OF COMPLEMENTARY RESOURCES WITH A TYPE II FUNCTIONAL RESPONSE**

Strategy	Conditions	Consumption Functions
Opportunistic	$R_2 > \frac{\beta(1 + a_1 h_1 R_1)}{\alpha a_2 h_2}$ and	$C_1 = \frac{a_1 R_1}{1 + a_1 R_1 h_1 + a_2 R_2 h_2}$
	$R_2 > \frac{a_1 h_1 R_1 \beta - \alpha}{\alpha a_2 h_2}$	and $C_2 = \frac{a_2 R_2}{1 + a_1 R_1 h_1 + a_2 R_2 h_2}$
Modulate R_2 consumption	$R_2 > \frac{\beta(1 + a_1 h_1 R_1)}{\alpha a_2 h_2}$	$C_1 = \frac{\alpha a_1 R_1}{\alpha + \alpha a_1 R_1 h_1 + \beta(1 + a_1 R_1 h_1)}$
		and $C_2 = \frac{\beta(1 + a_1 R_1 h_1)}{\alpha h_2 + \beta h_2(1 + a_1 R_1 h_1) + \alpha h_2 a_1 R_1 h_1}$
Modulate R_1 consumption	$R_2 < \frac{a_1 h_1 R_1 \beta - \alpha}{\alpha a_2 h_2}$	$C_1 = \frac{\alpha(1 + a_2 R_2 h_2)}{\beta h_1 + \alpha h_1(1 + a_2 R_2 h_2) + \beta h_1 a_2 R_2 h_2}$
		and $C_2 = \frac{\beta a_2 R_2}{\beta + \beta a_2 R_2 h_2 + \alpha(1 + a_2 R_2 h_2)}$

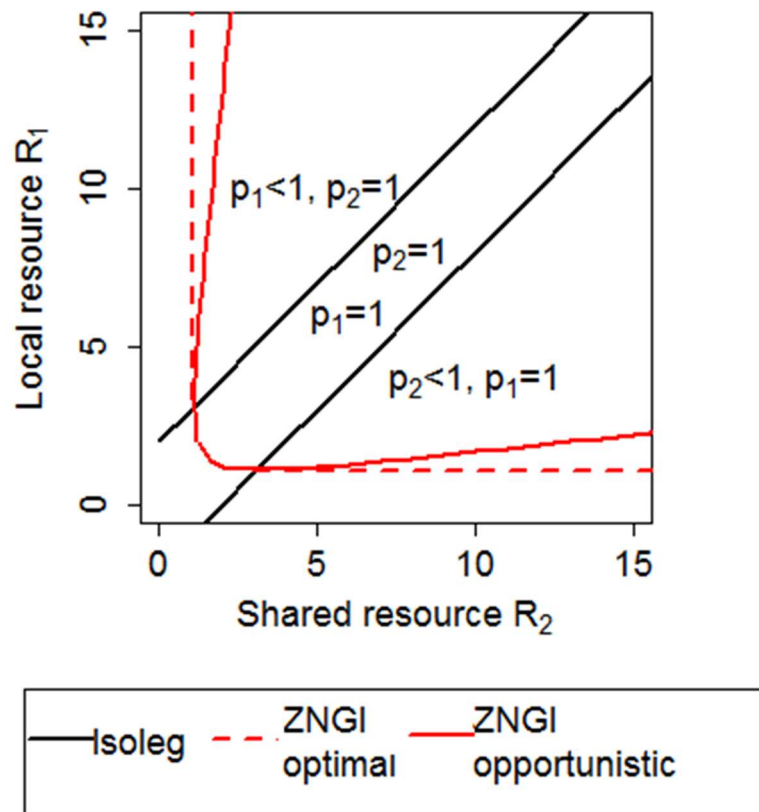


Figure 6. Opportunistic vs. optimal foraging with complementary resources in a Type II system. The shape of the zero net growth isocline (ZNGI) depends on the foraging strategy employed by consumers: optimal foraging (dotted red line) vs. opportunistic foraging (solid red line). Isolegs (black lines) divide the resource state space into three regions in which the optimal forager will have different probabilities of accepting an item of the local resource (p_1) or shared resource (p_2).

3. **Simulations**

For three nutritional types of resources (substitutable, essential and complementary) and two functional responses (Types I and II), we simulate population dynamics using a system of five ordinary differential equations. Two equations represent growth of consumers and two represent local resource growth in habitats A and B. The fifth equation represents growth of the shared resource.

The system of equations is solved using function ODE in package deSolve (Soetaert et al., 2010) in R (R Development Core Team, 2009). Simulations ran ≥ 100 time-steps, depending on the interval required to reach equilibrium. The system of equations did not lend itself to analytical solving, as has been found previously with similar equations (Amarasekare, 2008). Simulations determine conditions allowing coexistence of consumers, equilibrium population sizes, and resource levels. We overlay two graphing techniques to present our results: 1) ZNGIs depict all combinations of resources allowing for zero net growth of consumers and 2) depletion trajectories in the resource state space show inter-equilibrium resource dynamics that ultimately govern consumer coexistence vs. displacement. The depletion trajectories show how resources are depleted by consumers over time, beginning at the resource supply point and ending at the ZNGI if the system reaches equilibrium, or beneath the ZNGI if consumers are displaced. ZNGIs are solved analytically, except in the case of complementary resources with a Type II functional response and optimal foraging which did not lend itself to analytical solving and for which we use function "uniroot" in R (R Development Core Team, 2009).

Herein, we focus on a two-consumer system with shared and local resources in two distinct habitats, A and B, as depicted in Figure 5 (our primary system). We assume that habitat A is of superior quality for consumers compared to habitat B. We compare the primary system to a system in which consumers in either habitat A or B are removed (one-consumer systems).

We also compare the primary system to a system wherein habitats A and B are identical in terms of consumers, local resources, and parameters governing consumption of resources. We refer to the latter system as a system of "duplicate habitats." The models for one-consumer and duplicate habitat systems are variants of single consumer models described by Tilman (1980) and Vincent et al. (1996). In making these comparisons among systems, we develop model intuition about how resource levels at equilibrium are affected by the configuration of consumers and resources. Then, using the primary system, we perform parameter sweeps of local resource carrying capacity in a Type I system, and handling time in a Type II system, to illustrate conditions facilitating coexistence vs. displacement.

D. **One- vs. two-consumer systems**

In a one-consumer system wherein one habitat and its consumers and resources exist in isolation, the intersection of the ZNGI and consumption vector in the resource state space determines equilibrium resource levels. Assuming opportunism, the depletion trajectory is a straight line from resource supply point to origin. Compared to the primary system (Figure 5), which has two consumer species, the level of the shared resource at equilibrium is higher in one-consumer systems. This outcome is unsurprising; adding consumers depletes the shared resource. The level of shared resource at equilibrium in the primary system falls between equilibrium levels of the shared resource levels when both habitats are identical to habitat A or to habitat B (duplicate habitat systems) (Figure 7). This is true of substitutable, essential or complementary resources.

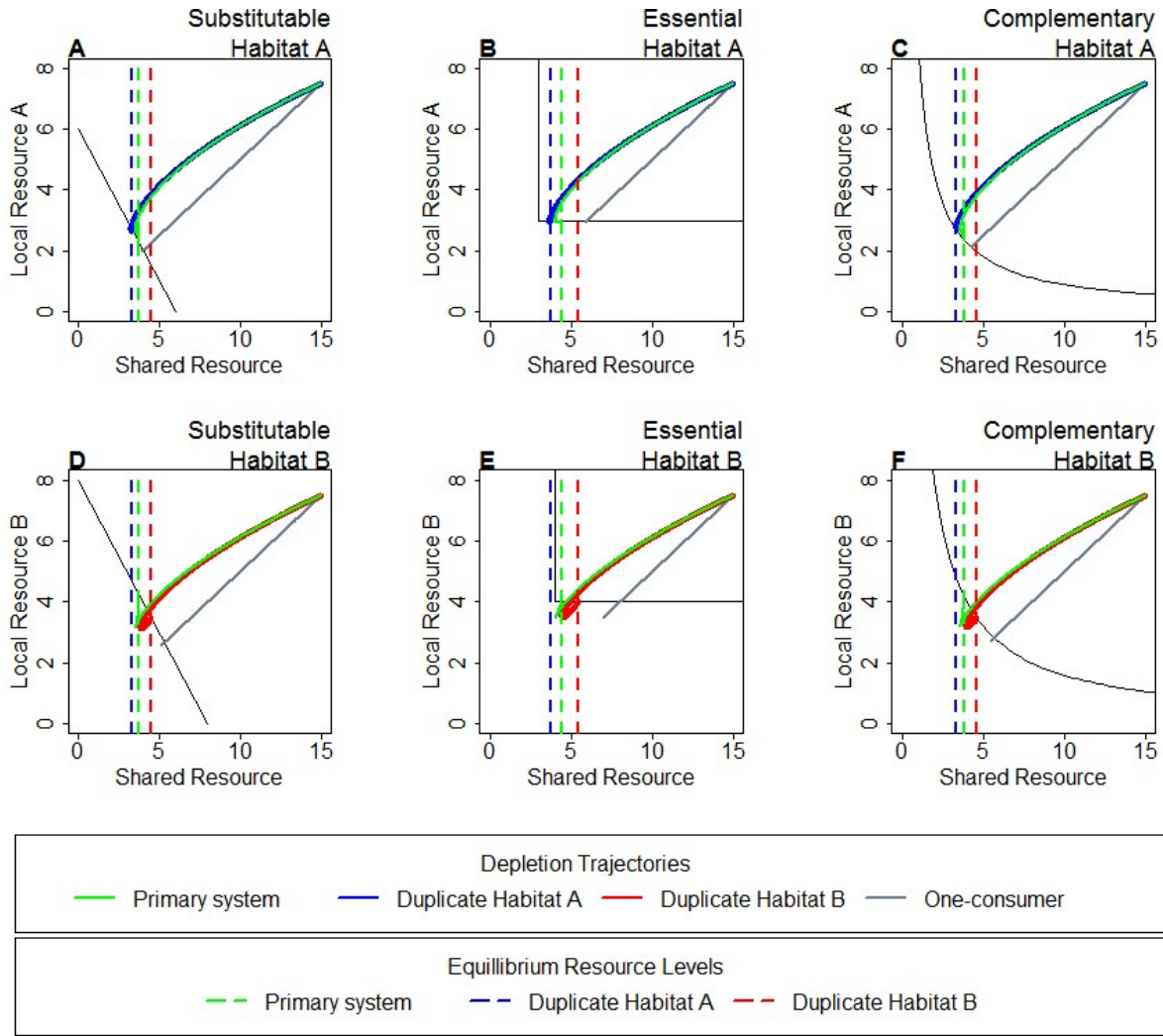


Figure 7. Comparison of four configurations of consumers and resources with substitutable, essential, or complementary resources. Equilibrium shared resource levels (dotted lines) in the primary system (green) are intermediate between equilibrium levels in systems in which both habitats are identical to habitat A or to habitat B (duplicate habitat systems; blue and red respectively). Depletion trajectories for one-consumer systems (grey) go directly from the resource supply point to the origin, stopping where they intersect with the ZNGI (black). Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.8$. Other parameter values are as follows: for all panels, $\mu_1^A = \mu_1^B = \mu_2 = 1$, $a_1^A = a_1^B = a_2^A = a_2^B = 1$, $K_2 = 15$ and $K_1^B = K_1^A = 7.5$. For panel A and panel D, $b_1^A = b_1^B = b_2^A = b_2^B = 0.1$. For panel B and panel E, $b_1^A = b_1^B = b_2^A = b_2^B = 0.2$. For panel C and panel F, $b^A = b^B = 0.2$, $\alpha^A = \alpha^B = \beta^A = \beta^B = 0.5$.

E. **Displacement vs. coexistence**

Displacement vs. coexistence can be affected by modifying any parameter governing consumption. However, for simplicity of presentation, we focus here on comparing parameter sweeps in which we vary carrying capacity of a local resource in a Type I system, and handling time of a local resource in a Type II system. A number of results, including those pertaining to one- vs. two-consumer systems, are best demonstrated with a linear functional response (Type I). As would be expected, Type II systems exhibit similar behavior to Type I systems regarding increasing local resource carrying capacity. Of interest in this section is the comparison between handling time and carrying capacity in terms of coexistence vs. displacement. In the Type II system, we assume optimal foraging and the p values governing resource consumption follow the conditional rules laid out in the section of this article in which we describe functional responses.

1. **Substitutable resources**

In a two-consumer system with substitutable resources, consumers coexist if local resources are available regardless of shared resources. Changes in population sizes of consumers and shared resources are proportional and gradual in response to incremental increases in local resource carrying capacity in habitat A (Figure 8). Increasing local resource carrying capacity in habitat A increases the consumer population in habitat A. The larger consumer population draws down the shared resource which results in smaller consumer population size in habitat B. The only scenarios in which coexistence is not possible is in the absence of local resources, in which case the consumer with the lower ZNGI for the shared resource will prevail.

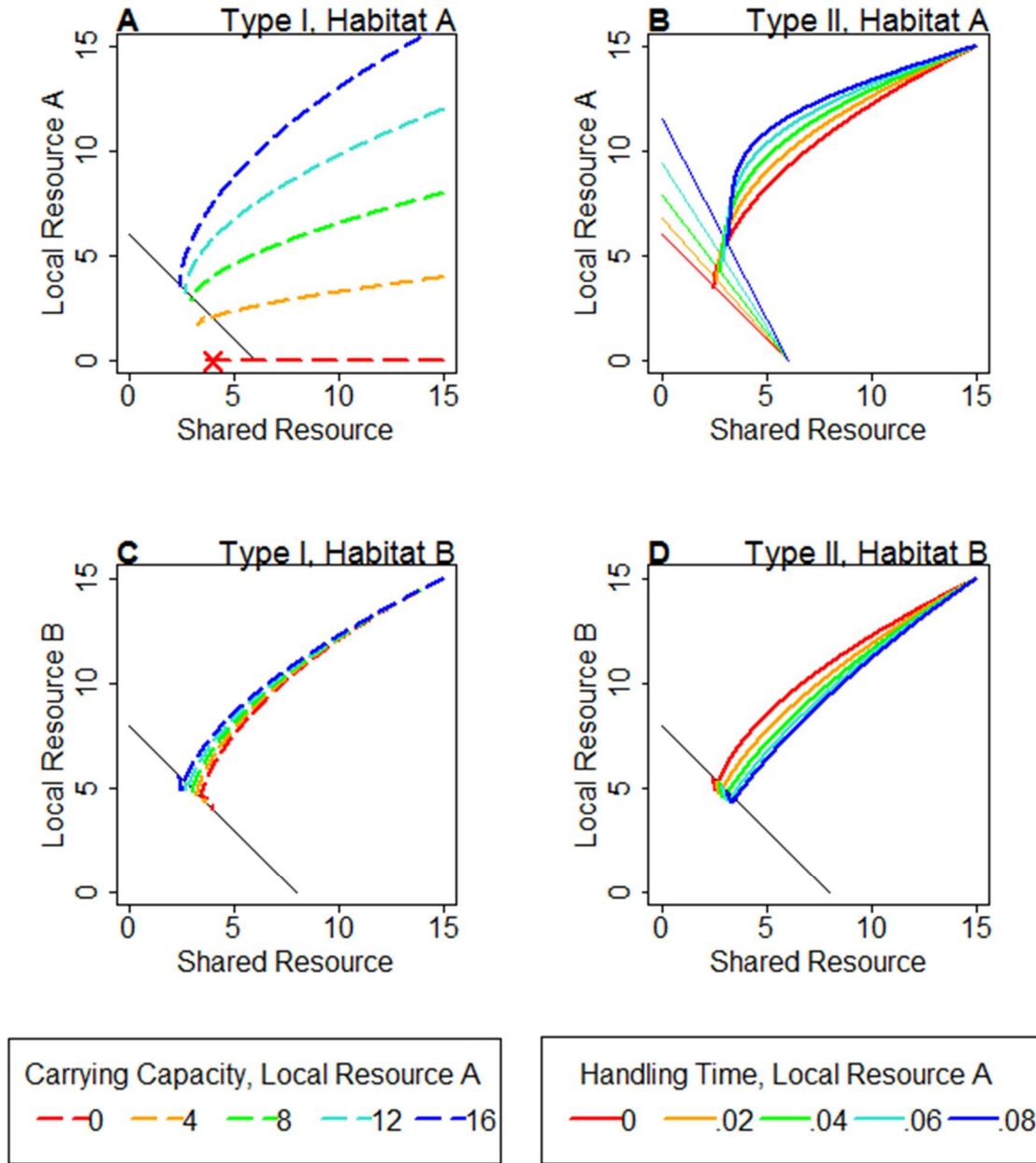


Figure 8. Simulations varying carrying capacity or handling time of a local, substitutable resource in habitat A show that all possible scenarios allow coexistence, except when there are no local resources. Depletion trajectories from the resource supply point to the intersection with the ZNGI, which indicates equilibrium, are shown. Increasing local resource carrying capacity results in gradual lowering of the shared resource at equilibrium (panel A). Decreasing handling time in habitat A has a similar effect to increasing carrying capacity (panel B). Corresponding changes in habitat B are shown (panels C and D). Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.8$. Other parameter values for all panels are as follows: $\mu_1^A = \mu_1^B = \mu_2 = 1$, $a_1^A = a_1^B = a_2^A = a_2^B = 1$, $K_2 = 15$, $K_1^B = 7.5$, $b_1^A = b_1^B = b_2^A = b_2^B = 0.1$. For panel A and panel C, $K_1^A \in \{0, 4, 8, 12, 16\}$. For panel B and panel D, $h_1^A \in \{0, 0.02, 0.04, 0.06, 0.08\}$ and $h_2^A = h_2^B = h_1^B = 0$.

Unlike changing carrying capacity, which moves the resource supply point, changing handling time moves the ZNGI because the amount of local and shared resources required to maintain a population at equilibrium is greater when time is spent handling resources (Figure 8). The exception is the x-axis (shared resource) intercept of the ZNGI which remains the same, indicating the amount of shared resource required to sustain consumers in the absence of local resources is unaffected by local resource handling time. When local resource handling time increases, the y-axis (local resource) intercept of the ZNGI increases thus decreasing the slope and increasing the area beneath the ZNGI. The area beneath the ZNGI encompasses resource levels that do not support consumer populations at equilibrium. All values of handling time allow coexistence provided there are local resources. If handling time of the local resource in habitat A is so large that the local resource becomes essentially unavailable to consumers in habitat A, the consumers in habitat A become vulnerable to displacement if the consumers in habitat B drive the shared resource level below the ZNGI in habitat A (Figure 9).

Decreasing local resource handling time in habitat A has a similar effect on consumer population sizes compared to increasing carrying capacity. Decreasing local resource handling time in habitat A results in a gradual increase in consumer population size at equilibrium in habitat A (Figure 9). The larger consumer population in habitat A consumes more shared resources, which results in a gradual decrease in consumer population size at equilibrium in habitat B (Figure 9).

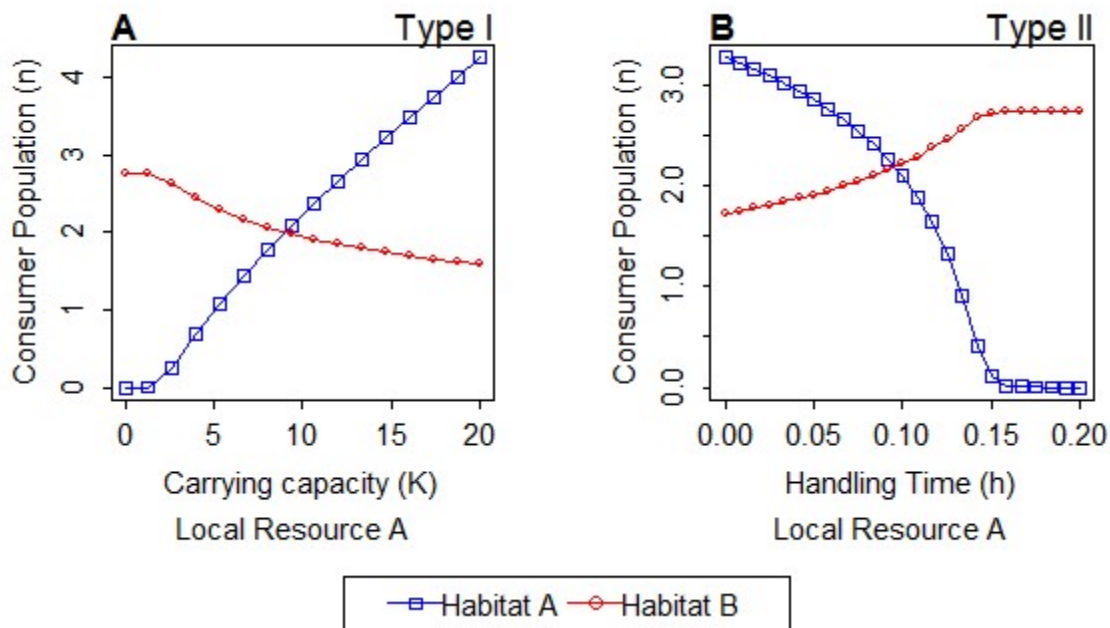


Figure 9. Consumer population sizes at equilibrium corresponding to simulations varying carrying capacity (panel A) or handling time (panel B) of the local, substitutable resource in habitat A. When the local resource in habitat A is available, coexistence is possible. Displacement occurs when carrying capacity of the local resource in habitat A is 0 or if handling time of the local resource in habitat A is so high that it becomes essentially unavailable. Depletion trajectories for a subset of values in this parameter sweep are depicted in Figure 8. Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.8$. Other parameters are listed in the caption for Figure 8.

2. Essential resources

Changing local resource consumption in one habitat can affect consumer populations in a separate habitat through the shared resource when resources are essential, even when the shared resource level at equilibrium is unchanged. For example, in Figure 10, when carrying capacity is 4 units, the local resource is limiting and the amount of local resource in the system is beneath the consumer's ZNGI, so consumers in habitat A are displaced.

Increasing the carrying capacity of the local resource in habitat A from 4 units to 8 units makes it possible for habitat A to sustain consumers. In both scenarios (local resource carrying capacity in habitat A is either 4 or 8 units), consumers in habitat B, which are limited by the shared resource, draw the level of the shared resource down to the ZNGI in habitat B. However, even though the level of the shared resource does not change at equilibrium, inter-equilibrium dynamics are such that some of the shared resource is taken up by the consumers in habitat A, so the consumer population size in habitat B at equilibrium is reduced when carrying capacity of the local resource in habitat A increases (Figure 11). Consumption of the shared resource by consumers in habitat A, who are limited by their local resource in these scenarios, is called "spiteful consumption" because it does not directly benefit the consumers in habitat A, but it does negatively affects their competitors in habitat B. With essential resources, gradual increases in local resource carrying capacity can cause abrupt changes in consumer population sizes. Abrupt changes occur when consumers switch from being limited by one resource to another. For example, when local resource carrying capacity in habitat A is relatively low (<12 units in Figure 10), consumers in habitat A are limited by the local resource. When local resource carrying capacity in habitat A exceeds a threshold (≥ 12 units in Figure 10), the shared resource becomes limiting, at which point consumers in habitat B, also limited by the shared resource, are displaced.

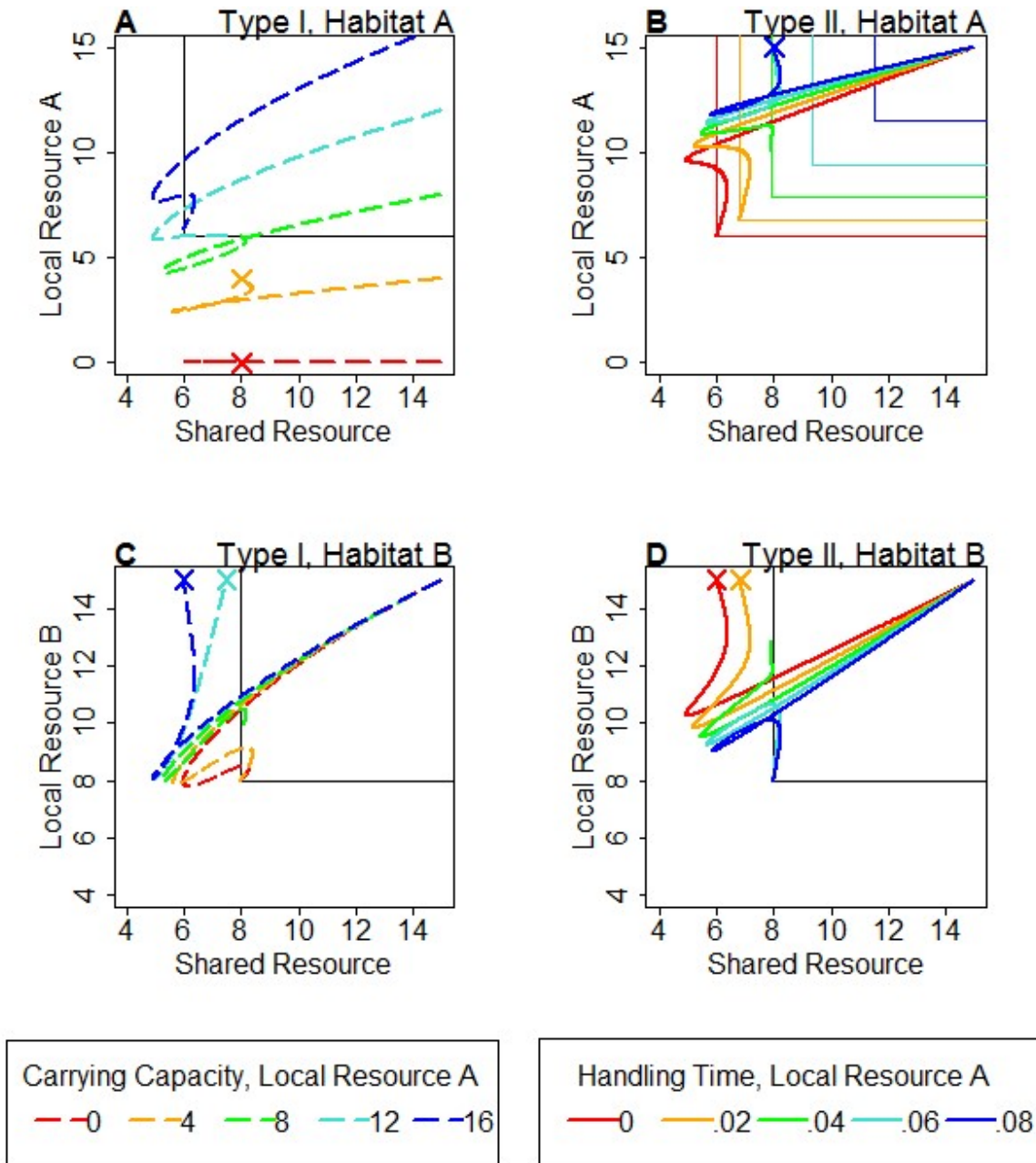


Figure 10. With essential resources, increasing carrying capacity or decreasing handling time of a local resource can displace consumers from a separate habitat. Depletion trajectories from the resource supply point to the intersection with the ZNGI, which indicates equilibrium, are shown. Increasing local resource carrying capacity in habitat A from 12 to 16 units switches the limiting resource in habitat A (panel A). Decreasing local resource handling time in habitat A lowers the shared resource at equilibrium (panel B). Displacement of consumers in habitat B, indicated with an X, results when habitat A draws down the shared resource below the ZNGI in habitat B (panel C). When handling time of the local resource in habitat A decreases from 0.04 to 0.02, the shared resource is driven lower than the ZNGI in habitat B, displacing consumers (panel D). Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.8$. Other parameter values are indicated in the caption of Figure 8.

Decreasing local resource handling time in habitat A can trigger a switch of which resource is limiting in habitat B (Figure 10), resulting in a large abrupt shift between one equilibrium population size and another. In the scenario in which consumers in habitat B are limited by the shared resource, reducing local resource handling time in habitat A can result in displacement of consumers from habitat B (Figure 10, consumer population sizes shown in Figure 11). Therefore, consumers in habitat B are vulnerable to displacement when they are limited by the shared resource. In this regard, decreasing handling time on the local resource is similar to increasing carrying capacity of the local resource; decreasing local resource handling time in habitat A can displace consumers from habitat B. Unlike changing carrying capacity, the mechanism via which consumers in habitat A outcompete those in habitat B involves moving the ZNGI. With greater local resource handling time in habitat A, both horizontal and vertical legs of the ZNGI move to greater values (Figure 10), which can result in the limiting resource switching. Both the horizontal and vertical legs of the ZNGIs change when handling time of a local resource changes because the handling time of all accepted resources contributes to the amount of resources necessary to maintain the consumer population at equilibrium.

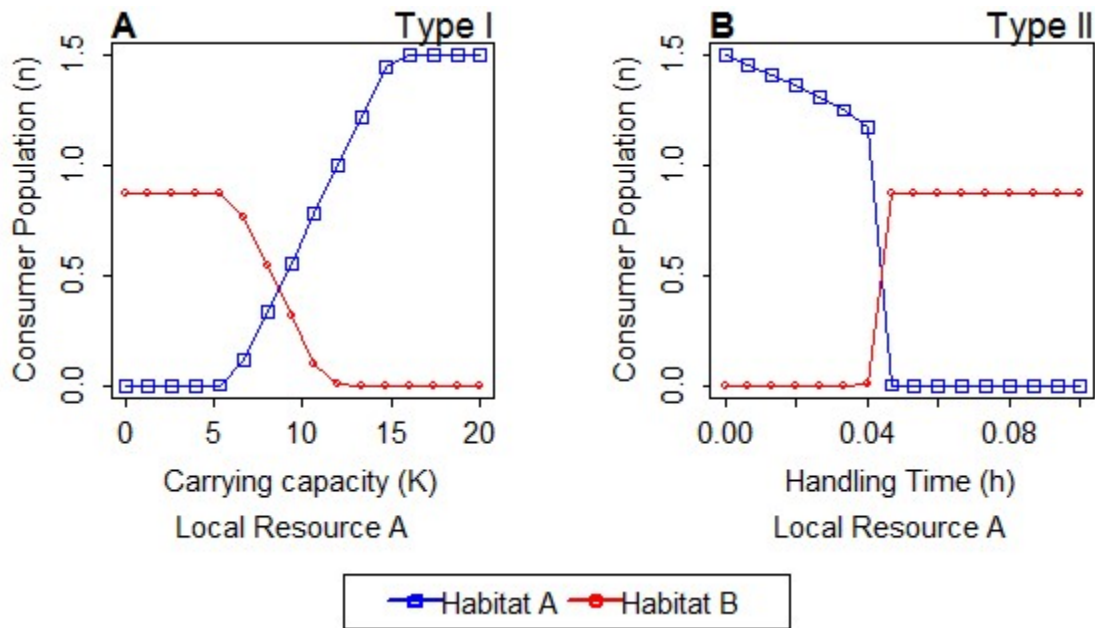


Figure 11. Consumer population sizes at equilibrium corresponding to simulations in which carrying capacity (panel A) or handling time (panel B) of the local resource in habitat A varies, and resources are essential, showing multiple scenarios that result in displacement of consumers. Only intermediate values of carrying capacity and handling time allow for coexistence of consumers in both habitat A and habitat B. Depletion trajectories for a subset of values shown in this parameter sweep are depicted in Figure 10, with ZNGIs. Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.8$. Additional parameters are listed in the caption for Figure 8.

We investigated the effects of introducing additional consumer species into the primary system with essential resources. With two consumer species in one habitat, both consumers in that habitat coexist when resource levels are at the intersection of their ZNGIs. If we add additional consumers to habitats A and B (four consumer species total), the habitat with the lower ZNGI for the shared resource drives the shared resource level below the intersection in the other habitat, disallowing coexistence. The singular situation permitting coexistence is when intersection of ZNGIs in habitats A and B occur at the same shared resource level (Figure 12).

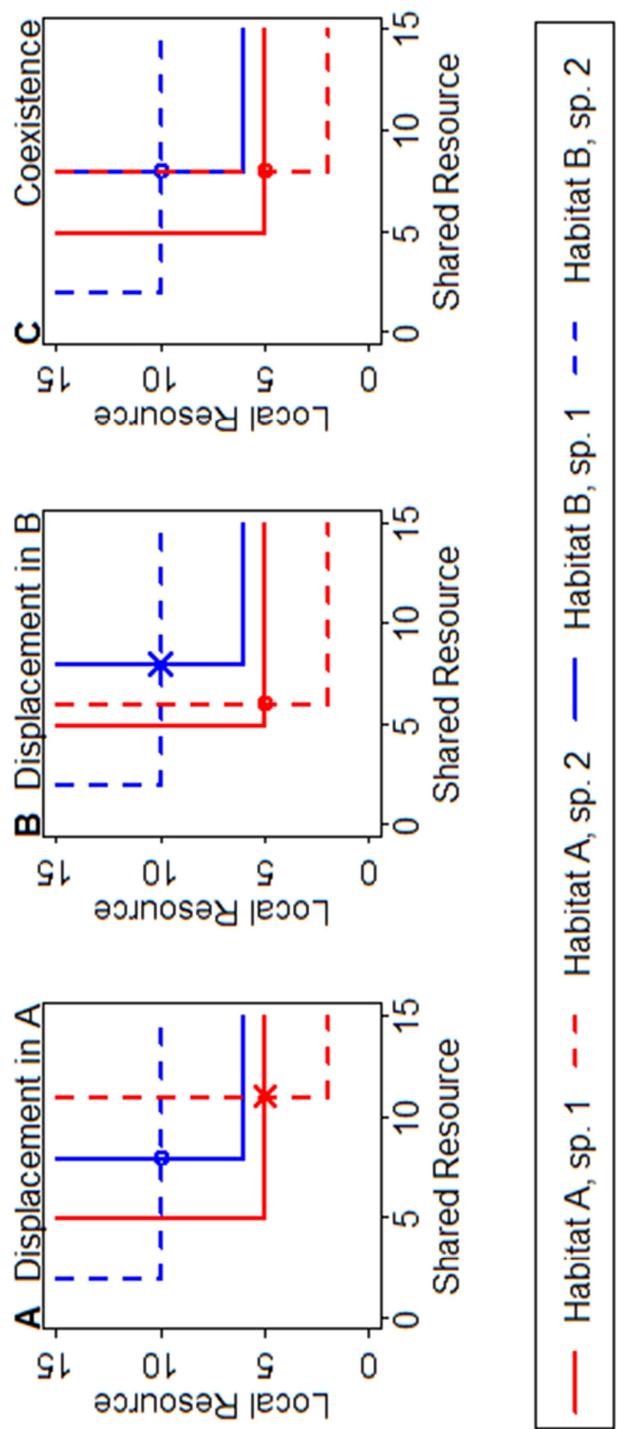


Figure 12. The system with essential resources and four consumer species supports, at most, three consumer species, with one singular exception. Panel A shows that when the intersection of the ZNGIs for consumer species in habitat A is at a greater value of the shared resource than the intersection of ZNGIs in habitat B, a consumer species in habitat A will be displaced. Panel B shows the opposite scenario from panel A, where the intersection of the ZNGIs for consumer species in habitat B is at a greater value of the shared resource than the intersection of ZNGIs in habitat A, and a consumer species in habitat B is displaced. Panel C shows the only possible scenario in which four consumer species (two in habitat A and two in habitat B) can coexist with essential resources. In panel C, the intersections of the ZNGIs for the two species in habitat A (red) and habitat B (blue) must occur at precisely the same level of the shared resource.

3. **Complementary resources**

With complementary resources, changes in equilibrium resource levels and consumer population sizes are gradual in response to incremental increase in local resource carrying capacity in habitat A when resource levels land in the curved elbow region of the system's ZNGI (Figure 13; consumer population sizes in Figure 14). This pattern is similar to that of substitutable resources. When resource levels land in the region of the ZNGI approaching straight lines, abrupt changes in population size as a result of incremental changes to carrying capacity are possible, akin to a system with essential resources. Consumer displacement from habitat B depends on local resource carrying capacity in habitat B when shared resource levels approach limiting levels (Figure 14). This is because increasingly large quantities of the local resource are needed to reach the ZNGI in such a system due to the diminishing returns nature that is characteristic of complementary resources.

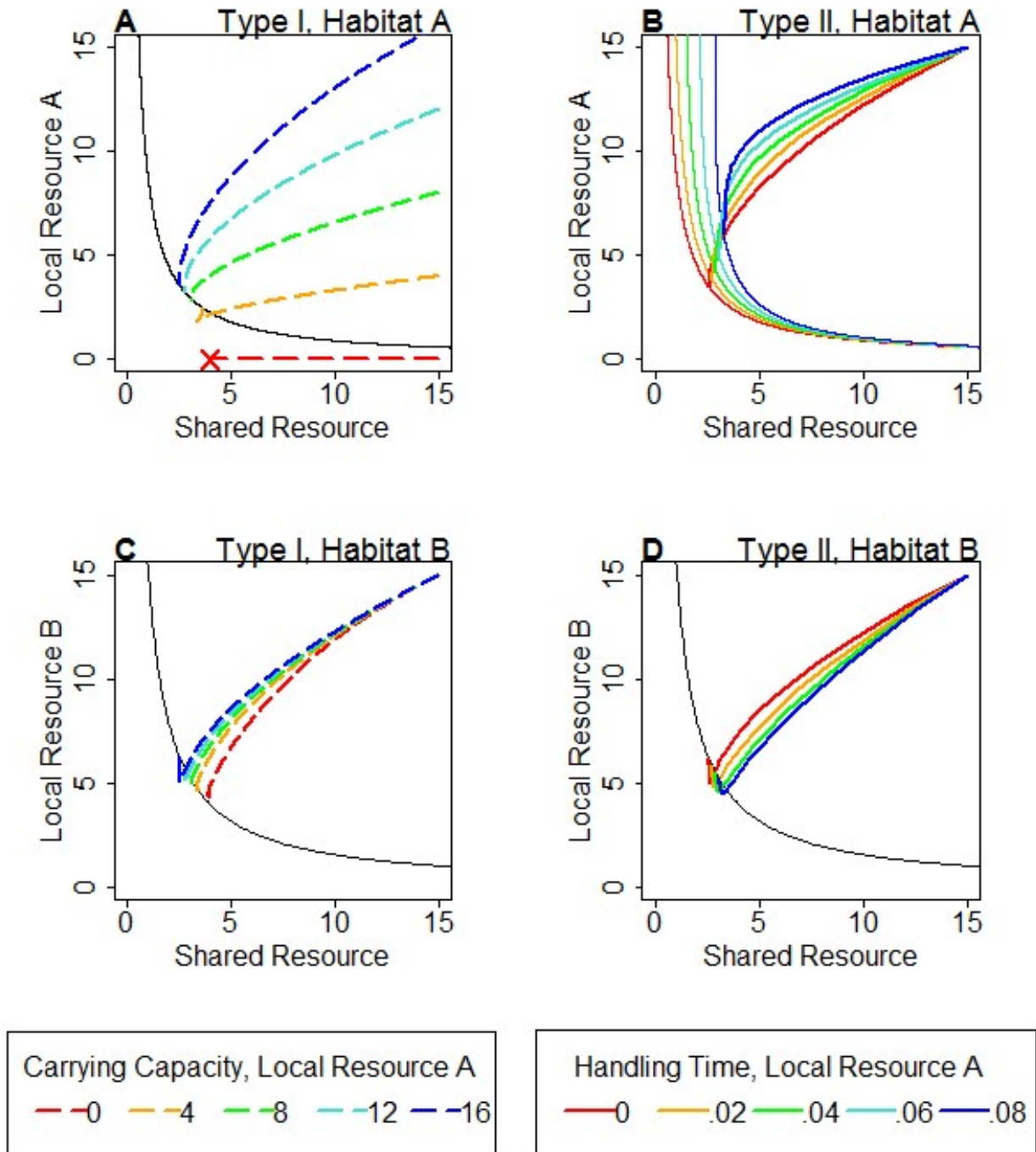


Figure 13. With complementary resources, changes in resource concentrations at equilibrium are gradual resulting from varying carrying capacity (panel A) or handling time (panel B) of a local resource in habitat A, when resource levels land in the curved region of the ZNGI. Corresponding effects in habitat B are shown (panel C and panel D). All panels show depletion trajectories from the resource supply point to the intersection with the ZNGI, which indicates equilibrium. Mortality differs per habitat: $d^A = 0.6$ and $d^B = 0.8$. Other parameter values for all panels are as follows: $\mu_1^A = \mu_1^B = \mu_2 = 1$, $a_1^A = a_1^B = a_2^A = a_2^B = 1$, $K_2 = 15$, $K_1^B = 15$, $b^A = b^B = 0.2$. For panels A and C, $K_1^A \in \{0, 4, 8, 12, 16\}$. For panels B and D, $h_1^A \in \{0, 0.02, 0.04, 0.06, 0.08\}$ and $h_2^A = h_2^B = h_1^B = 0$ and $K_1^A = 15$.

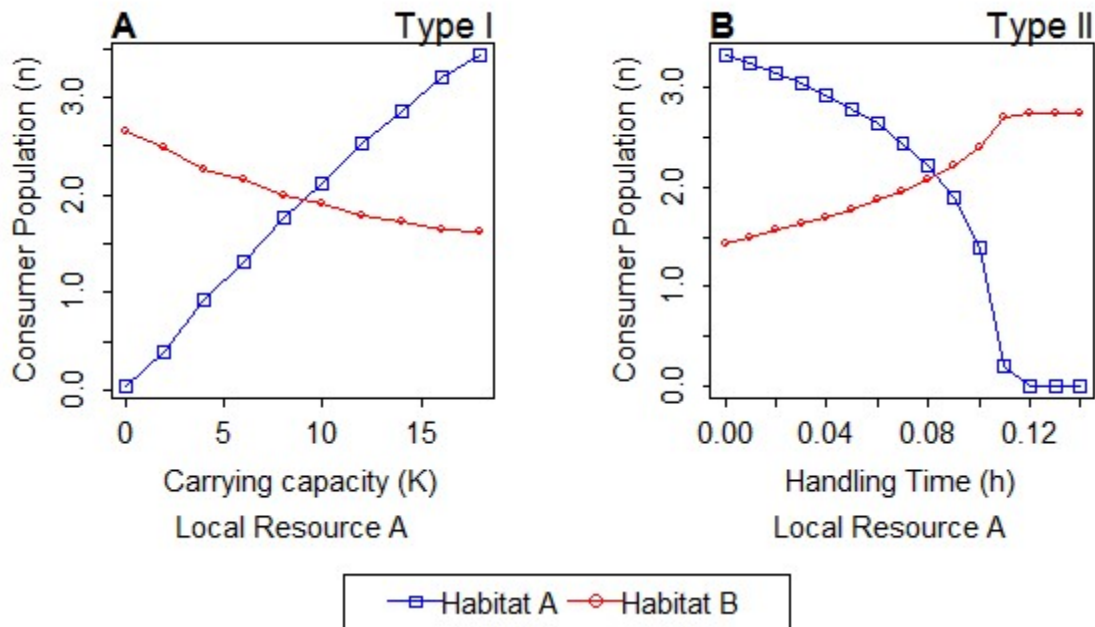


Figure 14. Consumer population sizes at equilibrium corresponding to simulations in which carrying capacity (panel A) or handling time (panel B) of the local resource in habitat A is increased and resources are complementary show displacement of consumers in habitat A occurs only when carrying capacity of the local resource in habitat A is 0, or handling time is so large that the resource becomes essentially unavailable. Depletion trajectories for a subset of values shown in this parameter sweep are depicted in Figure 13. Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.8$. Other parameters are in the caption for Figure 13.

In a Type II system, decreasing handling time of a local resource in habitat A results in a gradual increase in consumer population size in habitat A and a decrease in consumer population size in habitat B when resulting resource levels at equilibrium land in the curved region of the system's ZNGIs. Decreasing local resource handling time in habitat A can displace consumers in habitat B, but consumers in habitat B are buffered against this effect relative to

the consumers of essential resources. For example, in Figure 10 with essential resources, reducing handling time for the local resource in habitat A could result in displacement of consumers from habitat B when the only difference was a mortality rate of 0.6 in habitat A and 0.8 in habitat B. Displacement of consumers in habitat B with complementary resources is not observed at these parameter values (Figure 13). When the difference between habitats is extreme (e.g., mortality rate of 0.2 in habitat A and 0.9 in habitat B), displacement can occur in habitat B when handling time of a local resource in habitat A is reduced (Figure 16, consumer population sizes in Figure 17).

We observe two main differences between optimal and opportunistic foraging: the shape of the system ZNGIs is such that more of the limiting resource is required at high values of the non-limiting resource when foraging is opportunistic (Figure 16), and optimal foraging changes the depletion trajectory because the consumer conditionally specializes on the less available (more limiting) resource. Trends regarding handling time and coexistence are the same for opportunistic and optimal foraging strategies.

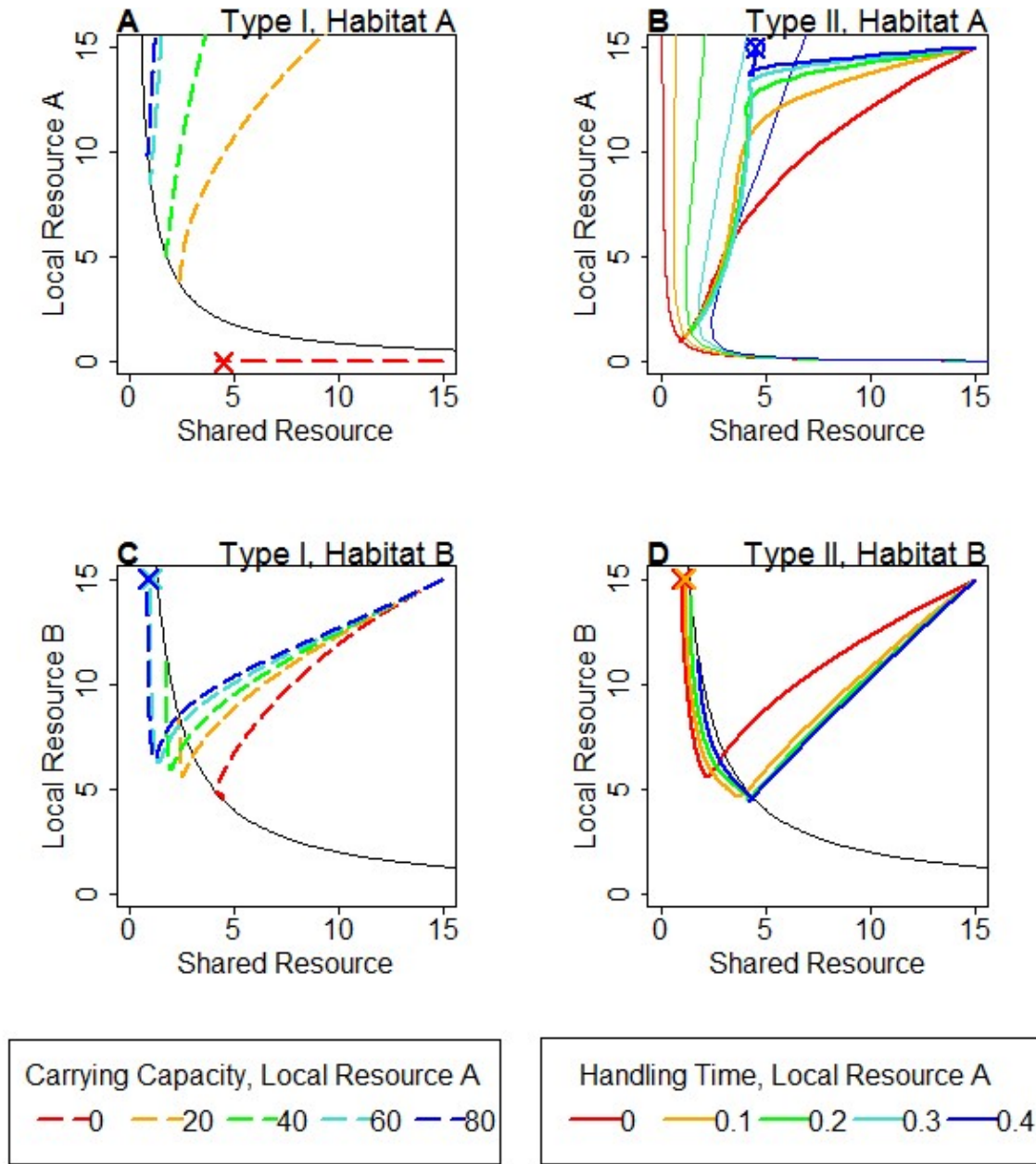


Figure 15. Increasing carrying capacity or decreasing handling time of a local resource can displace consumers of a complementary resource from a separate habitat when the difference in mortality between habitats is extreme. Increasing local resource carrying capacity in habitat A from 0 to 80 units results in equilibrium resource levels in the vertical region of the ZNGI (panel A). With opportunistic foraging, decreasing local resource handling time in habitat A from 0.6 to 0 moves the ZNGI to the left, and the elbow of the ZNGI moves to a lower value than the limit for the shared resource (vertical part of ZNGI) in habitat B (panel B). Corresponding effects in habitat B are shown in panel C and panel D. Displacement of consumers in habitat B is observed at high local resource carrying capacity in habitat A, or at low local resource handling times in habitat A. Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.9$ in panels A and C; $d^A = 0.2$ and $d^B = 0.9$ in panels B and D. Other parameters are listed in the caption for Figure 13.

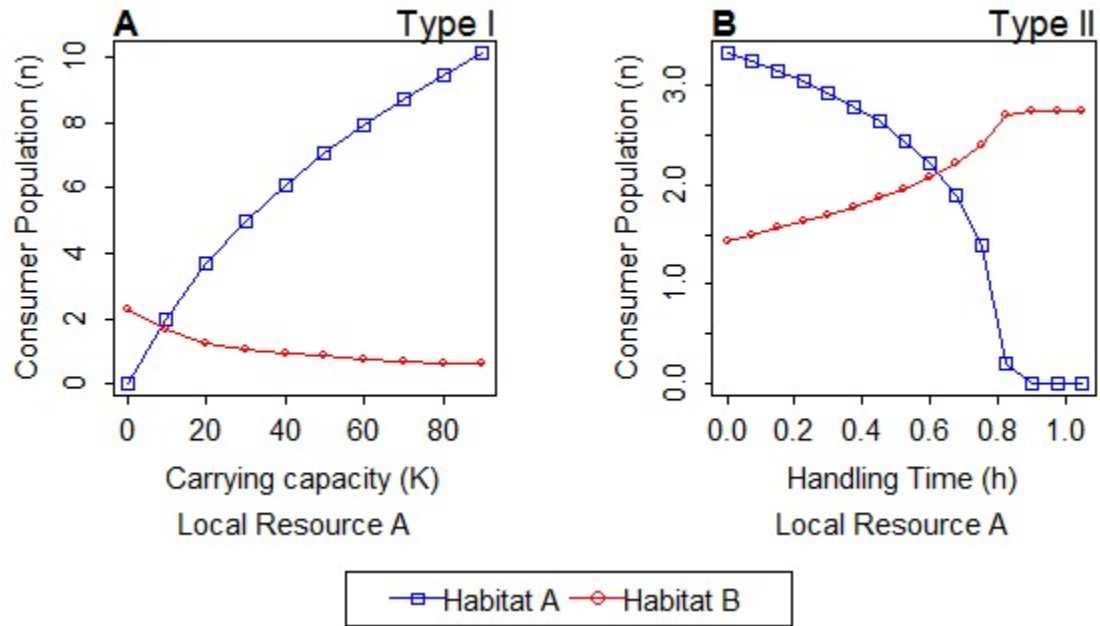


Figure 16. Consumer population sizes at equilibrium corresponding to simulations in which carrying capacity (panel A) or handling time (panel B) of the local resource in habitat A varies, resources are complementary, foraging is opportunistic, and there is an extreme difference in mortality between habitats. Depletion trajectories for a subset of values shown in this parameter sweep are depicted in Figure 15. Habitats differ in per capita mortality: $d^A = 0.6$ and $d^B = 0.9$ in panel A; $d^A = 0.2$ and $d^B = 0.9$ in panel B. Other parameters are listed in the caption for Figure 15.

F. Discussion

We have developed models for consumer-resource systems with both shared and local resources. Our analysis reveals that in the case of limiting resources (essential or complementary), increasing the local resource carrying capacity in one habitat can displace consumers from a spatially separate habitat. Decreasing local resource handling time can have

a similar effect to increasing carrying capacity. For anyone studying these systems, the local scale may serve their purposes, but there is a cautionary tale here regarding study design. One might casually expect effects of increasing availability of resources in a spatially separate habitat would, if anything, have a greatly attenuated effect on the study habitat. However, we found that a small change in carrying capacity or handling time in one habitat could have an amplified effect on spatially separate consumers, even when the observed effect on shared resources is small, due to the threshold nature of limiting resources. If only one habitat is considered, such phenomenon could appear very mysterious. Studies must encompass habitats occupied by consumers of any potentially shared resource to illuminate such effects.

We recognize that this model omits much of the complexity of natural systems. Following convention (e.g., Vincent et al. 1996; Haegeman and Loreau 2015), we assume no interactions between resources and consumers aside from consumption of resources by consumers and competition amongst consumers for resources. This assumption may be particularly problematic when extending our findings to natural systems with complex interactive dynamics and feedback loops (Franco et al. 2014). However, this model could serve as a module helping to illuminate one component of dynamics of such systems.

Previously developed models account for dispersal of consumers but not of resources. This may be because predatory consumers tend to be the focus of such models, and we typically think of predators, e.g., raptors, as having large ranges. However, we imagine many examples wherein resources have a greater capacity for dispersal than consumers. In this spirit, we are expansive in this discussion of systems for which the model might apply.

Various upwelling systems and systems with pulsed resources such as salt water tidal flats, estuaries, and mud flats have both local and shared resources amongst habitat patches (Odum et al., 1995). Alternatively, a competent invasive host species could serve as a shared

resource for multiple parasitic species parasitizing different native hosts (Kelly et al., 2009). Resources might be shared due to foraging behavior of consumers, e.g., seabirds compete for shared fish in the ocean and locally for nest sites within a colony. We imagine this model applying to territorial animals with some pool of local prey that have a small home range and migratory prey serving as a shared resource across many territories. This could apply to lions (*Panthera leo*) on the Serengeti or birds of prey along a migratory flyway.

We consider the case of systems with subsidized local resources because our analysis indicates that such subsidization could displace spatially separate consumers. Colonies of feral cats (*Felis catus*) are subsidized by humans, which provide them with a local food source. Feral cats also hunt and compete with non-domestic wildlife for a common pool of small mammal prey. We hypothesize that supplemental anthropogenic food sources provided to urban wildlife in general may detrimentally affect wildlife in non-urban areas via depletion of shared prey.

Plants provide an intriguing application that could possibly scale up to global climate change and intra- and inter-biome interactions. Light and soil nutrients represent local resources whose scale of interaction encompasses nearest neighbors and perhaps some distance beyond. When viewed as a resource, carbon dioxide is much better mixed over much larger spatial scales and so qualifies as the shared resource. So at scales of square kilometers, plants may be interacting through depression of carbon dioxide. While such depression might be too small to be consequential, it might exist nonetheless and create some of the effects seen in our model.

At larger scales we know that plants during the northern hemisphere summer demonstrably depress carbon dioxide levels (Graven et al., 2013). In this way plants in the temperate zone may share this carbon dioxide with plants in the tropics. So we offer this rather wild but intriguing conjecture; it seems plausible that if the globe were entirely “tropics”, then

the equilibrium value of carbon dioxide would be lower than for an all “temperate” globe. If so, then the presence of the temperate zone would actually decrease the R^* for light and soil nutrients in the tropics and vice-versa for the effect of the tropics on the temperate zone. Wouldn't it be amazing if this model and the presence of the temperate zone adds “darkness” and lower soil fertility to tropical rain forests? This may be far-fetched, but it illustrates the opportunities for applying this model and the need for extensions of consumer-resource models and graphical theory to above and belowground plant production (Grover 1997, Lynch et al., ms).

As a next step, we recommend empirical testing of the predictions made by these models using phytoplankton (diatoms) in a well-mixed chemostat. This model system has been used in some of the most rigorous tests of Tilman's (1981) classical graphical models (Wilson et al., 2007). Recent work of Alexander et al. (2015) illuminates that closely related species of phytoplankton use different nitrogen sources: *Skeletonema spp.* primarily use inorganic nitrogen, and *Thalassiosira rotula* use organic nitrogen. Thus species-specific nitrogen sources could serve as local resources for different diatom species. Diatoms require other essential nutrients, e.g. phosphorous and silicon, which could serve as the shared resource in a well-mixed chemostat. If model predictions are demonstrated in a simplified study environment, we believe this would support inclusion of this work as a module in complicated system models.

G. **Acknowledgments**

Joel Brown coauthored this work. The authors thank Rosalyn Rael and Paul Orlando for providing many helpful comments that greatly improved the manuscript. Maria Luisa Jorge provided us with information about an option for formatting the ZNGI figures. This work was inspired by the work of Vincent, T. L. S., D. Scheel, J. S. Brown, and T. L. Vincent in "Trade-Offs and Coexistence in Consumer-Resource Models: It all Depends on what and where you Eat" published in 1996 in *The American Naturalist*.

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III. ECOLOGY OF EASTERN COTTONTAIL RABBITS IN AN URBAN PARK

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A. **Abstract**

Eastern cottontail rabbits (*Sylvilagus floridanus*) are common, conspicuous denizens of urban environments. They are associated with human-wildlife conflict due to vegetation damage. Prior to this study, population dynamics of this species in urban environments remained largely uncharacterized. For three consecutive winters, we used classic field ecology methods (mark-recapture and mark-resight surveys) to estimate demographic parameters of rabbits in a city park in Chicago, Illinois. Rabbits occurred in densities as high as 16.3 rabbits/ha, which is comparatively high for the Midwestern United States. An annual survivorship of 30.4 ± 12.9 % SE was similar to that observed in natural environments in similar climates. This result refuted our hypothesis that urban rabbits would have higher annual survival rates than rabbits in natural settings due to food subsidies supplied by landscaping in parks. Mean distance between trap locations for rabbits trapped three or more times was 43.14 ± 30.01 m SD, suggesting that rabbits in the urban study area had smaller home ranges than rabbits in non-human-dominated habitats. This study contributes to our understanding of population dynamics of a human-wildlife conflict species in urban environments and provides useful information for managers dealing with damage caused by rabbits. The mark-resight method

employed here could be used by managers to estimate pre- and post-management population sizes of other conflict species, for example Canada geese (*Branta Canadensis*) in parks and green spaces, provided that the species is trappable, visible, and individuals have relatively small home ranges.

B. **Background**

Wildlife damage in North America costs approximately \$3 billion per year (Conover et al., 1995) and human-wildlife conflicts are on the rise (Conover and Decker, 1991) particularly in urban areas (Messmer, 2000). Herbivore damage to commercial property including crops, timber (Conover et al., 1995), and nurseries (Mason et al., 1999) contributes to these losses. Herbivores including eastern cottontail rabbits (*Sylvilagus floridanus*) (Feinstein, 2011), white-tailed deer (*Odocoileus virginianus*) (Conover et al., 1995) and Canada geese (*Branta canadensis*) (Washburn and Seamans, 2012) can damage vegetation in urban green spaces and gardens.

Recent literature on rabbit management focuses on European rabbits (*Oryctolagus cuniculus*), which have been widely introduced and are invasive (Smith and Boyer, 2008), especially in Australia (Conover, 2010; Williams et al., 2007). In Australia, European rabbits compete with livestock, cause soil erosion (Conover, 2010), damage crops, and threaten native species (Conover, 2010; Williams et al., 2007). Consequently, Australia engages in rabbit population control using poison baiting (McIlroy and Gifford, 1991; Twigg et al., 2001), immunocontraception (McLeod et al., 2007; Williams et al., 2007) and introduced diseases (Bruce and Twigg, 2005). In Great Britain, rabbits damage crops resulting in loss of £115 M per year (Smith et al., 2007) and are controlled by fumigating burrows, trapping, and electric fencing (Conover, 2010; Smith et al., 2007). In the European rabbit's native range on the Iberian Peninsula, the

species is beneficial as prey for endangered predators (Ferreira, 2012), and detrimental as an agricultural pest (Barrio, Bueno, et al., 2010; Barrio et al., 2013, 2011; Ferreira, 2012).

Relative to the European rabbit, there is a dearth of recent research on eastern cottontail rabbit management, although the species cause similar problems e.g., damage to commercial property (Conover et al., 1995; Mason et al., 1999). Like European rabbits (Letty et al., 2000), eastern cottontail rabbits are a game species and most early research on eastern cottontail rabbits focuses on this (Allen, 1938; Boland and Litvaitis, 2008; Chapman and Trethewey, 1972; Haugen, 1942; Rose, 1977), or on rabbits as disease reservoirs (Lepitzki et al., 1992; McGowan et al., 1979; McKeever et al., 1958; Peavey et al., 1997; Smith and Cheatum, 1944; Woolf et al., 1993). In the winter, snow cover limits grazing options and eastern cottontail rabbits resort to foraging on bark and woody perennials (Schwartz et al., 2002), causing damage to urban parks (e.g., Ford, 2003). Eastern cottontail rabbits increasingly colonize urban gardens (Feinstein, 2011), resulting in aesthetic and monetary damage (Hygnstrom, 2010).

The Chicago metropolitan area is home to 8.4 million people (Chicago Metropolitan Agency for Planning, 2011), contains expansive green spaces (Moskovits et al., 2004) and provides ample opportunity to study human-wildlife conflict. Long-term urban wildlife research initiatives in the area include the Cook County, Illinois, Coyote Project (Gehrt et al., 2009) and Project Squirrel (van der Merwe et al., 2005). Rabbit damage at Grant Park, a 129 ha public green space in Chicago, cost \$50,000 in a single winter and fall (Ford, 2003) and cost \$19,000 annually at our 13.4 ha study site in Chicago, as estimated by horticulture surveys.

We hypothesized that eastern cottontail rabbits inhabiting urban parks would have higher population densities than cottontails in natural areas due to higher food availabilities, as is true of brown rats (*Rattus norvegicus*) (Traweger et al., 2006) and raccoons (*Procyon lotor*) (Graser et al., 2012). We used mark-resight surveys which have previously been used for estimating population abundance of color-marked eastern cottontail rabbits (Edwards and Eberhardt, 1967). Mark-recapture would likely yield similar results, and has been used with rabbits (Woolf et al., 1993) but requires significantly more effort and resources, as animals must be captured repeatedly in a short window of time (White and Burnham, 1999).

Alternative methods for estimating rabbit (multiple species) population densities include warren counts (Palomares, 2001; Rueda et al., 2008), pellet counts (Palomares, 2001; Rueda et al., 2008), line transects (Palomares, 2001) and counts of individuals, including roadside counts (Woolf et al., 1993) and spotlight counts (Barrio, Acevedo, et al., 2010). Warren counts are not possible for eastern cottontail rabbits because they do not dig burrows (Schwartz et al., 2002) and pellet counts are unreliable (Palomares, 2001). Line transects depend on habitat type (Palomares, 2001) and in our study area, visual obstructions preclude their use. Lastly, counting individuals is labor intensive and involves extensive trapping (Palomares, 2001).

Humans in urban areas provide food for herbivores via landscaping, and therefore we expected that rabbits in our study area would have higher survival rates, as is true for Canada geese (Balkcom, 2010). Survival rates of rabbits (multiple species) have previously been determined using radio-marked animals (Cabezas et al., 2007; Woolf et al., 1993), mark recapture surveys (Rose, 1977; Williams et al., 2007), and mark resight surveys (Letty et al., 2000).

In this multi-year study, we used classic field ecology methods (mark-recapture and mark-resight surveys) to characterize demographic processes of eastern cottontail rabbits in an urban park. Our objectives were: 1) estimate population density, 2) estimate survival rates and 3) characterize movement and spatial distribution of rabbits. We sought to meet these objectives in a manner that could be applied elsewhere to study urban wildlife and inform human-wildlife conflict management.

C. **Materials and methods**

1. **Study area**

Our study area consisted of the main grounds of the Lincoln Park Zoo, Chicago, Illinois (41°55'17.25"N 87°38'0.28"W). A metal fence enclosed the property, but eastern cottontail rabbits (hereafter, rabbits) were able to pass under the fence and were observed doing so when flushed from hiding. Gardening staff continually maintained vegetation in the park, which consisted of turf, and both native and non-native ornamental shrubs and trees. Forty-one percent of the 13.4 ha property consisted of green space, defined as any non-path, non-building area that appeared qualitatively green in an aerial map. Selected trap locations were accessible to research staff, out of public view, protected from the elements on at least one side, and were distributed so as to survey the entire property.

2. **Population dynamics**

a. **Capture and mark-resight**

For three successive winters in late January to early March we live-trapped rabbits across the study area. We trapped on 840 trap-nights: 228 in 2010, 384 in 2011, and 228 in 2012. The number of traps deployed per night (mean 24.7 \pm 5.8 SD, range: 18 – 32 traps) depended on available equipment and weather. Traps

were set out in an array across the study area, and were moved at weekly intervals to reduce predation. We inferred the presence of predator species in the park using motion-triggered video cameras (Bushnell Trophy Cam HD Max Game Camera; Bushnell, Overland Park, KS), which were employed as part of another study.

We used baited 1-door traps (model #1078; Havahart, Lititz, PA) with dimensions of 61 cm × 18 cm × 18 cm. Bait was refreshed daily, and consisted of lettuce and vegetables in 2010 and 2011, and apples, timothy hay (*Phleum pratense*) and apple cider in 2012. The change in type of bait was due to the lack of snow cover and subsequent lack of food-motivation in the rabbits in 2012. The more appealing bait in 2012 achieved a comparable percentage trap success as observed in 2011 and 2010. Changing the bait did not affect comparability of our population estimates across years, as the estimates did not depend on trapping rates, but depended instead on the proportion of marked to unmarked rabbits observed in resight surveys.

Researchers wearing latex gloves and protective barrier clothing restrained unanesthetized rabbits with a cloth sack during processing. We sterilized all tagging equipment (ear tags and tag applicators) with rubbing alcohol. When a rabbit was caught for the first time, we applied individually numbered monel ear tags (model #1005-3; National Band and Tag Company, Newport, KY) to both ears (Edwards and Eberhardt, 1967; Haugen, 1942). After the first year, tags were colored with nail polish indicating year of capture to differentiate release cohorts during resight surveys.

Estimates of population size were derived from resight surveys, rather than recapture surveys, allowing us to avoid extensive recapturing. If field-readable marks can be applied, as is true for rabbits, resight surveys have many advantages over recapture surveys: they are less expensive, less invasive, and less stressful (White and

Burnham, 1999). We conducted resight surveys in the two weeks immediately following trapping during two time periods: mornings between 8:00 hours and 10:00 hours, and afternoons between 15:30 hours and 17:00 hours. At these times, rabbits were relatively inactive and we were able to detect rabbits without flushing them out, which reduced the likelihood of double counting.

During resight surveys, researchers performed walking transects along paths through the study area and counted marked and unmarked rabbits seen with the aid of binoculars. We were unable to read individually labeled ear tags from a distance and therefore we treated tagged rabbits from a given year as a release cohort based on color of ear tags. We used a double-observer approach (Borchers et al., 1998; Melville et al., 2008) to validate our resight procedure. The second observer never detected a rabbit that was missed by the first observer.

b. **Analysis**

Rabbit population size per year was estimated using the Joint Hypergeometric Estimator (JHE) as implemented in the Mark-Resight model in the program MARK (White and Burnham, 1999). JHE, a maximum likelihood estimator used to determine population abundance from mark-resight survey data, assumes all animals in the population have equal probability of resighting on all sampling occasions (White, 1996). Due to the brevity of the period in which we conducted resight surveys each year (mean 8 ± 1 day SD) we assumed a provisionally closed population for population abundance estimation. Figure 17 shows a schematic of the experimental design used for population abundance estimation.

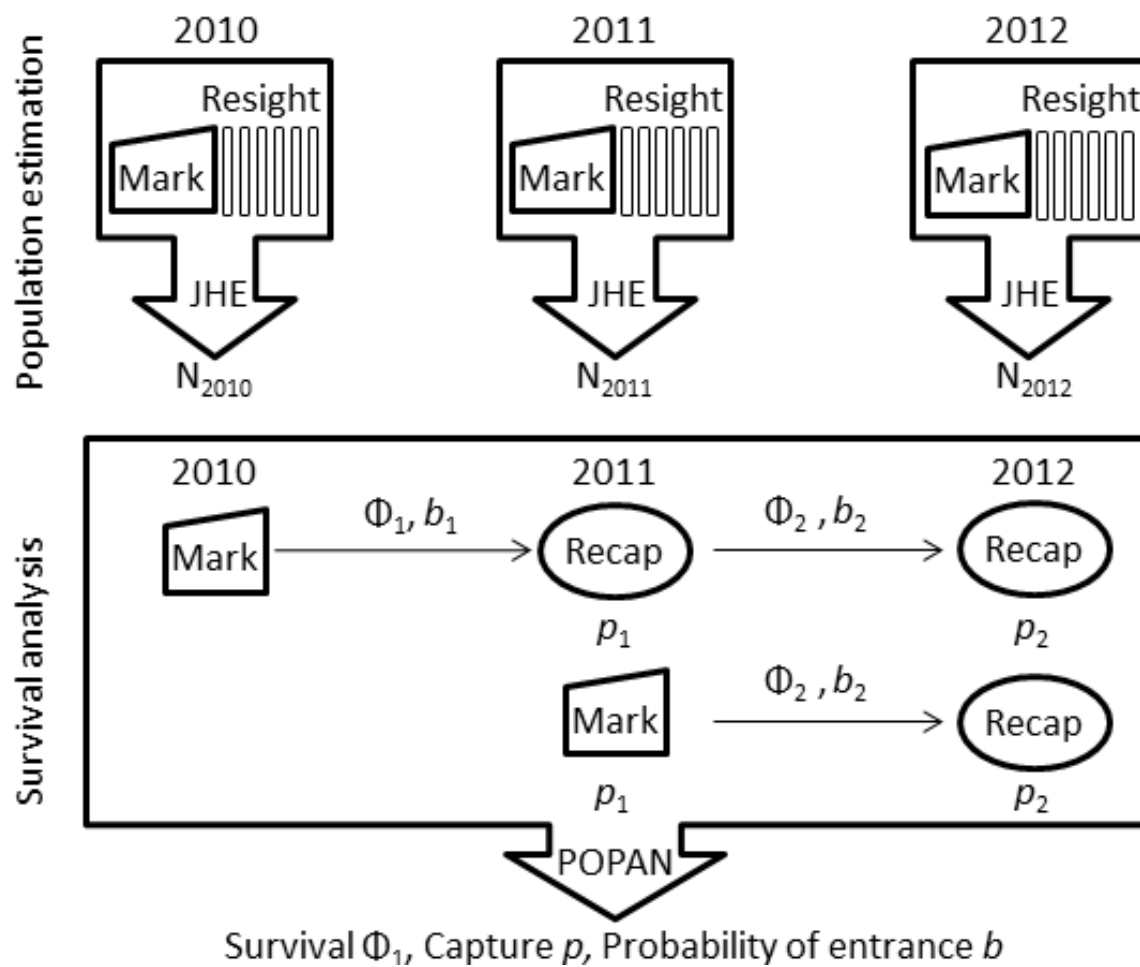


Figure 17. Schematic of experimental design for population estimation and survival analysis of rabbits in Lincoln Park.

We determined annual survival rates for urban rabbits using mark-recapture surveys in 2010, 2011 and 2012. Encounter histories for survival analysis were based on one primary sampling period per winter for each of the three winters in which we live-trapped rabbits (see process model in Figure 17). The sampling periods were 21 January to 17 February in 2010, 19 January to 4 March in 2011, and 31 January to 17 February in 2012. Each encounter history included three sampling occasions: winter 2010, winter 2011 and winter 2012. Using these encounter histories, we implemented the POPAN (POPulation ANalysis) model (Arnason and Schwarz, 1995) in the program MARK to estimate apparent survival (White and Burnham, 1999).

We assessed survival between winters, not within each sampling period. When the entire winter sampling period was considered, we made every effort to equally survey the entire property. In contrast, we periodically relocated traps within our primary sampling periods because we lacked adequate equipment to cover the entire study area concurrently. Consequently, the probability of trapping a given rabbit was unequal within the sampling period, as we were more likely to trap a given rabbit when traps were situated within the rabbit's home range. By summarizing trap nights per winter into primary sampling periods, we avoided location bias. Thus, the manner in which we formulated our recapture encounter histories both addressed our focal question of annual survival and compensated for a limitation in our study design.

We used POPAN, a model based on Jolly-Seber estimation (White and Burnham, 1999), to analyze survival. In the POPAN model, encounter histories consisted of multiple sampling occasions. At each sampling occasion, captured unmarked animals were marked with uniquely identifiable tags and any captured marked animals were recorded. The model assumed that unmarked animals were equally likely to be captured

as marked animals (White and Burnham, 1999). The proportion of marked animals that were recaptured at a given sampling occasion was a product of apparent survival (ϕ) and the probability of being captured (p), given that the animal was alive (White and Burnham, 1999).

By using POPAN, we assumed that the marked animals used for survival analysis comprised a sample taken from a super-population. Not all individuals in the super-population were expected to be trappable at any particular encounter occasion. The POPAN model was appealing because it did not assume population closure and we knew that rabbits could enter and exit the study area through the property's fence. Additionally, we expected that over the course of the three-year study, individuals were born into the population. The POPAN model included a parameter for probability of entrance (PENT; b) in addition to apparent survival (ϕ) and probability of capture (p). We tested a suite of six POPAN models in MARK varying 1) designation of parameters as variable over time or constant, 2) link functions for apparent survival (ϕ) and probability of capture (p), and 3) method of variance estimation (Table II). The most parsimonious model given the encounter histories was determined by corrected Akaike information criterion (Table II). White and Burnham (1999) advocate use of corrected Akaike information criterion for determining the model that best explains variation in the data using the minimum number of parameters. We used \hat{c} to assess overdispersion, where $\hat{c} > 1$ reflected lack of fit (White and Burnham, 1999).

TABLE II
COMPETING RECAPTURE MODELS FOR RABBITS IN AN URBAN PARK

Model ^a	Parameters		ΔAIC_c	Var. ^b
	Constant	Variable by time		
$\phi(t)p(t)b(t)$		Surv, Capt, PENT	0	2 nd Part
$\phi(.)p(.)b(t)$	Surv, Capt	PENT	3.4	2 nd Part
$\phi(t)p(t)b(t)$		Surv, Capt, PENT	6.6	Hessian
$\phi(.)p(t)b(.)$	Surv, PENT	Capt	110337	2 nd Part
$\phi(t)p(.)b(.)$	Capt, PENT	Surv	110337	2 nd Part
$\phi(.)p(.)b(.)$	Surv, Capt, PENT		110339	2 nd Part

^a ϕ = survival (Surv), p = capture (Capt), b = probability of entrance (PENT).

^b Var. = variance estimation method.

Each time a rabbit was captured, it was weighed with a spring scale accurate to 0.1 kg. To estimate body mass for each rabbit, masses for the same rabbit over multiple captures in the same winter were averaged. The period over which masses for each rabbit per year were averaged comprised relatively short time intervals: 21 January to 17 February in 2010, 19 January to 4 March in 2011, and 31 January to 17 February in 2012. Due to the brevity of the sampling window, we did not expect that averaging the masses taken from repeated measurements on individuals masked any actual change in size. Averaging reduces potential errors from misreading the spring scale or from double counting individuals when estimating the overall mean mass of the population. Mean masses of individuals were averaged to determine the overall mean mass.

Gender of live-trapped rabbits was not determined due to difficulties in sexing rabbits in the winter when the testes of male rabbits were not reliably detectable (Haugen, 1942; Petrides, 1951). Utilizing previously published data (Boyd and Henry, 1991), we attempted to assign age-classes to rabbits according to an established weight classification scheme. However, in our study system, known adult rabbits (rabbits that were captured in multiple years) were misclassified as juveniles at an unacceptable rate (86%) using this scheme. Without a tool to reliably assess age, we do not report age-classes of rabbits.

3. **Spatial variability in activity**

We used spatial variability in capture rate as an index of spatial use by the population (Hill, 2005) across the study area. Trap locations at which we caught rabbits on at least one occasion, and for which we had data on three or four occasions were included in the spatial analysis. All other trap locations, for example trap locations where we trapped on only one occasion, were excluded from the spatial analysis. The capture rate for each sampled trap location was calculated as incidents of capture divided by number of sampling occasions. Bait and trap odors may influence capture rate (Boitani and Fuller, 2000). To minimize this potential bias, we used the same bait across the study area.

We performed kriging in the ArcGIS 10.1 extension Spatial Analyst (Environmental Systems Research Institute, Redlands, CA) to interpolate capture rate from sampled locations across the study area. We overlaid this visualization of capture rate on top of an aerial map of the study area obtained from the Illinois Natural Resources Geospatial Data Clearing House (University of Illinois at Urbana-Champaign, 2004).

D. **Results**

1. **Population dynamics**

a. **Trapping and mark-resight surveys**

We live-trapped and marked 166 rabbits and recaptured rabbits 163 times. We trapped 78 rabbits and had 39 recaptures in 2010, 38 rabbits and 56 recaptures in 2011, and 50 rabbits and 68 recaptures in 2012. In a study assessing techniques for maximizing capture rate, Young and Henke (1999) achieved their highest capture rate of 29.6% using urine as bait. In comparison, we achieved high rates of capture (Table III): 51.7% in 2010, 24.5% in 2011, and 51.3% 2012.

TABLE III
RABBIT CAPTURE RATE BY DATE

Sampling Occasion	Traps	Capture rate ^a
21 Jan, 2010	24	0.083
26 Jan, 2010	24	0.417
27 Jan, 2010	24	0.458
28 Jan, 2010	18	0.667
2 Feb, 2010	24	0.500
3 Feb, 2010	24	0.458
4 Feb, 2010	24	0.708
9 Feb, 2010	20	0.650
16 Feb, 2010	22	0.727
17 Feb, 2010	24	0.583
19 Jan, 2011	32	0.156
20 Jan, 2011	32	0.187
15 Feb, 2011	32	0.125
16 Feb, 2011	32	0.156
17 Feb, 2011	32	0.250
18 Feb, 2011	32	0.250
23 Feb, 2011	32	0.218
24 Feb, 2011	32	0.281
1 Mar, 2011	32	0.281
2 Mar, 2011	32	0.375
3 Mar, 2011	32	0.281
4 Mar, 2011	32	0.375
31 Jan, 2012	19	0.368
1 Feb, 2012	19	0.368
2 Feb, 2012	19	0.632
3 Feb, 2012	19	0.737
7 Feb, 2012	19	0.526
8 Feb, 2012	19	0.368
9 Feb, 2012	19	0.421
10 Feb, 2012	19	0.580
14 Feb, 2012	19	0.474
15 Feb, 2012	19	0.421
16 Feb, 2012	19	0.684
17 Feb, 2012	19	0.579

^a Incidents of capture divided by number of sampling occasions.

To estimate rabbit density per habitable area, we divided population estimates based on resight surveys (Table IV) by the study area, excluding buildings and bodies of water. Uninhabitable areas comprised 2.5 ha of the 13.4 ha property. Population density per habitable area was 16.3 rabbits/ha in 2010, 10.0 rabbits/ha in 2011 and 9.4 rabbits/ha in 2012 (Table V).

TABLE IV
RABBIT RESIGHT SURVEY OUTCOMES

Sampling Occasion	Marked	Observed	Observed \cap Marked
25 Feb 2010	76	45	22
26 Feb 2010	76	60	27
1 Mar 2010	76	39	16
2 Mar 2010	76	42	19
3 Mar 2010	76	54	21
4 Mar 2010	76	59	20
5 Mar 2010	76	62	28
7 March 2011	41	21	9
8 Mar 2011	41	21	8
9 Mar 2011	41	16	5
9 Mar 2011	41	30	10
10 Mar 2011	41	28	9
11 Mar 2011	41	24	8
14 Mar 2011	41	25	11
27 Feb 2012	57	11	4
28 Feb 2012	57	18	7
29 Feb 2012	57	16	10
1 Mar 2012	57	16	9
2 Mar 2012	57	19	10
5 Mar 2012	57	16	9
6 Mar 2012	57	16	12
7 Mar 2012	57	20	12

TABLE V
RABBIT POPULATION DYNAMICS BY YEAR

	Year: 2010	2011	2012
Population estimate (rabbits)	178 rabbits	109	102
SE	± 9.07	± 9.73	± 7.07
95% CI	$162 \leq x \leq 198$	$93 \leq x \leq 131$	$90 \leq x \leq 118$
Density (rabbits/ha)	16.3	10.0	9.4
Mean body mass (kg \pm SD)		1.15 ± 0.14	1.21 ± 0.16
Annual survival (% \pm SE)		30.4 ± 12.9^a	

^a Estimate applies to the time period between sampling in 2010 and sampling in 2011.

We observed five mortalities, all of which were likely caused by raccoons as indicated by raccoon prints. Raccoon predation on trapped animals is a common problem in urban areas where raccoon densities are high (Prange et al., 2003). To reduce such mortality, we moved traps frequently.

b. **Survival**

We estimated annual apparent survival as $30.4 \pm 12.9\%$ SE and capture probability as $56.6 \pm 20.8\%$ SE between 2010 and 2011 using the POPAN model in the program MARK (Table V). In the most parsimonious implementation of the POPAN model as determined by Akaike information criterion, \hat{c} was equal to 1, indicating that data were not overdispersed (White and Burnham, 1999). Following the method and notation of White and Burnham (1999), mark-recapture models including POPAN operate on the premise that proportion of marked animals recaptured at a given

sampling occasion, return rate (R), is a product of apparent survival (ϕ) and probability of capture given the animal is alive (p).

$$R = \phi \times p$$

It follows that the estimate for annual apparent survival (ϕ) from the POPAN model could be compared to an estimate derived from the observed return rate, to assess whether the two are roughly in agreement. This was possible because in addition to observed return rates, we had population size estimates generated using resight surveys and the Joint Hypergeometric Estimator (JHE). In 2010, 78 rabbits were trapped and 11 (14.1%) were recaptured the following year. On the basis of resight surveys, the population estimate from 2011 was 109 rabbits. The probability of capture for 2011 was 34.9%, as we captured and marked a total of 38 rabbits in 2011, out of a total of 109 rabbits estimated to be in the population. We divided the observed return rate of 14.1% by the 34.9% probability of capture to estimate apparent survival as 40.4%. This crude secondary estimate fell within one standard error of the survival estimate obtained with POPAN, suggesting our annual survival estimate was reasonable.

c. **Body mass**

Mean body mass of rabbits was 1.18 ± 0.15 kg SD, ranging from 0.8 kg to 1.6 kg. We used a 2-tailed t-test to compare masses of rabbits in 2011 and 2012 (Table V). Body masses in 2012 were greater than in 2011 ($P = 0.02$, $df = 94$).

2. **Spatial characteristics**

Mean distance between recaptures for rabbits captured three or more times was 43.14 ± 30.01 m SD, $n = 41$. To illustrate spatial variation in capture rate across our study area, we performed kriging in the ArcGIS 10.1 extension Spatial Analyst (Environmental Systems Research Institute, Redlands, CA). We used the output to interpolate a map of capture rate across the study area (Figure 18). Overall, we achieved high capture rates: 51.7% in 2010, 24.5% in 2011, and 51.3% in 2012.

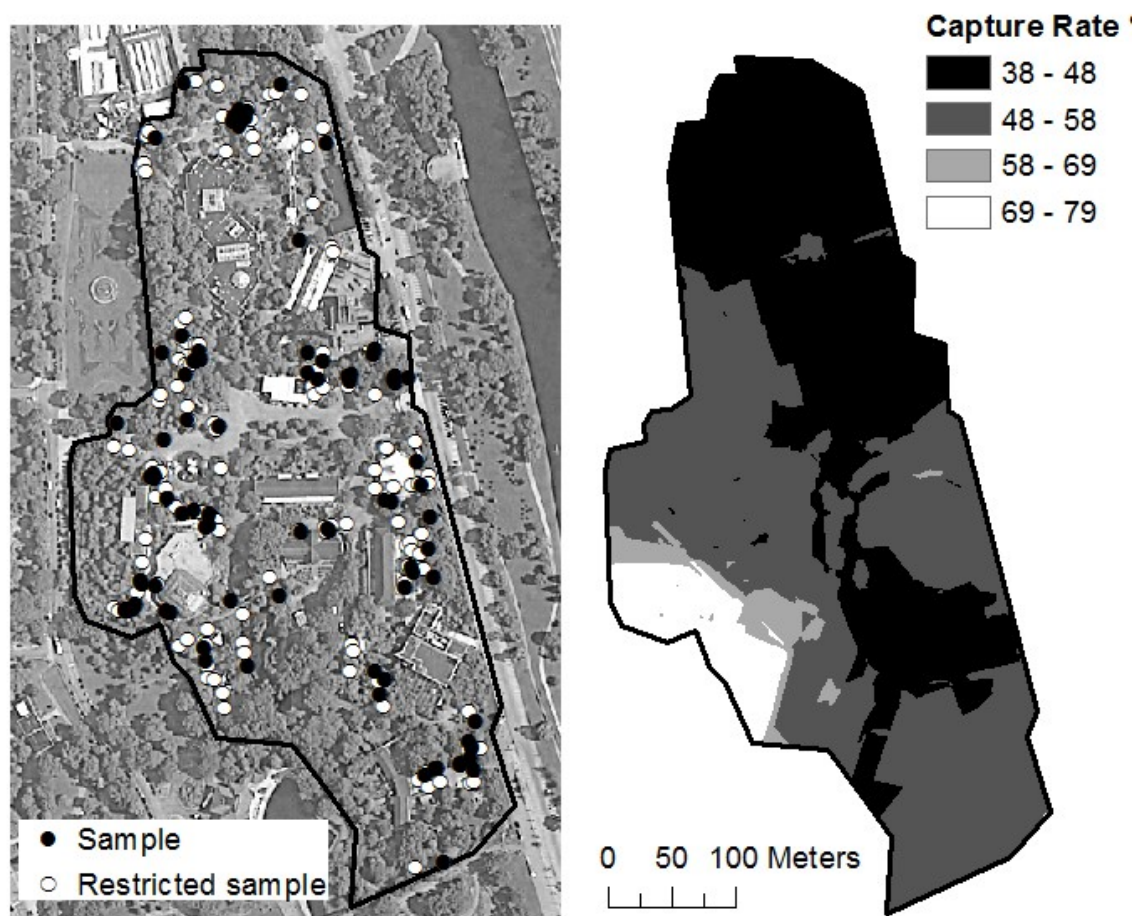


Figure 18. Map of the study area with trap locations and interpolated capture rates of rabbits in Lincoln Park.

E. **Discussion**

This comprehensive study quantitatively investigated population dynamics and spatial habitat use in eastern cottontail rabbits in an urban park setting, the Lincoln Park Zoo in Chicago, Illinois. The methods used here could be applied to determine rabbit population density in a range of urban, suburban, and even rural situations in which rabbit damage to gardens or agricultural crops is of concern. Rabbits in the study area occurred in dense populations: 9.4 to 16.3 rabbits/ha. Annual apparent survival in the study population was $30.4 \pm 12.9\%$ SE and the mean body mass was 1.18 ± 0.15 kg SD, both of which are similar to populations in natural habitats in the same season. Mean distance between capture locations for rabbits trapped three or more times was only 43.14 m, suggesting that the rabbits in our study area covered a smaller area than rabbits in undeveloped habitats. Spatial distribution of capture rate across the study area (Figure 18) showed fine scale variation, supporting the generalization that urbanization can heighten spatial variation in abundance (Marchetti et al., 2006; Trubl et al., 2012).

1. **Population dynamics**

a. **Population density**

The population density in our study site was 16.3 rabbits/ha in 2010, 10.0 rabbits/ha in 2011, and 9.4 rabbits/ha in 2012 (Table V). For comparison, in an undeveloped habitat in Michigan in the fall, rabbit densities were 0.08-0.35 rabbits/ha (Haugen, 1942). In an agroecosystem in northern Italy (37.1% cropland), density of eastern cottontail rabbits was 0.54 rabbits/ha, determined by spotlight counts along transects (Rosin et al., 2010). Edwards and Eberhardt (1967) report densities of 1.2

rabbits/ha and 1.6 rabbits/ha. Density estimated for rabbits in the playa lake basins of the Texas panhandle matched more closely with our own: 8.2 rabbits/ha and 11.6 rabbits/ha (Scribner, 2012). Hence, for the Midwestern United States, the density of rabbits in our study area was comparatively high.

b. **Survival**

Annual apparent survival of adult rabbits in our system was $30.4 \pm 12.9\%$ SE (Table V), which is similar to annual survival of populations in natural areas. Haugen (1942) determined that in undeveloped settings, approximately 20% of juvenile rabbits survived until the fall in the year of their birth. Rose (1977) reported that annual survival of adult rabbits was 25% in populations without hunting. By following radio-collared rabbits at Cape Cod National Seashore in Massachusetts for an 8.5 month period in 2006 between hunting seasons, Boland and Litvaitis (2008) determined that survival rates of hunted and non-hunted populations were similar: 33% and 40% survival respectively.

We recaptured fewer rabbits between 2011 and 2012 than between 2010 and 2011; 14.1% of tagged rabbits were recaptured the following year in 2010, but only 6.1% were recaptured the following year in 2011. This decline in return rate may have been due to the harsh winter in 2011, as harsh winter conditions reduce survival in eastern cottontail rabbits (Boland and Litvaitis, 2008). We only trapped rabbits in the winter when capture rate is greatest (Chapman and Trethewey, 1972) and therefore we did not detect urban sources of juvenile mortality such as destruction of nests by mowers (Schwartz et al., 2002). Survival in our study system may also have been reduced by coyote predation. Several coyotes regularly hunted in the park between 2010 and 2012, evidenced by 1) remains of predated rabbits in association with coyote

footprints, 2) photos of multiple coyotes, distinguishable from one another by color, size and field-tags, recorded by motion-triggered video cameras, and 3) sightings of coyotes by park employees and visitors.

c. **Body mass**

Eastern cottontail rabbits show range-wide variation in size in agreement with Bergmann's rule (Olcott and Barry, 2000). As per Bergmann's rule (McNab, 2002), body size increases with increasing latitude and decreasing temperature (Olcott and Barry, 2000). Eastern cottontail rabbits also show variation in mass by season and sex, with females weighing more than males (Haugen, 1942). Haugen (1942) determined that female rabbits in the winter weighed 1.36 kg, and males weighed 1.29 kg, similar to the mean value observed in our study system:

1.18 ± 0.15 kg SD.

Body masses of rabbits in 2012 were greater than in 2011. Additionally, year influenced frequency of weight categories as the mode shifted upwards from 1.1 kg in 2011 ($n = 16$) to 1.2 kg in 2012 ($n = 18$). The shift upward in body mass from 2011 to 2012 (Table V) may have resulted from extreme weather. In 2011, Chicago experienced the third largest blizzard on record with 51 cm of snow (Chicago Weather Center, 2011). In contrast, 2012 was one of the mildest winters on record. Body mass of rabbits has been shown to decline as a result of stormy winter weather (Boland and Litvaitis, 2008; Haugen, 1942).

2. **Spatial characteristics**

a. **Distance**

Mean distance between trap locations for all rabbits trapped three or more times was 43.14 m, suggesting that the rabbits in our study area covered

smaller areas than rabbits in undeveloped habitats. The small distance between trap locations was not due to lack of possibilities, as we trapped at locations throughout the 13.4 ha park. In comparison, rabbits in undeveloped habitats have home ranges of 0.4-2.0 ha (Schwartz et al., 2002). In a study design similar to our own in the playa basins of the Texas panhandle, rabbits that were trapped two or more times during 7-10 day trapping periods in February traveled mean distances of 96.4 m and 95.6 m (Scribner, 2012).

b. **Distribution**

Capture rate mapped across the study area showed clusters of sampling locations with high capture rates (Figure 18). The 0.92 ha area of high capture rate (indicated on the map in Figure 18 as the quarter equal interval polygon with capture rate of 69-79%) included a service yard behind a building, adjacent to a fenced woodland habitat. The map of capture rate suggested fine scale variation in population abundance that supported the generalization that urban areas can heighten spatial variation, as has been documented in black widows (*Latrodectus Hesperus*) (Trubl et al., 2012) and some fish species (Marchetti et al., 2006).

We suggest using giving-up densities (GUDs) to investigate the unevenness of population abundance suggested by our interpolated map of capture rate (Abu Baker and Brown, 2009; Brown, 1988). Abu Baker and Brown (2009) used GUDs to characterize the response of cottontail rabbits to resource patch characteristics including substrate depth and prey richness (Abu Baker and Brown, 2009). Predation risk also affects giving up densities (Brown, 1988) as foragers facing increased predation risk may react by increasing vigilance behavior at the expense of foraging. Therefore, giving up densities increase (more food is left behind in the patch) with increased predation

risk. If rabbits perceived the 0.92 ha area of high capture rate, which included a service yard and associated woodland habitat, as being particularly safe, this perception could be assessed using GUDs.

3. **Implications for rabbit management in urban landscapes**

Little has been formally studied about urban rabbits, with a noteworthy exception: Abu Baker and Brown (2009). However, Abu Baker and Brown (2009) focused exclusively on foraging behavior. Herein, we expand the knowledge base of urban wildlife population dynamics by documenting the use of visual mark-resight surveys to obtain precise population estimates for rabbits in an urban setting. This method could be used by managers to estimate pre- and post-management population sizes of rabbits or other conflict species in parks and green spaces. Mark-recapture would likely yield similar results but requires significantly more effort and resources (White and Burnham, 1999).

Mark-resight allowed us to obtain a rabbit population estimate with adequate precision to theoretically inform management. This technique, paired with damage surveys, could be used to determine the relationship between population size and vegetative damage. Reduction in the number or density of a nuisance species is a common response to human-wildlife conflict (Messmer, 2009), but without data supporting the relationship between population size and damage, efforts to reduce population size may not meet management objectives. Also, removal of rabbits may be complicated in high density areas, because adjacent areas may provide a source for rabbits following removal (Conover, 2010). Notwithstanding the difficulties associated with removal of rabbits, if population size and damage are correlated, management

programs with the objective of ameliorating vegetative damage caused by rabbits should focus on reducing population size.

This research adds to a growing body of knowledge about the function of urban ecosystems, and the role of one of its most commonly encountered urban wildlife inhabitants, the cottontail rabbit. While there is an increasing interest in urban wildlife (Magle et al., 2012), information on this common and conspicuous species is lacking. The chief objective of this research was to provide background information that would inform sound management decisions. The mark-resight method employed here could be used by managers to estimate pre- and post-management population sizes of conflict species in parks and green spaces, e.g., Canada geese, provided that the species is trappable, visible, and individuals have relatively small home ranges. This type of small-scale research is an example of applying scientific rigor to improve understanding of a human-wildlife conflict and has the potential to serve as a model for institutions that face herbivore damage-management challenges.

F. **Acknowledgments**

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IV. HABITAT SELECTION OF BLACK-CROWNED NIGHT-HERONS

This research was published in the following article:

Hunt, V. M.: Reproductive Success and Habitat Selection in Black-crowned Night-Herons (*Nycticorax nycticorax*) in a City Park. Am. Midl. Nat.; in press.

A. **Abstract**

Black-Crowned Night-Herons (BCNH; *Nycticorax nycticorax*) increasingly colonize urban areas, demonstrating they consider the value of such habitat to outweigh the risks. However, it is unclear if cities support reproductively successful populations of BCNH. To begin to address this question, I evaluated if a park in Chicago, Illinois, provided suitable breeding habitat or was an ecological trap for a colony of approximately 400 BCNH. Nest densities were 217 nests/ha in 2010 and 315 nests/ha in 2011, which were higher than nest densities observed in North American BCNH colonies in natural habitats. Ratios of young to active nests were 1.22 in 2010 and 0.76 in 2011, similar to ratios observed in nearby BCNH colonies. Within the park, BCNH selected between two neighboring habitat patches. Logistic regression was used to predict habitat patch selection as a function of colony size and year. In the model the probability of selecting a larger, more exposed habitat patch versus a smaller, more secluded habitat patch, increased with colony size. This trend in habitat patch selection demonstrated behavioral flexibility which may have facilitated successful colonization of a human-modified landscape. My findings support the conclusion that in 2010 and 2011, an urban park in Chicago supported a locally endangered BCNH population and was not an ecological trap.

B. **Background**

As urbanization progresses it becomes increasingly important to understand the role of human-modified landscapes as wildlife habitat (Dearborn and Kark, 2010). Some wildlife populations thrive in urban areas, but for other populations urban areas are ecological traps in which wildlife choose low-quality habitat over high-quality habitat based on faulty or incomplete information (Battin, 2004). Black-Crowned Night-Herons (BCNH; *Nycticorax nycticorax*) increasingly occupy urban areas (e.g., Kelly et al. 2006) but it is unclear if such areas provide suitable breeding habitats because anthropogenic disturbance potentially disrupts BCNH breeding (Parsons and Burger, 1982; Tremblay and Ellison, 1979). Therefore, it is unknown whether BCNH colonies which select urban areas for breeding have found refugia, or have unwittingly fallen into ecological traps.

BCNH have colonized human-modified landscapes including cities and suburbs for decades (Hothem and Hatch, 2004; Kelly et al., 2007). For example a suburban colony in Penngrove, California, has been active since the 1930s (Kelly et al., 2007). Other suburban colonies in California include West 9th St. of Santa Rosa and the Napa State Hospital campus (Kelly et al., 2007). BCNH also colonized Alcatraz Island in California, a popular tourist attraction with more than a million visitors per year (Hothem and Hatch, 2004; Kelly et al., 2007). Examples of urban colonies can be found on the East Coast of the United States as well; BCNH colonized an urban estuary in New York Harbor (Craig et al., 2012) and forage on and around Staten Island, New York (Bernick, 2004). Erwin et al. (1991) describe a colony of more than 300 BCNH pairs in Baltimore Harbor, Maryland, and posit that the colony benefits from proximity to urban lights which attract fish. Some colonies of egrets and herons (family *Ardeidae*) including BCNH become so successful in urban areas that they are considered nuisances because of

their odors, guano, loud vocalizations, and the perception they pose a health risk (Grant and Watson, 1995; Parkes et al., 2012).

BCNH choose to colonize urban areas in a variety of scenarios but such areas may be unsuitable for breeding. Evidence suggests urban areas become ecological traps for some BCNH colonies when colony abandonments result from nest tree removal by private residents in suburbs (Kelly et al., 2006), similar to an oft-cited ecological trap in which grassland bird nests are mowed over (Battin, 2004; Best, 1986; Schlaepfer et al., 2002; Sih et al., 2011). Even in the absence of direct management against breeding colonies, BCNH are susceptible to human disturbance which can result in nest abandonment, nest failure, behavioral changes in nestlings, young mortality, and inhibition of egg laying (Kelly et al., 2007; Parsons and Burger, 1982; Tremblay and Ellison, 1979). Fernández-Juricic et al. (2007) determined that nestling BCNH increase vigilance and decrease maintenance behaviors such as grooming in response to disturbance by pedestrians and boats. Consumption of environmental contaminants is hazardous to BCNH foraging in industrialized areas (Levenson and Schaeffer, 2010; Newman et al., 2007; Padula et al., 2010). In Illinois where this study occurred, the selection of urban areas by BCNH may in part reflect limited alternatives. BCNH have been listed as endangered in Illinois since 1977 based on small population size, a history of decline, and extensive wetland habitat loss (Illinois Natural History Survey and Illinois Department of Natural Resources, 2011; Illinois Endangered Species Protection Board, 2011).

Assessment of behavioral flexibility can provide insight into why some wildlife populations thrive under human induced rapid environmental change (HIREC) including urbanization, and others do not (Sih et al., 2011). Generally the more behavioral

flexibility exhibited by a wildlife population, the better their chances of initially surviving HIREC, and of subsequently adapting to novel conditions (Sih et al., 2011). For example, urban Northern Goshawks (*Accipiter gentilis*), which have successfully colonized cities throughout Europe, demonstrate specialized hunting techniques that use novel features in the urban environment, such as hunting from perches on television aerials (Rutz, 2006). Urban Northern Goshawks also display flexible habitat use that includes both patches of green space and built-up habitat (Rutz, 2006). Northern Goshawks spend most of their time in green spaces (parks) where they nest and make frequent hunting forays into surrounding built-up habitat (Rutz, 2006).

In this article, my objective was to conduct a quantitative assessment of reproductive success and habitat selection and use this assessment to consider whether or not Lincoln Park in Chicago, Illinois, was an ecological trap for a breeding colony of BCNH. To this end, the results of regular monitoring efforts were used to: (1) determine how reproduction in the colony compared with colonies in natural habitats, and (2) assess behavioral flexibility in terms of habitat patch selection in an urban park.

C. **Methods**

1. **Study area**

The study took place in Lincoln Park, Chicago, Illinois (41°55'1.95"N, - 87°37'56.12"W). Lincoln Park contains 485 ha of landscaped, public-use park habitat. The park is located 4 km north of the Chicago Loop, the downtown business district (Figure 19). Human use of the park is high throughout the year, particularly from April to August when thousands of people visit and attend events including concerts, fairs, organized picnics, and carnivals. For example multiple charity events for cancer

awareness co-occurred with this study, each of which brought more than a thousand participants to Lincoln Park (e.g., Pancreatic Cancer Action Network, 2010).

The study area consisted of two distinct habitat patches in Lincoln Park: a small 0.18 ha grove of several trees in a pond (hereafter the grove) and a 0.67 ha tree-lined avenue located 40 m south of the pond (hereafter the avenue). Figure 19 illustrates the spatial arrangement of the two habitat patches using an aerial map of the study area obtained from the Illinois Natural Resources Geospatial Data Clearing House (University of Illinois at Urbana-Champaign, 2011).



Figure 19. Map of study area showing two Black-crowned Night-Heron habitat patches (avenue and grove) in Lincoln Park, Illinois, in 2011.

The circumstances of the grove changed over the course of the study due to restoration efforts which involved draining (November 2008) and refilling the pond (summer 2011), and stocking the pond with fish (July 2011). The grove and drained pond were fenced off from the public in 2009 and 2010 while the pond was empty. Wildlife are increasingly challenged to adapt to rapid environmental changes caused by humans (Sih et al., 2011) and the changes that occurred in Lincoln Park are prime examples. Furthermore some restoration efforts unintentionally become ecological traps (Robertson et al., 2013). Thus restoration efforts in Lincoln Park created an opportunity to observe BNCH responses to HIREC, as well as to anthropogenic disturbance in general.

The grove habitat patch contained linden (*Tilia americana*), ash (*Fraxinus americana*), and white birch trees (*Betula papyrifera*). Although many small saplings less than 3 m tall grew in the grove, it was estimated that only 7 trees were sturdy enough to be selected by the BCNH to support BCNH nests. The grove's overgrown understory included buttonbush (*Cephalanthus occidentalis*), blackhaw (*Viburnum prunifolium*), red dogwood (*Cornus sericea*), and riverbank grape (*Vitis riparia*). Understory characteristics of BCNH breeding areas are important because undergrowth can harbor and conceal predators (Baker et al., 2015). BCNH in Lincoln Park in 2007-2009 nested in the grove, therefore restoration of the pond did not result in immediate relocation of the colony.

South of the grove, the avenue habitat patch was characterized by approximately 50 regularly spaced ash and linden trees. A popular public path bisected the avenue and mowed turf grass grew beside the path. There was no understory in the avenue. BCNH were never observed nesting in the avenue before 2010.

Motion-triggered wildlife cameras (Bushnell Trophy Cam HD Max Game Camera; Bushnell, Overland Park, Kansas) were used to determine which species of mammalian predators occurred in the study area. Cameras revealed raccoons (*Procyon lotor*), coyotes (*Canis latrans*), and foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*). Raccoons and coyotes occur in high densities in the Chicago region (Gehrt et al., 2010; Prange et al., 2003). Additionally, domestic dogs (*Canis lupus familiaris*) and cats (*Felis catus*) frequented the park, often unattended by their owners. Aerial predators including Peregrine Falcons (*Falco peregrinus*), Cooper's Hawks (*Accipiter cooperii*), American Crows (*Corvus brachyrhynchos*), and gulls (family *Laridae*) were observed during the BCNH breeding season. On one occasion a Ring-billed Gull (*Larus delawarensis*) was observed eating a BCNH chick in the avenue in 2010; this was the only direct observation of predation in the study area.

2. **Censuses**

I conducted 192 censuses: 113 in 2010 and 79 in 2011. During each census the number of BCNH in three age classes (adults, juveniles greater than 1-year-old, and young born in the concurrent breeding season), locations of BCNH (grove, avenue, or other), number of active (occupied) nests, and number of trees containing active nests were recorded.

With assistance from three trained observers, I began daily censuses when adult BCNH arrived at the park (2 April 2010 and 30 March 2011) and continued until all young had dispersed (20 September 2010 and 12 August 2011). Censuses were taken from the ground using binoculars, beginning 2-3 hours after sunrise (Hoeftler, 1980; Ralph et al., 1981). Censuses were unconstrained by time, requiring up to 2 hours when the population was at its peak. Where birds occur at high density, such as in BCNH

colonies, birds are not necessarily detected in the earlier portions of such censuses and total time spent conducting censuses is important for detecting all birds (Slater, 1994).

During each census, I or another trained observer walked the entire way around the pond which contained the grove habitat patch, and down and around the complete length of the avenue habitat patch. A boardwalk allowed me to census the grove from a distance of less than 100 m from three cardinal directions: north, east and south (Figure 19). In the avenue I was able to observe from directly beneath nest trees and therefore viewed the nests from a distance determined by the nest height, which I estimated to be approximately 10 m in most cases. Movement of BCNH during censuses was minimal and consisted primarily of nest building and courtship. To avoid double counting I did not count BCNH that startled and flew into parts of the colony that had not yet been surveyed (Levengood et al., 2005).

3. **Analysis of reproductive success**

Peak abundance of active nests can be reliably determined from a single count conducted during peak nesting season because of the conspicuous nature of active BCNH nests (Kelly et al., 2007). The nests are conspicuous for two main reasons. First, nests are active for long durations because BCNH incubate eggs for approximately 24 days (Levengood et al., 2005) and nestlings remain in the nest for several weeks after hatching. Second, BCNH deposit copious quantities of guano and prey items under active nests (Bent, 1963; Kelly et al., 2006). In Lincoln Park, BCNH also deposited egg shells, prey items, and sticks beneath active nests. BCNH young are loud and parents are frequently observed actively feeding hatchlings, making active nests all the more obvious (Kelly et al., 2006). I counted active nests daily and was confident I determined the peak abundance because of the conspicuous nature of the nests. Active nests

included all nests occupied by adult or young BCNH. Density of active nests was determined by dividing the peak abundance of active nests by spatial area of the associated habitat patch (0.18 ha for the grove and 0.67 ha for the avenue).

The ratio of young to active nests, or young to nesting pairs, is frequently used to quantify reproductive success in colonial birds including BCNH (e.g., Tremblay and Ellison, 1979; Hoefler, 1980; Crouch et al., 2002; Hothem and Hatch, 2004; Levensgood et al., 2005; Kelly et al., 2007). However, there is no commonly accepted definition of young. Young may include eggs, nestlings and fledglings (Crouch et al., 2002), or it may only include fledglings of a certain age, e.g., 7 days (Kelly et al., 2007), 15 days (Levensgood et al., 2005), 28 days (Tremblay and Ellison, 1979), or 35 days (Hoefler, 1980). In this study young were counted as soon as they were visible from the ground, therefore my definition of young included fledglings and nestlings. Nestlings fledge at approximately 2 weeks of age and attain flight at around 6 weeks of age (Levensgood et al., 2005).

To estimate the number of young produced by the colony, I used the peak abundance of young as determined by daily censuses. This peak count of young was actually the minimum possible produced by the colony; the count excluded young that died before the peak abundance census and young born after the peak abundance census. Young were unlikely to have dispersed before the peak abundance censuses on 14 June 2010 and 8 June 2011 because BCNH disperse at approximately 58 days of age (Levensgood et al., 2005) and peak abundances of young occurred less than 58 days after the first young hatched.

Because of the endangered status of BCNH in Illinois and under advisement of the Illinois Department of Natural Resources observation methods involving touching

BCNH (e.g., banding) were avoided (Maggie Cole, pers. comm.). I was unable to use the Mayfield Method to determine nest success or similar methods involving following the fate of specific nests (Mayfield, 1975) because eggs in the nest could not be observed. BCNH in Lincoln Park nested approximately 10 m up and were only viewable from the ground. I did not have equipment necessary to view or photograph nests from above; therefore, I could not record the fate of specific eggs. Use of hydraulic lift vehicles (Crouch et al., 2002) should be considered in future study efforts.

4. **Fine-scale habitat patch selection**

The close proximity of two habitat patches (grove and avenue) and my ability to census the entire BCNH colony daily presented an opportunity to investigate whether the colony exhibited behavioral flexibility in terms of fine-scale habitat patch selection in response to fluctuations in colony size. If BCNH were to exhibit behavioral flexibility in terms of habitat patch selection, this was of interest because it may have aided the colony in adapting to urban living (Sih et al., 2012).

To determine the effect of colony size on habitat patch selection, I used logistic regression wherein the habitat patch selection of an individual BCNH was the binary dependent variable of interest. Habitat patch selection was determined for the two mutually exclusive habitat patches (avenue and grove), where habitat patch referred to the cluster of trees occupied by an adult BCNH during a given census. Habitat patch selection was determined for each censused BCNH in the subset of censuses collected prior to and including the peak population censuses. Therefore, census dates included were 2 April 2010 to 16 June 2010 and 30 March 2011 to 10 May 2011, which included 43 censuses in 2010 and 30 in 2011. These censuses represented 5,314 habitat patch selections by BCNH in 2010 and 3,195 in 2011. I restricted censuses taken after the

population peaks because at that time BCNH migrated away from the study area and I could no longer determine their habitat patch selections. Censuses taken in 2010 for the approximately 2-week period before I realized BCNH were selecting the avenue habitat patch and began conducting censuses there were also restricted (Figure 20).

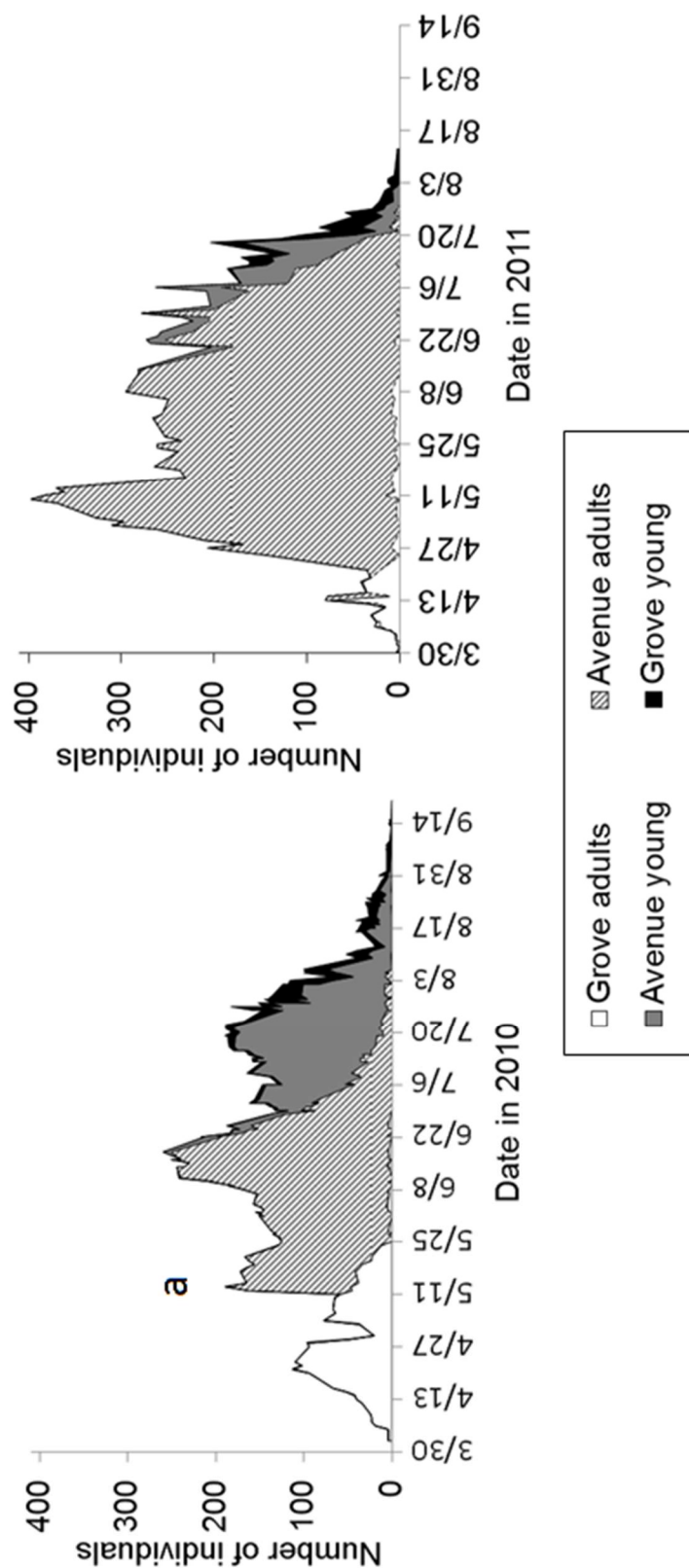


Figure 20. Stacked area counts of adult and young Black-Crowned Night-Herons at two habitat patches (avenue and grove) in Lincoln Park, Illinois. The left panel shows counts in 2010 from arrival on 2 April 2010 to departure on 20 September 2010. The right panel shows counts in 2011 from arrival on 30 March 2011 to departure on 12 August 2011.

^a The first census in the avenue in 2010.

Two predictor variables in the logistic regression were included. The first predictor was colony size (n_{colony}), defined as the number of adult BCNH in the colony determined via census. The second predictor was year (y), a categorical variable with two levels: 2010 and 2011. Procedure GLM in the R statistical environment was used to perform the logistic regression, employing a binomial link function (R Development Core Team, 2009). To determine which model was best supported by census data, AIC values were used (Akaike, 1974).

D. **Results**

1. **Reproductive success**

BCNH nested in very high density in Lincoln Park, with 217 nests/ha in 2010 and 315 nests/ha in 2011. Some trees contained as many as 13 simultaneously active nests. The adult BCNH colony size peaked at 251 in 2010 and at 397 in 2011. Despite 58% larger colony size, the colony produced fewer young in 2011 compared to 2010. Peak abundance of young was 180 in 2010 and 160 in 2011 (Figure 20). The ratios of young to active nests were 1.22 in 2010 and 0.76 in 2011.

In 2010 although many BCNH pairs initially began nesting on the grove, only one pair remained there for the entire breeding season and they did not produce young. The other 146 active nests were in the avenue in 2010. In 2011 all 211 active nests were in the avenue. After young BCNH were able to fly, they frequently left the avenue for the grove before dispersing from the park, which is reflected in censuses of the two habitat patches (Figure 20). Young BCNH, less than 1-year-old, were observed using the grove to practice flying and foraging, in addition to roosting and congregating in small groups. Therefore, in Figure 20, which shows censuses of the grove and avenue habitat patches, the BCNH young observed in the grove were not born there, but were simply censused

there while roosting, foraging, etc. The wandering behavior of small pods of young BCNH at the end of the summer breeding season is typical for this species (Semenchuk and Federation of Alberta Naturalists, 1992)

2. **Fine-scale habitat patch selection**

Four models with all combinations of two predictors (colony size and year) and interaction between predictors were considered (Table VI).

TABLE VI
 CANDIDATE LOGISTIC REGRESSION MODELS OF BLACK-CROWNED NIGHT-HERON
 HABITAT PATCH SELECTION WITH BINOMIAL LINK FUNCTION

Model	Description	Equiv. DF ^a	Δ AIC ^b
$p_{avenue} \sim n_{colony} \times y$	Probability of selecting the avenue is a function of colony size, year, and the interaction between colony size and year.	4	0
$p_{avenue} \sim n_{colony} + y$	Probability of selecting the avenue is a function of colony size and year.	3	133
$p_{avenue} \sim n_{colony}$	Probability of selecting the avenue is a function of colony size.	2	248
$p_{avenue} \sim y$	Probability of selecting the avenue is a function of year.	2	4365

^a Equivalent degrees of freedom.

^b AIC scores identified the model with the most support from data. The data consisted of 5,314 habitat patch selections in 2010 and 3,195 in 2011, collected between 2 April 2010 to 16 June 2010, and between 30 March 2011 to 10 May 2011.

The model with the most support from the census data, as determined by AIC (Akaike, 1974), was given by

$$p_{avenue} \sim n_{colony} \times y$$

where p_{avenue} was the probability of selecting the avenue habitat patch, n_{colony} was number of BCNH in the colony overall, and y was a categorical variable for year (2010 or 2011). Coefficients for n_{colony} , y , and the interaction between n_{colony} and y were all significant ($p < 0.001$).

In both 2010 and 2011, it was more probable that a BCNH would not select the avenue, and would therefore select the grove at low overall colony sizes, and would select the avenue at high overall colony sizes (Figure 21). For each increase in n_{colony} of one BCNH, the odds of selecting the avenue increased 1.05 times (determined from the antilog of the coefficient for n_{colony} , 0.05). Interaction between year and overall colony size was such that the odds of selecting the avenue were 59 times greater in 2011 than in 2010, controlling for n_{colony} and interaction between y and n_{colony} (antilog of the coefficient for y , 4.1).

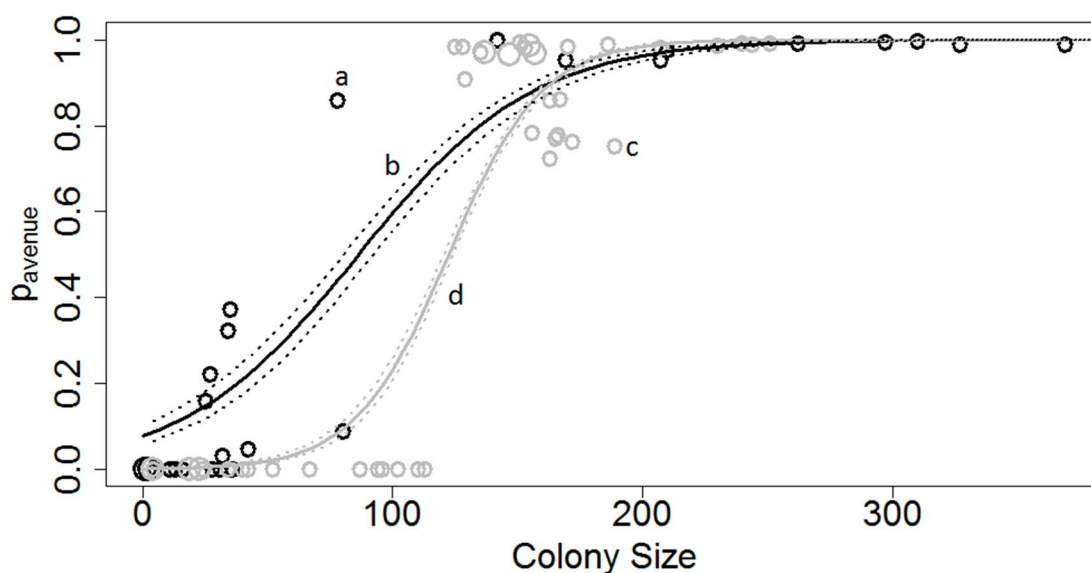


Figure 21. Logistic regression model of the probability of selecting the avenue habitat patch as a function of overall colony size in 2010 and 2011. Sample size consists of 5,314 habitat patch selections in 2010 and 3,195 in 2011. Census dates included were 2 April 2010 to 16 June 2010 and 30 March 2011 to 10 May 2011. Dotted black lines indicate 95% confidence intervals.

^a Black circles indicate observations from 2011 and symbol size scales with number of observations.

^b The solid black line is the logistic regression equation for 2011:

$$p_{avenue} = \frac{1}{1 + e^{-(-6.5 + 0.05 \times n_{colony})}}$$

^c Gray circles indicate observations from 2010 and symbol size scales with number of observations.

^d The solid gray line is the logistic regression equation for 2010:

$$p_{avenue} = \frac{1}{1 + e^{-(-2.5 + 0.03 \times n_{colony})}}$$

E. **Discussion**

1. **Reproductive success**

BCNH in North America in natural habitats typically nest in high densities such as 62 nests/ha (Bent, 1963) and 88 nests/ha (Hoffman and Prince, 1975). Table VII lists more examples and associated details. Nevertheless, densities observed in Lincoln Park, 217 nests/ha and 315 nests/ha in 2010 and 2011 respectively, were markedly high, although higher nest densities have been reported (e.g., Kazantzidis et al., 1997; Nam et al., 2007). Davis (1986) observed BCNH nested with only one pair per tree in 95% of cases on Clark's Island, Plymouth, Massachusetts, and Bent (1963) also found that the majority of nest trees had only one nest per tree in Cape Cod Bay, Massachusetts. In California, Crouch et al. (2002) observed some trees containing 15 BCNH nests, which was similar to densities observed in Lincoln Park (13 active nests per tree). Bent (1963) reported surveying 854 trees, only two of which had 13 and 14 nests respectively; the remaining 852 trees surveyed contained fewer nests.

TABLE VII
BLACK-CROWNED NIGHT-HERON NEST DENSITY IN LINCOLN PARK COMPARED WITH LITERATURE

Area	Nests/ ha	Year	Location	(Source) Habitat
16.2 ha	124	1910	Cape Cod Bay, Massachusetts	(Bent, 1963) ^a Wooded area, sand hills.
1.4 ha	88	1973	Monroe County, Michigan	(Hoffman and Prince, 1975) Wood lot.
185 × 141 m	79	1996	Napa State Hospital, California	(Kelly et al., 2006) Hospital campus with lawns, dorms, sport fields.
265 × 215 m	12	2004	Penngrove, California	Residential area.
280 × 60 m	149	1995	Brooks Island, California	Natural island habitat, no bridge (boat access only).
106 × 36 m, 22 × 11 m	478	2001	West 9th St., California	Residential area, in the median of a 4 lane street.
0.67 ha	217, 315	2010, 2011	Chicago, Illinois	(This study) Tree lined avenue in an urban city park.

^a Colony size given as 0.125 mi by 0.5 mi with 2,000 pairs, which I converted to nests.

Nesting in high density may be an adaptation to life in an urban environment as has been found in Eurasian Tree Sparrows (*Passer montanus*) and House Sparrows (*Passer domesticus*) (Møller et al., 2012). Supporting this hypothesis, Kelly et al. (2006) described a suburban nest site at West 9th St. in Santa Rosa, California, in which BCNH nested in very high density: approximately 200 active nests were located in two sub-colonies in the median of a four lane street measuring 106 m by 36 m and 11 m by 22 m in 2001. Nesting in high density is adaptive if fecundity increases in a density-dependent manner due to an allee effect in which social stimulation is requisite for reproductive success (Davis, 1993). Alternatively nesting in high density is maladaptive if there is an overabundance of urban nest sites but inadequate food, as has been documented in urban European Kestrels (*Falco tinnunculus*) (Sumasgutner et al., 2014). More nests does not necessarily equate increased reproduction; Bennetts et al. (2000) determined reproductive parameters were negatively associated with number of Little Egret (*Egretta garzetta*) nests in a heronry, presumably due to competition for suitable nest sites.

Ratios of young to active nests in the Lincoln Park colony, 1.22 in 2010 and 0.76 in 2011, were similar to ratios observed in other BCNH colonies in North America (Table VIII). The colonies closest to the study area are in Lake Calumet, 30 km south of Lincoln Park. Ratios of young to active nests in Indian Ridge Marsh, a hemi-marsh in Lake Calumet, were 1.74 in 2002 and 2.22 in 2003 (Levengood et al., 2005). Therefore, I observed smaller ratios of young to active nests in Lincoln Park than were observed at Indian Ridge Marsh. However a BCNH colony nesting in cottonwoods (*Populus deltoides*) in the vicinity of an active steel mill near Indian Ridge Marsh had ratios of young to active nests similar to those I observed: 0.52 in 2002 and 1.27 in 2003 (Levengood et

al., 2005). Mean number of young produced per nest attempt observed in California in Central San Francisco Bay, San Pablo Bay, Russian River and Laguna de Santa Rosa (1.28, 0.79 and 0.78 respectively) were also similar to ratios I observed (Kelly et al., 2007). Ratios observed in Lincoln Park were smaller than those observed in Horicon and Mead Wildlife Areas in Wisconsin (1.98) (Hoefer, 1980) and on multiple undisturbed islands in Québec (1.5, 1.3 and 2.1) (Tremblay and Ellison, 1979). Although the values observed in Lincoln Park were similar to values obtained in nearby natural habitats, they may signal reproduction that is lower than necessary to sustain the population over the long term (Henny, 1972; Levensgood et al., 2005).

TABLE VIII
RATIOS OF YOUNG TO ACTIVE NESTS IN BLACK-CROWNED NIGHT HERONS IN
LINCOLN PARK COMPARED WITH LITERATURE

Nests	Young ^a /Active nest	Year	Location	(Source) Habitat
18	0	1975	Gros Pèlerin, Québec	(Tremblay and Ellison, 1979) Uninhabited island, before egg laying.
46,64	1.5, 1.3	1975, 1976	Gros Pèlerin, Québec	Uninhabited island.
43	2.1	1975	Ile Brûlé, Québec	Uninhabited island.
66	0.5	1976	Ile Brûlé, Québec	Uninhabited island, before egg laying.
82	1.98	1978, 1979	Horicon, Mead Wildlife Areas, Wisconsin	(Hoefler, 1980) Wildlife Areas, associated wetlands.
2,187	0.74	1990- 2002	Alcatraz Island, California	(Hothem and Hatch, 2004) ^b Island 2 km north of San Francisco. Tourist attraction.
1,285 ^c	1.28	1993- 2005	Central San Francisco Bay, California	(Kell et al., 2007, habitat descriptions in Kelly et al., 2006) Urban development and interspersed wetlands, small islands, parks.
259 ^c	0.79	1993- 2005	San Pablo Bay, California	Large wetland complex and restored pasture and salt evaporation ponds. Some colonies in residential areas.
170 ^c	0.78	1993- 2005	Santa Rosa, California	Cultivated bottomlands, forested hillsides along a river and 8100 ha of ands, grasslands and woodlands.
48, 55	1.74, 2.22	2002, 2003	Indian Ridge Marsh, Illinois	(Levengood et al., 2005) Hemi-marsh in polluted, former industrial area.
11,17	0.52, 1.27	2002, 2003	Inland Steel, Indiana	Vicinity of an active steel mill, cottonwood tree grove.
147, 211	1.22, 0.76	2010, 2011	Chicago, Illinois	(This study) Urban park habitat.

^a Young defined as surviving to 28 days (Tremblay and Ellison, 1979), 35 days or flying (Hoefler, 1980), 15 days (Hothem and Hatch, 2004), at least 7 to 15 days (Kelly et al., 2006), and 15 days (Levengood et al., 2005). Hoefler (1980) reported young per pair.

^b Range of young/active nest ratios for different study years was 0.46 - 1.27.

^c Sample sizes were reported for nest survivorship estimates. See Kelly et al. (2007) for the method used to calculate number of young produced per nest attempt.

The observed 58.2% increase in colony size between 2010 and 2011 likely resulted from an influx of adult BCNH from another nesting site, not from intra-colony reproduction. The increase in colony size in Lincoln Park came in the form of BCNH in adult plumage, which supported the hypothesis that the influx resulted from immigration because acquisition of adult plumage takes several years (see descriptions of immature and breeding plumages in DeVore et al., 2004). Therefore, the BCNH that constituted the influx were not young from the previous year that had hatched in Lincoln Park. Large fluctuations in BCNH colony sizes due to immigration, emigration, and colony abandonment are common (Gross and Siefken, 2007; Hoefler, 1980; Kelly et al., 2007).

I identified a possible source of the BCNH influx I observed. Shortly before the Lincoln Park colony experienced an influx, a BCNH colony was at least partially abandoned in Lake Calumet (Maggie Cole, pers. comm.). The colony had nested at Lake Calumet and was documented by Levensgood et al. (2005) since 1984 and declined from 1,600 adult BCNH in 1992 to fewer than 600 adult BCNH in 2000 (Marcisz et al., 2005). Vetted census data submitted to eBird, an online database hosted by Cornell Lab of Ornithology, supports the hypothesis that BCNH left Lake Calumet and joined the Lincoln Park colony in 2011 (Cornell Lab of Ornithology, 2013). The peak colony size recorded in Lake Calumet in 2010 was 113 BCNH compared with only 24 BCNH in 2011 (Cornell Lab of Ornithology, 2013).

2. **Fine-scale habitat patch selection**

I determined that selection of habitat patches by BCNH depends on colony size and year, thus demonstrating behavioral flexibility. Behavioral flexibility has been implicated in the success of wildlife under conditions of HIREC (Sih et al., 2011); therefore it is hopeful that BCNH displayed flexibility in this study. BCNH typically display

high nest site fidelity, reusing nests in 86% of cases (Davis, 1986), making this demonstration of behavioral flexibility all the more remarkable. The propensity to select the avenue habitat patch in 2011 may have been influenced by the tendency to reuse nests (Davis, 1986) or learning, e.g., BCNH learned the previous year that at high colony sizes the avenue provided more nesting sites.

The logistic regression model I developed supports the conclusion that colony size affects habitat patch selection, but it does not explain why. I hypothesize BCNH selected habitat patches to strike the optimal balance between avoiding overcrowding and nesting in adequate density for social stimulation for breeding (Davis, 1993). Before 2010 the BCNH colony was smaller (approximately 30 adult BCNH in 2007) and nested exclusively on the grove. The grove may have been easier to defend at small population sizes, but overcrowding made it unsuitable at large population sizes. Considering that the grove contained only approximately seven suitable nest trees and the trees were relatively small and short compared to trees in the avenue, it seems likely that the BCNH moved to the avenue when the colony would have been too crowded in the grove (Burger and Gochfeld, 1993). The grove and the avenue were close together and therefore it is likely the same predators accessed both sites. However, the grove may have been a more defensible nest site with better visibility, making vigilance more effective. Alternatively, if larger colony size attracted more predators, perhaps the understory of the grove concealed those predators (Baker et al., 2015) therefore rendering the grove more dangerous at higher colony sizes.

That BCNH selected nest sites in a busy, urban area such as Lincoln Park demonstrated the BCNH perceived the value of these nest sites to be greater than risks perceived from anthropogenic disturbance. However, the question remains: is the urban environment an ecological trap for BCNH? One factor in whether a site is an ecological trap is if the wildlife are able to read and respond to novel cues in their environment, and wildlife that exhibit behavioral flexibility typically perform better in novel situations such as those associated with urbanization (Sih et al., 2012). Results from the logistic regression model I present suggest BCNH show behavioral flexibility in fine-scale habitat patch selection to adjust for colony size fluctuations. This observation, coupled with the observation that productivity in the colony was similar to that of in colonies in nearby natural environments, supports the conclusion that for this colony over the two-year time period I investigated, a city park served as a refuge and not as an ecological trap, and behavioral flexibility may have played a role in the colony's success. This approach consisting of assessment of reproductive success and behavioral flexibility using fine-scale habitat selection could contribute to evaluations of whether or not other urban bird colonies have fallen into ecological traps.

F. **Acknowledgments**

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V. DATA MANAGEMENT FOR COLLABORATIVE NATURAL RESOURCE MONITORING AND MANAGEMENT

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A. Abstract

Collection, processing, and long-term storage of data for broad-scale, collaborative natural resource monitoring and management projects poses technical and administrative challenges that, if not properly addressed, result in suboptimal management and learning. Data from many cooperators, often spanning multiple organizations, must be efficiently centralized and processed, and must be consistent in content and quality over the lifespan of such projects. We present a data management system for natural resource monitoring and management consisting of two components: a centralized, web-based platform for data entry and a connected relational database for data processing, modeling, and analysis. After the data management system has been customized to meet the needs of a specific project, operation and system maintenance require minimal external technical support, making it suitable for long-term projects that face potential staffing and budgeting constraints. We discuss the scope of projects for which this approach is applicable and document two U.S. Fish and Wildlife Service and U.S Geological Survey adaptive management case studies demonstrating this data management system: 1) Native Prairie Adaptive Management and 2) Wetland

Restoration and Sediment Removal. The standardized approach presented within is broadly applicable in collaborative natural resource monitoring and management settings and has the potential to improve management outcomes and facilitate deeper ecological understanding of systems being managed.

B. **Background**

The complexity of natural resource monitoring and management increasingly necessitates sharing data and lessons learned from management experiences across geopolitical and administrative boundaries (Groves et al., 1995; Knutson et al., 2010; Moore et al., 2011, 2013). The aim of this collaboration is to improve ecological and conservation outcomes of management decisions (Knutson et al., 2010, Moore et al., 2013). Such 'distributed decision-making,' in which coordinated monitoring and decision-making responsibilities are shared among many cooperators, often involves collecting, analyzing, and storing monitoring data from the study system (Mason et al., 2006; Moore et al., 2013). Cooperators participating in such programs need practical solutions for maintaining long-term data sets (Ballard et al., 2002) and obtaining timely decision support (Marzluff et al., 2000). Much literature focuses on theory and modeling in distributed decision-making; little addresses the issue from an operational standpoint (notable exceptions include Williams et al. [2009]). Technological advances in data management provide opportunities to better inform natural resource management decisions, and to deepen our collective understanding of natural systems (Sampson and Delgiudice, 2006). However, because the technological component of natural resource monitoring and management projects is usually not focal, it is often glossed over in the literature, providing inadequate guidance for managers (Sampson and DelGiudice, 2006).

Our objectives in this article are to: 1) describe the data management challenges presented by broad-scale natural resource monitoring and management projects and explain the drawbacks of existing data management systems; 2) present a data management system consisting of an online database for data entry and a locally stored companion relational database that analyzes and archives data; and 3) present case studies from two long-term U.S. Fish and Wildlife Service (USFWS) projects demonstrating successful implementation of the data management system.

1. **Data management challenges**

On account of the slow nature of many ecological processes, natural resource monitoring and management projects may require a decade or more to see meaningful results (Moir and Block, 2001; Stankey et al., 2003; Williams et al., 2009; Williams, 2011). However, managers working within these systems often require immediate decision support. To address this dichotomy, data management systems for long-term projects must provide continuity and facilitate refinements over the duration of projects while simultaneously providing useful guidance to cooperators (Ballard et al., 2002; Williams, 2011).

In distributed decision-making environments, collection, analysis, and use of monitoring data from multiple collaborating parties often poses administrative challenges (Groves et al., 1995, Williams 2011). Such challenges include 1) many cooperators (e.g., hundreds of cooperators in multiple regions or agencies) must collect monitoring data and make management decisions in a coordinated fashion (Marzluff et al., 2000); 2) data from all cooperators must be consistent in content and quality over the duration of the project (Groves et al., 1995, Ballard et al., 2002); 3) timely reporting is required to inform time-sensitive decisions (Knutson et al., 2010); and 4) costs associated with

hardware, software, and database development and maintenance are of concern (Marzluff et al., 2000; Smiley, 2008; Stankey et al., 2003).

One cumbersome solution to these data management challenges is a distributed database (Bangia, 2010; O'Brien and Marakas, 2010). Because a distributed database, by definition, houses portions of a data set in parallel across multiple computer systems, database maintenance requires redundancies and duplicative efforts (Costa and Furtado, 2011). Detecting and correcting inconsistencies among copies of distributed databases is difficult (Fan et al., 2014). Additionally, distributed databases require that all cooperators have the same software, limiting the pool of potential cooperators (O'Brien and Marakas, 2010).

An alternative to a distributed database is a web-based, centralized, relational database (e.g., a Structured Query Language [SQL] server [<http://www.microsoft.com/en-us/server-cloud/products/sql-server/>; Microsoft, Redmond, WA], DB2 [<http://www-01.ibm.com/software/data/db2/>; IBM Corporation, Armonk, NY], or Oracle database [<https://www.oracle.com/database/index.html>; Oracle Corporation, Redwood City, CA]). The principle drawback of such centralized relational databases is that they require expertise in computer science to develop and maintain. Requisite expertise may be unavailable in-house, requiring prolonged involvement of external contractors or professional Information Technology (IT) support. The high cost of retaining a dedicated database administrator may render such an arrangement unsustainable for long-term natural resource monitoring and management projects.

To overcome data management challenges posed by broad-scale natural resource monitoring and management projects, we have developed a comparatively inexpensive data management system that combines the data centralization capability of a web-based database with a locally housed relational database that is relatively simple to develop and maintain.

C. **Data management system**

We describe a data management system for long-term distributed decision-making projects. The data management system comprises two components: an online database for data entry and dissemination of results and a locally stored relational database for analysis and archiving (Figure 22). In developing this system, we prioritized ease of database maintenance and accessibility of stored data over the long term. The system facilitates online data entry and centralization, rapid data analysis, and dissemination of results including situation-specific management action recommendations.

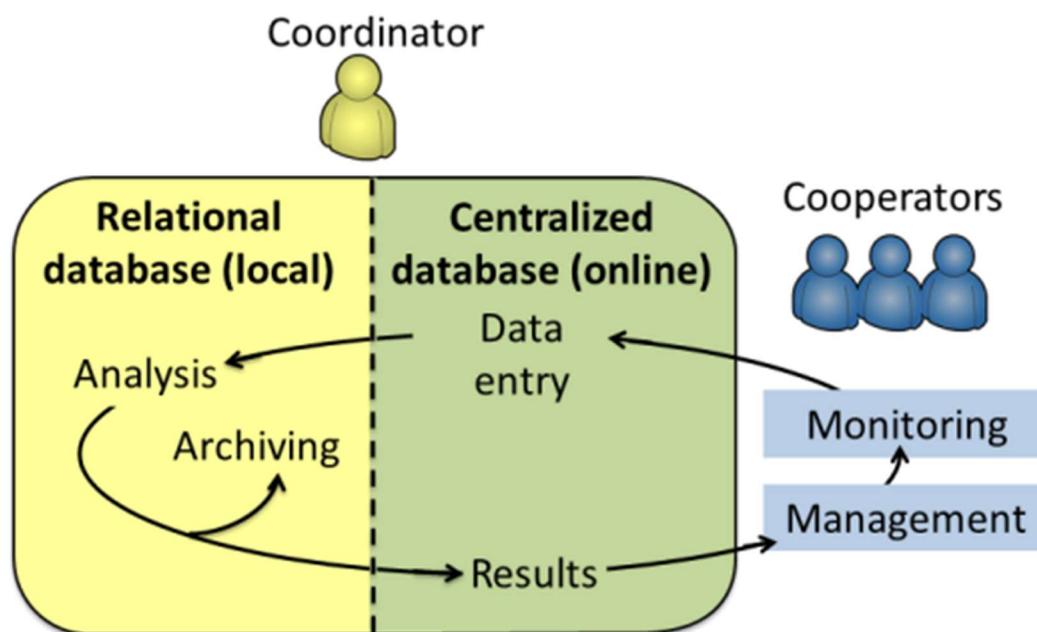


Figure 22. Schematic of a data management system for natural resource monitoring and management. The coordinator administers both the local relational database and the online database. Cooperators perform management actions, collect monitoring data, and enter their data into an online database. The local relational database imports data from the online database, performs archiving and analyses, and generates results that are uploaded back to the online database. Cooperators retrieve results and use them to inform subsequent management actions.

Data entry, centralization, and associated validation (quality control) occur in the online component of the data management system. We host the online component on a Microsoft SharePoint website (<http://products.office.com/en-us/sharepoint>; Microsoft). The website also serves as a hub for communication and document sharing. The project coordinator periodically imports data from the online database into a local relational database that performs analysis and archiving. We use Microsoft Access (<http://products.office.com/en-us/access>; Microsoft) for our data management system's local relational database. Access and SharePoint are compatible and can be coupled (Figure 22).

1. **Development**

Setting up the data management system requires an individual with a working knowledge of database development. We refer to such individuals as database architects. A database architect, in the context of this article, is not necessarily an IT professional or someone with a degree in computer science. In the case studies we present, individuals with diverse backgrounds, including conservation biology and environmental engineering serve as database architects.

First, a development team explains project specifications, including Quality Assurance and Quality Control requirements, to the database architect. The development team consists of the project coordinator, other project leaders, and stakeholders. The database architect uses information provided by the development team to implement a data management system that addresses project needs in a predominantly automated manner.

After the data management system has been set up, the database architect transfers system control, with accompanying documentation and user-guides, to the

project coordinator. The project coordinator oversees subsequent operation of the data management system.

2. **Workflow**

a. **Data entry**

The first step in the workflow facilitated by the data management system (Figure 23) is online centralization of monitoring data. Data can be entered online by cooperators via two possible routes: record-by-record using a form-based interface, or in batches using a data sheet filled out offline previously by the cooperator.

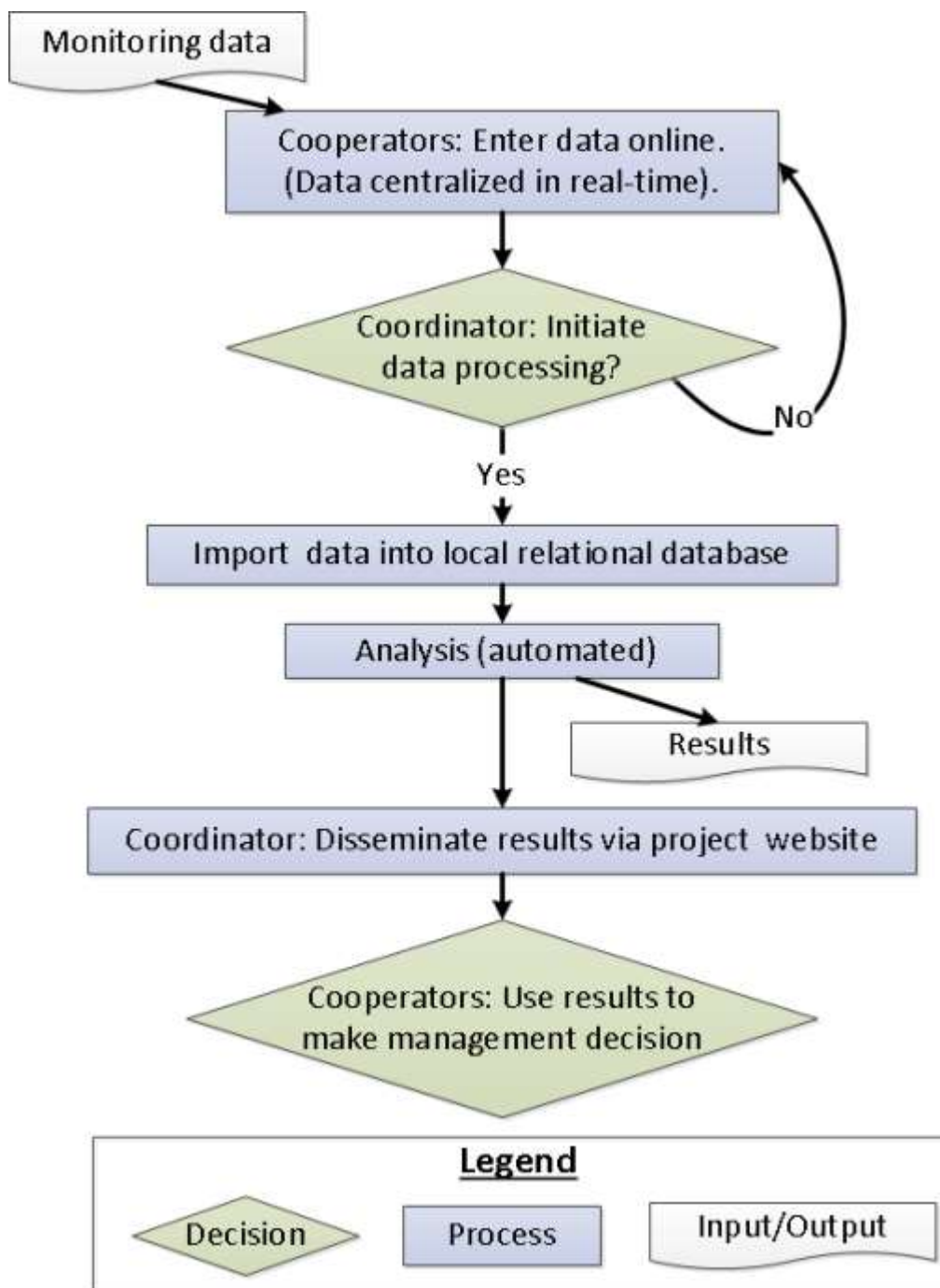


Figure 23. One iteration of the general workflow performed by a generalized data management system for natural resource monitoring and management.

If internet access is available, cooperators enter data record-by-record into a form-based interface on the project website. Cooperators can access the online data entry interface with tablets in the field, or can transcribe records from paper data sheets into online forms. The interface provides quality control via validation rules and alerts the cooperator when field values are out of range.

The second route for data entry entails using an online data sheet interface to import batches of data. When internet access is not immediately available, cooperators temporarily store data on GPS, tablet, or other data storage devices used in the field. Cooperators then transfer data directly into the online data sheet once they regain internet access.

b. **Import of data into local relational database**

Depending on decision support needs, the project coordinator may choose to run data processing routines annually or every few years (the first decision node in Figure 23). To initiate data processing, the coordinator clicks a button in the local relational database, which triggers the import of data from the online database into the relational database where analyses occur.

c. **Analysis**

The data management system performs analytical functions tailored to the specifications of each natural resource monitoring and management project. Different projects require different functions. For example, a data management system may use plant survey data to calculate the frequency of observations of each plant species recorded within a management unit.

The database architect builds the functions required by a specific project during the data management system's development phase. Functions are coded in SQL and

VBA (Visual Basic for Applications) on the back-end. The project coordinator initiates these functions by clicking buttons on a front-end graphical user interface.

After data analysis, the project coordinator initiates archiving routines. Archiving entails moving records from their original locations in active data tables into separate archive tables. Archiving serves two purposes: it creates a back-up copy of data that are available regardless of whether or not there is internet access, and it frees up server space for active data tables used in analyses.

d. **Dissemination of results**

Decision guidance and results of analyses are assembled in reports in the relational database component of the data management system. The project coordinator uploads the reports to the same website used for data entry. Cooperators retrieve reports from the website and use the results to inform management action decisions.

D. **Case studies**

We present case studies from two USFWS and USGS adaptive management projects that use the data management system we describe. Adaptive management is a structured decision-making approach that produces robust management recommendations by learning from the outcomes of repeated management decisions (Holling 1978, Lyons et al. 2008, Williams et al. 2009, Maser and Pollio 2011). Adaptive management projects are one type of long-term, collaborative natural resource monitoring and management, in which uncertainty about the system's response to management actions is reduced over time (Lyons et al. 2008).

Adaptive management entails making predictions from monitoring data and updating our confidence in two or more competing models using these predictions.

Competing models represent alternative hypotheses about the study system's response to management actions. Each competing model predicts different outcomes for each alternative management action.

1. **Native prairie adaptive management**

In the Native Prairie Adaptive Management initiative (hereafter, Native Prairie initiative), USFWS cooperators use an adaptive management approach to address the invasion of native prairies by nonnative species and to resolve uncertainties about the relative effectiveness of management actions in two discrete sets of alternatives. Alternatives included but were not limited to controlled burn, graze, a combination of controlled burn and graze within the same season, and rest (no action; Grant et al. 2009, Gannon et al. 2013).

The Native Prairie initiative is a collaboration between USFWS, who contributed management and monitoring effort, and USGS, who contributed the decision support framework and analytical elements. After initial decision cycles of the Native Prairie initiative, the USFWS-USGS team envisioned creation of a product that integrated and streamlined the operational pieces of the Native Prairie initiative. The analytical components in the new system were reproduced from algorithms designed by USGS and already in use by the Native Prairie initiative. The Open File Report (Gannon et al. 2013) is the authoritative source for the description of the Native Prairie initiative and all of its constituent technical pieces. Gannon et al. (2012) also provides background and information about the Native Prairie initiative. Hunt et al. (2016) provide the authoritative description of the design and development of the data management system for the Native Prairie initiative.

Prior to 2012, the Native Prairie initiative used a distributed database. Copies of

the database were emailed to cooperators and compiled manually each year (details are described in Gannon et al. 2013). Replication, distribution, and manual compilation of the distributed database were slow and error-prone processes. Additionally, analytical pieces of the Native Prairie initiative that processed the data, that update the model weights, and that identify optimal actions were housed in separate programs that were written in proprietary software code not available to the USFWS. The initiative's development team sought a centralized alternative because of observed inefficiencies in the distributed database. The data management system described in the following sections replaced the distributed database, eliminating sources of error in data processing and providing more rapid decision support for the cooperators. It also integrated analytical pieces of the initiative into a single tool accessible to USFWS managers.

The website of the Native Prairie initiative hosts online data entry and serves as a communication hub for cooperators and the coordinator. Like all other websites accessed through the U.S. Department of the Interior internet portal, the data entry website is password protected. Cooperators gain access to the website online through a browser of their choosing by submitting their approved user-name and password. Only the database architect and project coordinator can modify the website.

Cooperators collect three categories of data: monitoring data, management action data, and responses to management action recommendations. Monitoring data consist of plant-biodiversity transect surveys that characterize the conditions of a management unit in terms of the percent of native plant cover and the identity of the dominant invasive plant species on the management unit (Gannon et al. 2013). Monitoring data are collected before and after management actions are taken.

Management action data consist of detailed information about management actions taken (e.g., the temperature of a controlled burn). Lastly, response to management action recommendations are explanations as to how and why cooperators adhered to or deviated from management action recommendations issued the previous year. These responses document constraints and limitations on management and document personal choices regarding the recommended action (Gannon et al. 2013, Knutson et al. 2010). The ultimate purpose of this data collection is to refine estimates for the partial controllability model, as described in the Open File Report authored by Gannon et al. (2013).

An online, form-based data entry interface features extensive validation rules for quality control. Validation and quality-control rules existing in the distributed database were retained and augmented in the new system. For example, when entering management action data, specific fields are required depending on the management action that was taken (e.g., the percent of the management unit that was grazed must be recorded if the management action taken was a graze). Hundreds of such validation rules are applied in real-time while cooperators enter data online.

The data management system we describe automates the process by which confidence in each of a set of competing models is updated with the addition of new data. The Native Prairie initiative uses competing models to represent hypotheses about how the vegetation community behaves in response to management actions (Gannon et al. 2013). For example, one model represents the hypothesis that all defoliation management actions (controlled burn, graze, or burn–graze combination) are equally effective at promoting native prairie plant species. A second model represents the competing hypothesis that efficacy of different defoliation management actions depends

on a management unit's dominant invasive plant species. Gannon et al. (2013) provide complete descriptions of all models.

Each competing hypothesis is represented by a state and transition model that defines the likelihood of transitioning from one vegetation state to another under a specific management action (Gannon et al. 2013). Confidence in each competing model is represented by a model weight. Monitoring data are used to evaluate the performance of competing models and update the confidence in each model accordingly by applying Bayes' theorem (Gannon et al. 2013).

Value functions quantify the utility of predicted ecological outcomes from management actions under the competing models, weighted by confidence in each (Keeney 1992). The utility yielded by the value function answers the stakeholders' question, "How happy are we with the outcome?" In the context of the Native Prairie initiative, utilities reflect the predicted habitat quality resulting from a management action, factoring in cost (Gannon et al. 2013). The management action expected to maximize utility over the long-term is determined via a Markov decision process (Bellman 1954, Lubow 1995, Gannon et al. 2013) and is subsequently recommended. An adaptive version of stochastic dynamic programming was used for optimization, which accounts for information state in the optimization as well as vegetation and management history states (Moore and Conroy, 2006). The optimization was performed in a procedure outside of the data management system, and the full policy is stored in the data management system as a table of look-up values. The USGS formulated and performed the optimization (Gannon et al. 2013). Situation-specific management action recommendations for all participating management units are aggregated into a report.

The Native Prairie initiative provides management action recommendations for

native prairies on USFWS-owned lands in the northern Great Plains. To this end, the project coordinator uploads a report containing situation-specific management action recommendations to the initiative's website where it could be retrieved by the cooperators. Thus far, the coordinator has emailed recommendations to cooperators to facilitate dissemination. Cooperators must decide which management action to take annually to promote desired future conditions (increased composition of native prairie plant species). The data management system provides management action recommendations in a timely fashion to inform this recurring management decision. Automation of analyses (which were developed and in use prior to the data management system [Gannon et al. 2013]) used to update belief in competing models and to make management action recommendations take less than 24 hours. Cooperators take management action recommendations into consideration, but can also adjust for logistical, weather-related, and other constraints on management (Knutson et al. 2010, Moore et al. 2011, Gannon et al. 2013).

The Native Prairie initiative has used the data management system described herein for three management cycles in 2012, 2013, and 2014. Full functionality of the system was completed in 2014, while in prior years existing external analysis tools were used to varying degrees to complete the process. One hundred and twenty management units from 19 field stations participate in the initiative. Participating field stations are located across the Prairie Pothole Region in Minnesota, Montana, North Dakota, and South Dakota, spanning two USFWS administrative regions (Regions 3 and 6). Each year, approximately 50 cooperators enter 2,100 monitoring-data records based on plant biodiversity transect surveys. The predecessor of this data management system included a distributed database and operational analytical programs to process the data, compute

model likelihoods, update model weights, and select optimal management recommendations. Compared with its predecessor, (described in Gannon et al. 2013), the data management system described here reduces the administrative workload for the project coordinator, removes sources of user-error, and speeds up analyses used to generate situation-specific management action recommendations.

2. **Wetland restoration and sediment removal**

The Wetland Restoration and Sediment Removal project (hereafter, Wetland Restoration project) aims to answer two questions (Knutson et al., 2010): 1) Can the conservation outcomes of typical prairie pothole wetland restorations (including standard management practices such as ditch plugs and tile breaks) be improved by removing erosional sediment deposits during the restoration process? And, 2) is removal of the sediment layer worth the additional cost it incurs? In this project, management decisions occur only once at each site, at the start of the restoration; either the restoration includes removal of erosional sediment deposits, or the restoration does not include removal of erosional sediment deposits. Learning from the outcome of each restoration informs management action decisions on subsequent restorations (Knutson et al. 2010). The following sections focus on differences between the data management systems implemented for the Wetland Restoration project and the Native Prairie initiative to demonstrate the range of projects for which the described data management system is applicable.

In contrast to the Native Prairie initiative, in which cooperators collect and enter monitoring data annually, cooperators in the Wetland Restoration project collect monitoring data at several specified times: prior to management, four years after management, and eight years after management. The monitoring protocol includes

photographing management units (taking photo-points) during pre- and post-management assessments. Photo-points provide visual documentation of changes at each management unit.

Photo-point files, along with geographic information system survey maps and scanned data sheets, are stored as attachments on the data entry website. The cooperator first bundles the attachments for a specific assessment into a single compressed archival ('zipped') file and labels the file according to a naming convention specified on the data entry website. Each attachment is associated with observations collected during a corresponding management unit assessment.

Like the Native Prairie Initiative, the Wetland Restoration project evaluates competing hypotheses represented by state and transition models (Westoby et al. 1989). The Wetland Restoration project's competing models define the likelihood of transitioning from one system state to another state, depending on whether or not the restoration effort included sediment removal. System states are defined by the plant community and the hydrology of wetland management units.

In contrast to the Native Prairie initiative, which updates model weights annually (Gannon et al. 2013), cooperators in the Wetland Restoration project determined that the appropriate ecologically based time-scale to evaluate the weights of the competing models was 8 years. This lengthy time-step typifies environmental research because of the relatively slow nature of many ecological processes (Moir and Block 2001). Although the 8-year time-step was ecologically relevant, cooperators requested information at an intermediate point to assess progress after four years. For this reason, models with a shorter time-step were used with the understanding that the full evaluation of model weights would occur after eight years.

The Wetland Restoration project's data management system, like that of the Native Prairie initiative, includes web-based data entry, coupled with analyses performed by a local relational database. The local relational database imports monitoring data from the data entry website and uses Bayesian inference to produce updated model weights and expected utilities ('happiness scores') in response to the two alternative management actions. Utility indicates the expected outcome of each alternative management action in terms of attributes of habitat quality for waterfowl and grassland birds, and perceived ecological integrity (Knutson et al. 2010).

The data management system does not provide situation-specific management action recommendations because the Wetland Restoration project's primary objectives are to maximize ecological integrity of restored wetland management units, and to determine the ecological value of sediment removal in terms of increasing habitat quality for waterfowl and grassland birds (Knutson et al. 2010). Instead of providing recommendations, the data management system provides reports and graphs of model weights and utilities over the course of the project. The project coordinator uploads these results to the project website. Cooperators retrieve the report from the website and interpret the results to guide future wetland restorations.

The Wetland Restoration project began in 2009 and has used the data management system described herein since 2013. Five field stations in the western Minnesota prairie pothole region participate in the project. Currently 86 wetland basins (management units) are being monitored in this project and 23 cooperators enter monitoring data from pre- and post-management assessments via the data entry website.

The Wetland Restoration project is expanding; approximately twenty

management units are added annually. Because adaptive management projects such as this may initially have lower statistical rigor compared with traditional experimental design, facilitating inclusion of spatial and temporal replicates is particularly important (Marzluff et al. 2000). The project's data management system facilitates sharing data across administrative and organizational boundaries, which can increase sample size (Marzluff et al. 2000) and ultimately improve conservation delivery (Moore et al. 2013).

E. **Uses and limitations**

1. **Data storage**

We have found that SharePoint websites provide a pragmatic solution for centralizing and storing large numbers of monitoring-data records. SharePoint websites can house tables of >30,000,000 records (Microsoft 2014a). In our experience, tables of >30,000 records containing text and numerical fields have not limited data processing or analysis, with the caveat that tables of >2,000 records may result in slow performance of the online data entry interface.

The form-based data entry interface must access data tables to function properly (e.g., to populate dropdown fields). When data tables accessed by forms contain >2,000 records, forms may take several seconds or longer to retrieve necessary information. For this reason, data entry forms should be programmed to only query data tables when necessary and to filter data tables whenever possible (Microsoft 2014b). For example, if there is a dropdown field for plant species observed, and the list of possible species depends on field station, the form should determine field station first and subsequently only access the necessary records from the plant-species data table. We recommend expediting interface performance by archiving data immediately after analysis.

Projects that collect and archive geospatial data and photographs have used the

data management system we present. Cooperators sometimes choose to collect and archive data beyond those directly used to inform management action decisions. Such data may be of interest to cooperators for reporting purposes or for hypothesis testing. The data management system we present facilitates centralizing and archiving of such data in general.

2. **Analyses**

Six long-term USFWS (and USGS) natural resource monitoring and management projects currently use the data management system, all of which require unique analyses. The system is cable of performing analyses in which we 1) represent the study system's ecology in state and transition models, 2) use Bayesian inference to update our belief in competing models, and 3) determine optimal management actions via stochastic dynamic programming. The relational database component of the data management system performs these functions, which are coded in VBA and SQL, as needed on a project-by-project basis. Note that in the Native Prairie initiative case study optimization was performed externally by the USGS team and results were loaded into the data management system in tabular form, and that the data management system automated analyses that were developed by USGS and were in existence prior to development of the data management system.

We find that running analyses in a relational database using VBA- and SQL-based modules provides the flexibility necessary to address the needs of diverse natural resource monitoring and management projects. Additionally, performing analyses in this manner provides two critical benefits to project coordinators: the coordinator does not need technical expertise to obtain decision support because the processes are automated, and the system is self-contained; thus, it does not rely on outside software

such as SAS (<http://www.sas.com>; SAS Institute Inc., Cary, NC) or MATLAB (<http://www.mathworks.com>; MathWorks, Natick, MA).

3. **Development and maintenance**

In the development phase, involvement of a database architect familiar with relational databases is required. The database architect does not necessarily need expertise in software development and database administration at the level of a SQL Server database administrator or IT professional. The skills necessary to set up and maintain the system may be sourced in-house or contracted out. The level of involvement of the database architect and the related development cost depends on the project. We provide example costs for development and maintenance of the data management system in Table IX.

TABLE IX
APPROXIMATE COST COMPARISON OF DATA MANAGEMENT SYSTEMS

Project	Product or Service	Cost	Source ^a
Native Prairie Initiative	Year 1: Development, salary	\$22,000	1
	Year 2: Maintenance and updates, salary	\$17,500	1
	MS Office Professional 2013	\$290	2
	SharePoint license package	\$6,300	2
	Project subtotal	\$46,090	
Wetland Restoration Project	Year 1: Development, salary	\$13,000	1
	Year 2: Maintenance and updates, salary	\$5,500	1
	Microsoft Office Professional 2013	\$290	2
	SharePoint license	\$6,300	2
	Project subtotal	\$25,090	
Hypothetical project using SQL Server	Enterprise license	\$9,000	2
	Year 1: Development, SQL database administrator salary	\$91,000	3
	Year 2: Maintenance, salary	\$91,000	3
	Project subtotal	\$191,000	

^a 1: USFWS cooperative agreement, 2: softwaremedia.com, 2015, 3: Indeed.com, 2014.

We have applied this data management system to several adaptive management projects that perform similar analyses, allowing reuse of code in some cases. We found that reuse of code (e.g., the code used to import and archive data) in the relational database ultimately lowered the staff time needed for development of new databases because each database does not need to be built *de novo*. However, each project has unique features that require some customization of code in the development phase.

Before transferring system control to the coordinator, the database architect must provide thorough documentation of both the online and local components of the data management system. Documentation of the online component consists of systematic listing of validation rules and aggregation of all XML source files from the form-based interface of the data entry website. Documentation of the local relational database consists of a document listing all queries and tables in the database with associated descriptions and thoroughly commented VBA and SQL code.

By using foresight and building data management systems in a modular fashion, database architects can allow project coordinators to change validation rules on fields, edit dropdowns, and make other minor changes to system functions. Barring major changes (in which case involvement of a database architect may again be beneficial) there is minimal need for external assistance to operate and maintain the database in the long-term. This saves time and costs associated with database administration.

4. **System requirements**

The data management system described herein uses SharePoint and Access. However, only the database architect and coordinator interact with SharePoint and Access; cooperators interact with a data-entry website through a browser of their choosing and are not required to have proprietary software. We chose SharePoint and

Access because they are institutionally available to USFWS employees. If funds are limited and institutionally available software is inadequate, open-source options could be explored (e.g., MySQL [<http://www.mysql.com>; Oracle Corporation] paired with Python [<https://www.python.org>; Python Software Foundation, Wilmington, DE]).

F. **Conclusion**

Data management is critically important for long-term collaborative natural resource monitoring and management projects because collected and processed data must be comparable throughout the lifetime of projects to facilitate learning. The key components of the data management system we describe are web-based, centralized data entry and a connected local relational database that performs archiving and analysis. By providing a means to centralize standardized data across geopolitical and administrative boundaries, the system promotes the collaboration necessary to obtain adequate sample sizes to draw meaningful conclusions from natural resource monitoring and management projects (Groves et al., 1995; Marzluff et al., 2000).

The data management system allows project coordinators the flexibility to make changes with little to no technical assistance over the lifetime of natural resource monitoring and management projects and provides automated situation-specific decision support. Six long-term USFWS and USGS natural resource monitoring and management projects currently use the data management system, two of which we documented here as case studies. The data management system we describe facilitates the collection, storage and use of standardized data, which has the potential to deepen our ecological understanding of managed ecosystems, and to improve management outcomes from natural resource monitoring and management projects in general.

G. **Acknowledgments**

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VI. A DECISION SUPPORT TOOL FOR ADAPTIVE MANAGEMENT OF NATIVE PRAIRIE ECOSYSTEMS

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Hunt, V. M., Jacobi, S. K., Gannon, J. J., Zorn, J.E., Moore, C. T., Lonsdorf, E. V.: A Decision Support Tool for Adaptive Management of Native Prairie Ecosystems. Interfaces Articles in Advance; 1-11: 2016.

A. Abstract

The Native Prairie Adaptive Management initiative is a decision support framework that provides cooperators with management-action recommendations to help them conserve native species and suppress invasive species on prairie lands. We developed a Web-based decision support tool (DST) for the U.S. Fish and Wildlife Service and the U.S. Geological Survey initiative. The DST facilitates cross-organizational data sharing, performs analyses to improve conservation delivery, and requires no technical expertise to operate. Each year since 2012, the DST has used monitoring data to update ecological knowledge, which it translates into situation-specific management-action recommendations (e.g., controlled burn or prescribed graze). The DST provides annual recommendations for more than 10,000 acres on 20 refuge complexes in four U.S. states. We describe how the DST promotes the long-term implementation of the program for which it was designed and may facilitate decision support and improve ecological outcomes of other conservation efforts.

B. **Background of the Native Prairie Adaptive Management initiative**

Prairie dominated by endemic plant species (native prairie) is arguably the most endangered type of ecosystem in North America (Sampson and Knopf, 1994). As much as 82 to 99 percent of tallgrass prairie and 30 to 99 percent of mixed-grass prairie have been converted to agriculture in the past 200 years (Sampson and Knopf, 1994). Invasive grasses, including Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*), displace desirable native plant species and pose serious threats to remaining native prairie ecosystems (Grant et al., 2009). Endemic prairie plants evolved with periodic disturbance from fire and grazing. The management of native prairie strives to mimic historic disturbance regimes, thus promoting native species and suppressing invasive species (Sampson and Knopf, 1994).

The U.S. Fish and Wildlife Service, steward of significant tracts of native prairie in North America, recognized the potential to improve ecological outcomes of management-action decisions by strategically collecting and synthesizing information about invasive species management of prairies on National Wildlife Refuges (hereafter, refuges). To this end, the U.S. Fish and Wildlife Service (USFWS) and the U.S. Geological Survey (USGS) developed the Native Prairie Adaptive Management (NPAM) initiative in 2008 (Gannon et al., 2013). Hereafter, we refer to this collaboration as the NPAM development team. NPAM is a cyclical process of decision making, management implementation, and monitoring. Refuge biologists participating in the initiative (hereafter, cooperators) have enrolled 120 management units comprising more than 10,000 acres in 20 refuge complexes scattered across Minnesota, North Dakota, South Dakota, and Montana (Figure 24).

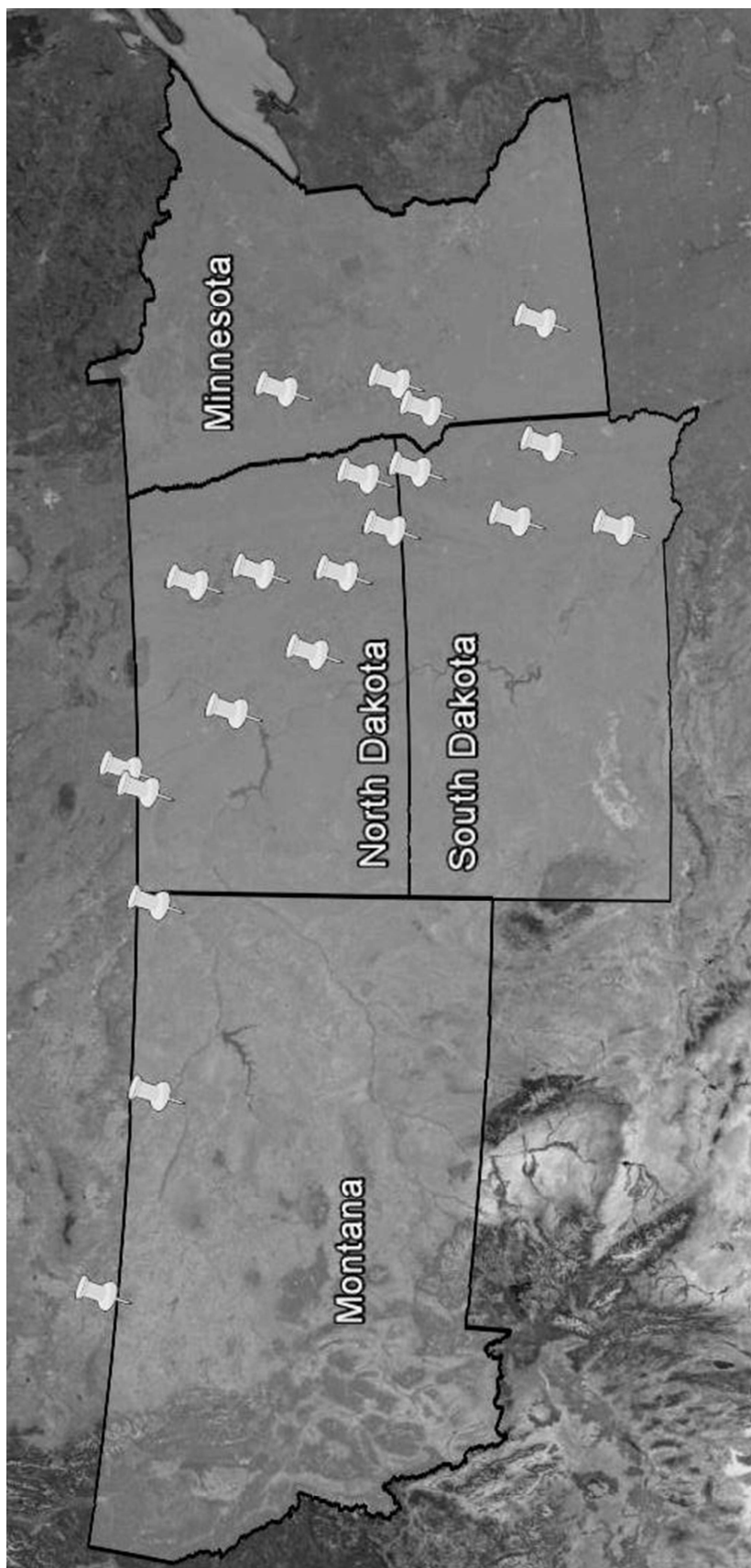


Figure 24. The map indicates 20 National Wildlife Refuge complexes that participate in the Native Prairie Adaptive Management initiative. Base map data: Google, Landsat, NOAA, April 9, 2013.

NPAM coordinates local efforts of refuges, provides transparent decision support for selecting management actions under uncertainty, maximizes learning from management outcomes, and improves decision making through time. To reduce uncertainty about the extent to which various management actions suppress invasive plants, NPAM uses adaptive management, a decision-analytic approach in which competing models represent hypotheses about the effects of management actions on the system being studied (Walters, 1986). Insights from repeated assessment of predictive abilities of competing models guide future management-action decisions (Walters, 1986). The combination of shared management challenges, biological uncertainties, and recurrent management-action decisions make adaptive management a natural fit for addressing concerns about invasive species on prairie lands.

The USGS provided technical expertise and specialized software during the first two adaptive-management cycles in 2010 and 2011, and in 2012 and 2013, as the work we describe was phased into operation. A formal transfer of the system from the USGS to the USFWS, at which point the USFWS would run the system autonomously, was envisioned from the beginning. However, inefficiencies in NPAM's original data management, quality-assessment, and analytical processes hindered this transfer. We developed a decision support tool (DST) that made this transfer feasible and promotes the long-term implementation and success of NPAM. The DST provides Web-based data entry, integrated analytical routines, and improved data-quality assessment. Herein, we describe the DST, which encapsulates NPAM's original analytical framework and workflow, and explain its benefits in comparison to the previous implementation of decision support.

1. **Adaptive-management framework**

Adaptive-management projects have four requisite components: objective(s), a monitoring plan, management actions (decision alternatives), and competing models (Williams et al., 2009).

Gannon et al. (2013) described these components in their implementation of NPAM:

(1) Objective: The NPAM management objective is to increase the relative proportion of native prairie plants by reducing the proportion of invasive plants, while minimizing management costs.

(2) Monitoring plan: Each summer, the dominant vegetation type is recorded along fixed 25 meter (m) belt transects. Each transect consists of 50 regular interval belts that are 0.1 m wide by 0.5 m long (Grant et al., 2004). Transects are used to sample vegetation in management units. Species or species-group observations recorded along transects are classified into four mutually exclusive categories: native prairie, invasive smooth brome, invasive Kentucky bluegrass, and other nondesirable species (i.e., the remainder) (Figure 25).

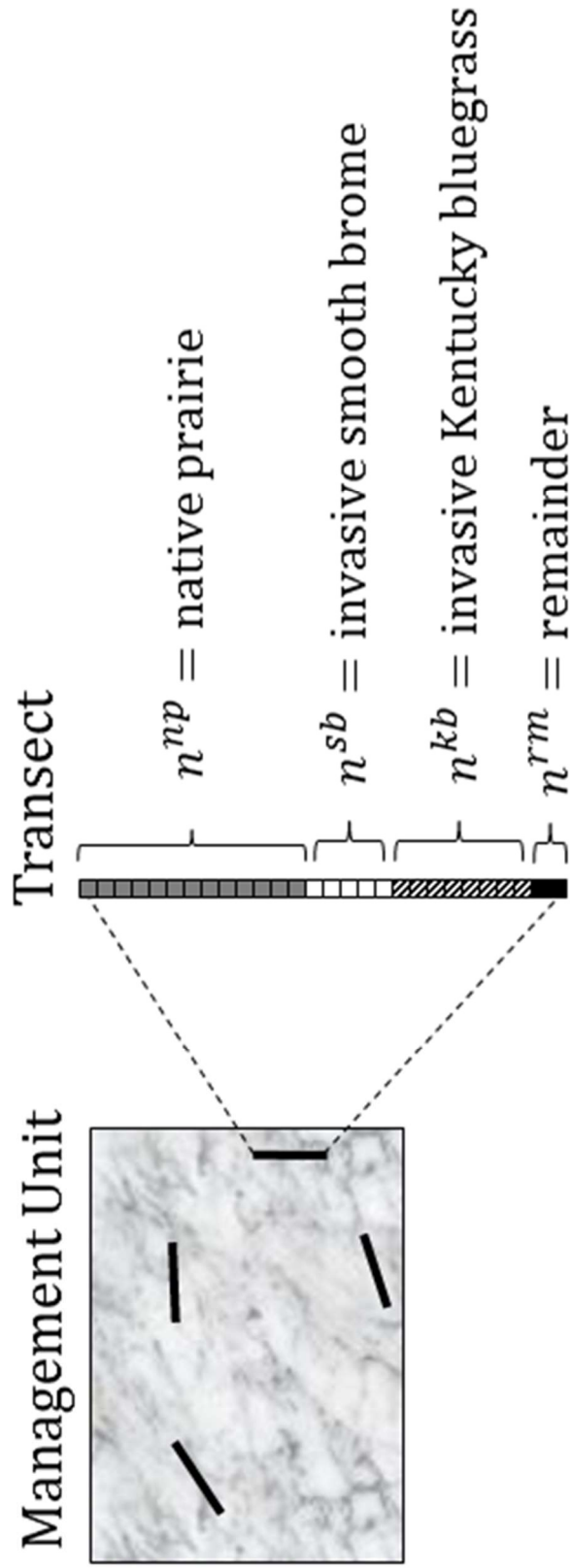


Figure 25. Observers annually collect data at 50 intervals along multiple transects randomly oriented within each management unit. A transect is characterized by a vector of 50 elements with each element taking one of four values shown .

Each management unit is assigned one of 16 possible vegetation states and one of seven management-history states based on monitoring data. Vegetation states have two components: proportion of native prairie (0 to 30 percent, 30 to 45 percent, 45 to 60 percent, or 60 to 100 percent) and a dominance classification of the remaining plant community (smooth brome dominant, Kentucky bluegrass dominant, smooth brome and Kentucky bluegrass codominant, or dominated by another nondesirable species) (Table X).

TABLE X
VEGETATION SYSTEM-STATES WHICH ARE ASSIGNED TO MANAGEMENT UNITS USING
MONITORING DATA COLLECTED ON TRANSECTS

Dominant invasive species	Proportion of native vegetation (%)			
	60 - 100	45 - 60	30 - 45	0 - 30
Smooth brome	1	5	9	13
Smooth brome and Kentucky bluegrass codominant	2	6	10	14
Kentucky bluegrass	3	7	11	15
Other nondesirable species	4	8	12	16

Management-history states convey the frequency of management actions that disturbed the vegetation community (e.g., controlled burn) in the preceding seven years and timing of the most recent disturbance. The combination of vegetation and management-history state is the basis of predictive models and decision support. Herein, references to state without modifier pertain to this combination of vegetation and management-history state; for simplicity we often refer only to vegetation state.

(3) Management actions (decision alternatives): One management action from a discrete set of actions may be applied during each iterative cycle per management unit. The set is specific to a geographic stratification to which the management unit belongs. For example, one set includes resting (no action), and three forms of disturbance: conducting a controlled burn, prescribed grazing, and performing a controlled burn and a prescribed graze in the same cycle (burn-graze combination).

(4) Competing models: Monitoring data are used to assess the performance of predictive models, which reflect specific uncertainties about the relative effectiveness of management actions under key scenarios. For example, one model proposes that compared with rest (no action), all methods of disturbance suppress invasive plants and increase the proportion of native plants equally well. A competing model hypothesizes that management-action efficacy depends on which invasive plant species dominates in the management unit; smooth brome may be more effectively reduced by prescribed grazing than by a controlled burn. Gannon et al. (2013) describe the competing models.

Competing models are represented by state and transition matrices. Each matrix contains probabilities of transitioning from one discrete state to another under a specific management action, for all possible combinations of states and management actions (Westoby et al., 1989) (Figure 26).

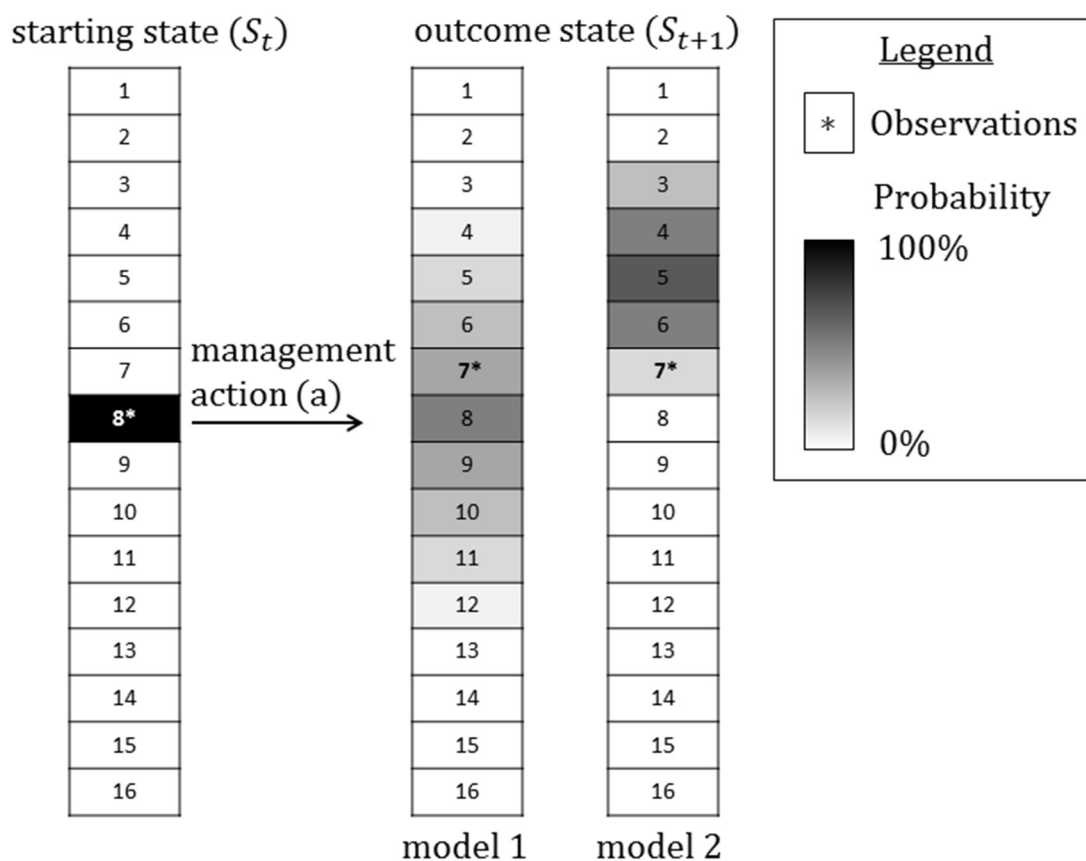


Figure 26. The graphic depicts the probabilities of transitioning from state 8 under management action (a) for two different models. Given that the observed final state was 7, model 1 has better predictive ability.

Monitoring data are used to assess the performance of predictive models and to incrementally learn through the application of Bayes' theorem (Moore et al., 2013):

$$P_{t+1,j} = \frac{P_{t,j}L_j(S_{t+1})}{\sum_i P_{t,i}L_i(S_{t+1})} \quad (1)$$

where $P_{t,j}$ is the weight of model j at time t , $P_{t+1,j}$ is the updated weight of model j after management actions are taken, and $L_j(S_{t+1})$ is the likelihood of outcome state, S_{t+1} under model j . The likelihood term incorporates state-to-state transition probability and uncertainty as a result of spatial heterogeneity of vegetation composition within management units. Bayes' theorem resolves a model's predictive performance with prior belief by assigning relatively more weight to models that support observed outcomes. In 2010, each competing model received equal weight reflecting a noninformative prior. Model weights are subsequently updated each cycle.

Each combination of starting vegetation state, outcome vegetation state, and management action has an associated utility value indicating the cooperators' relative strength of preference for one combination over another, factoring in cost. Given optimization of competing models and current model weights, management-action recommendations specific to the current state of each management unit are distributed to cooperators for use in the next iterative cycle (Figure 27).

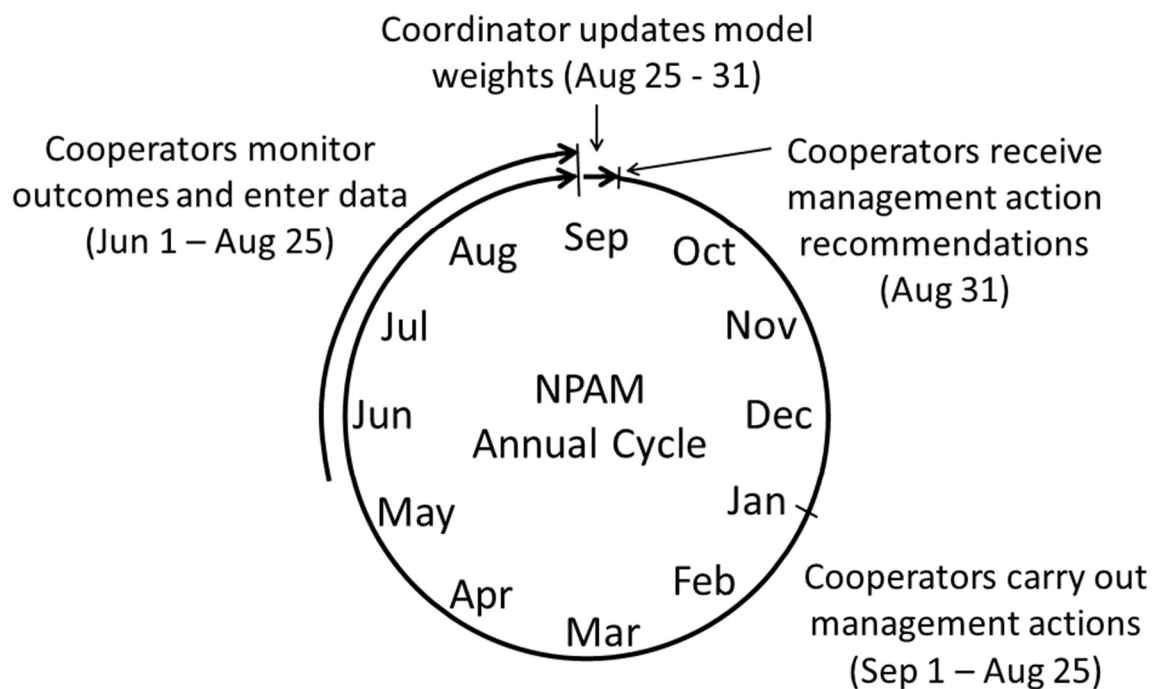


Figure 27. The Native Prairie Adaptive Management initiative's iterative adaptive management cycle spans from September 1 to August 31.

Optimization entails maximizing cumulative expected utility over 1,000 years (Gannon et al., 2013):

$$\max_{a_{t+1}} \sum_{t=t_0}^{t_{1000}} \lambda \times u(S_t, S_{t+1}, a_{t+1}) \quad (2)$$

where $u(S_t, S_{t+1}, a_{t+1})$ is the expected utility of a state transition (starting state S_t and outcome state S_{t+1}) under management action a_{t+1} chosen from a discrete set of alternatives, and λ discounts the value of the utility expected to be accrued in the distant versus near future. An adaptive stochastic dynamic-programming algorithm (Lubow, 1995, 1997) produces tables of recommended management actions.

2. **Original data management process**

In the first two adaptive management cycles of NPAM, data processing, analysis, and decision support required significant personnel resources, expertise, and oversight. Below, we describe methods used in 2010 and 2011, which we collectively refer to as the original process.

After completing management actions and data collection, the USFWS coordinator emailed copies of a compound Microsoft Access database to the cooperators. The database required a specific configuration of linkages that could easily be broken during data entry. Cooperators then entered management actions and monitoring data into local copies of the database. Because the database files were too large to email, the cooperators compressed the databases into archival (i.e., zipped) format and uploaded them to a FTP host. The coordinator retrieved and collated the data. A USGS member of the development team (hereafter, researcher) ran a SAS (SAS Institute Inc. 2010) program, translating monitoring data into state variables. The researcher computed likelihoods under competing models and updated model weights using SAS (Gannon et al., 2013). Updated model weights in combination with the state

of each management unit determined optimal management actions for the next iterative cycle.

Recommended management actions were drawn from static optimization tables generated by an adaptive stochastic dynamic-programming algorithm developed by Gannon et al. (2013). Technical expertise was required to run the SAS code and efficiently search large optimization tables. The researcher emailed the results to the coordinator. The coordinator emailed management-action recommendations to the cooperators. This concluded an iteration of the adaptive-management cycle.

3. **Evaluation of the original process**

Inefficiencies the NPAM development team observed in the 2010 and 2011 cycles, as we describe next, became development needs to be addressed with a DST that would replace the original process.

Ineffective communication and information transfer: The distributed database necessitated email-based communication among the coordinator and cooperators regarding protocols, deadlines, and management-action recommendations. This inefficient communication was prone to inconsistent and misunderstood messaging. The coordinator could not revise the database without disseminating a new product and could not observe data entry progress. Supervising cooperators could only verify data entered by field technicians if the supervisor and technicians accessed the same database copy.

The original process relied on a distributed database in which portions of the data set were stored in parallel across 20 computers. This introduced the possibility of data loss if database copies were corrupted or irretrievable (i.e., hard drive failure). The NPAM development team observed problems characteristic of distributed databases in

general: database maintenance required redundancies, isolating and correcting inconsistencies among database copies was difficult and time consuming, and the process required cooperators to have specific software.

Inefficient analytical performance: The original process was not robust in its ability to handle errors compounded across many users and multiple steps, thus complicating decision support. Rectification of questionable data values involved generation of a list of such values by the USGS researcher, who passed the list to the USFWS coordinator for resolution, who then passed the resolved list to a database manager for data entry. Model weight updating and the generation of optimal management-action recommendations were similarly labor-intensive processes.

Requirement for specialized technical expertise and proprietary software: The original process required specialized technical expertise and proprietary software. The original process required a USGS researcher to provide expertise in and access to proprietary software (SAS). The NPAM development team sought a system that could be operated by an in-house USFWS coordinator without requiring the coordinator to have specialized technical expertise.

C. **Development needs and literature review**

The NPAM development team required a DST that would increase the automation of decision support and result in a system that could be carried forward autonomously by the USFWS. Primary requirements were to facilitate cross-organizational data sharing, efficiently perform analyses, and eliminate the need for specialized software or technical expertise by the coordinator and cooperators. When we set out to develop a DST, we first looked for existing systems with requisite attributes. A literature review yielded no potential systems that we could adapt for our purposes.

Considering the logistical challenges of coordinated, broadscale monitoring and the need for rapid integration of monitoring data and updated learning, this finding was not surprising. Below, we describe existing DSTs for adaptive management in conservation, focusing on features NPAM required, and explain why we could not adapt an existing system.

Miradi, an open-source and popular DST for conservation applications, guides users through problem assessment, model design, implementation of management actions, and monitoring. Over 5,500 users downloaded Miradi and used it in 115 projects in the five years following its launch (Schwartz et al., 2012). However, Miradi does not facilitate cross-organizational data sharing and cannot perform analytical tasks related to knowledge updating and the selection of optimal management actions under uncertainty, making it unsuitable for NPAM.

We avoided using proprietary software for modeling Bayesian networks. For example, Netica (Norsys Software), which has been used in wetland-management decision support (Gawne et al., 2012), requires some technical expertise and does not adequately facilitate analyses for iterative decision making for our purposes. Open-source Bayesian software packages such as GeNIe (Decision Systems Laboratory) have been applied in natural resource management, for example, in decision support for fisheries surveillance (Tessem et al., 2009). We avoided open-source Bayesian software because of the technical expertise required.

We needed to centralize data across a large spatial area from multiple cooperators. Some DSTs support adaptive management; however, because they fall short of this requirement, they could not serve us as templates. For example, a DST for adaptive management of water resources developed by Westphal et al. (2003), the

CLAM model for integrated adaptive management of coastal lakes (Ticehurst, 2008), and Landscapes ToolKit (Bohnet et al., 2011) do not facilitate centralizing data contributed by multiple cooperators. These DSTs provide valuable decision support, but each lacks a critical element for distributed decision making. Thus, we concluded our literature review and developed a novel approach.

D. **A decision support tool for native prairie adaptive management**

We constructed a DST consisting of an online platform for data entry and an integrated database, which is maintained on the coordinator's local machine, that performed analyses and data processing. Next, we discuss the steps in our DST.

1. **Step 1: data entry**

Vegetation monitoring and management-action data are centralized in real-time and online. Cooperators interact with a secure Web portal maintained by the U.S. Department of the Interior. Data entry requires a four-character pass code specific to a refuge.

A standardized form-based interface (e.g., Figure 28) provides quality control by preventing the entry of duplicate information and disallowing incompatible field combinations. The DST strengthens and augments quality-control measures from the original data management process. Validation errors trigger descriptive screen tips, for example, "Start date of a management action must be before the end date." In the absence of errors, other screen tips confirm data entry. We developed the online data entry portal and form-based interface using Microsoft SharePoint and InfoPath. This software is institutionally available to USFWS employees and is thus cost effective.

Enter New Management Action(s)

Copy defaults :	<input type="button" value="Copy"/>		
Refuge complex:	Arrowwood ▼		
Password:	****		
Management Unit:	1A ▼		
Grassland type:	Mixed grass ▼		
Contact:	Cooperator 1 ▼		
Year:	2014: 9/1/13-8/31/14 ▼		
Management Action:	Graze ▼ Burn Rest		
Start date:	6/10/2014		
End date:	6/25/2014		
Acres:	78		
Acres treated:	78		
Special treatment applied?	<input checked="" type="checkbox"/>		
Comments:	<div></div>		

Graze Data

Number of animals:

Grazing animal type:

Stocking rate (AUMs/acre):

Grass Utilization:

Special Treatment Data

Description:

Spot mowing for weed control

Start date:

End date:

Acres treated:

Figure 28. An example data entry form on the Native Prairie Adaptive Management initiative's website illustrates how cooperators record details about management actions implemented.

2. **Step 2: data processing**

The coordinator imports data from the online database into a locally stored, relational database by clicking a button. The relational database archives data, making them accessible whether or not the Internet is available, and generates summaries of aggregated data (e.g., Figure 24). Summaries serve as the basis for potential hypothesis testing beyond NPAM. Cooperators consider summaries an added value of participation and use them for their personal records and reports.

Ten Plant Code Categories by U.S. State in 2014

Friday, April 10, 2015

4:49:47 PM

U.S. State	Description	Percentage	Number of Stops Along Transects
MN	Crested Wheatgrass	0.00%	0
MN	Kentucky Bluegrass	21.06%	1,411
MN	Low Shrub	2.66%	178
MN	Not Applicable	0.73%	49
MN	Native Grass-Forb	52.81%	3,538
MN	Noxious & Other Weeds	0.07%	5
MN	Other	2.10%	141
MN	Quackgrass	0.03%	2
MN	Reed-Canarygrass	4.12%	276
MN	Smooth Brome	13.72%	919
MN	Tall Shrub/Tree	2.70%	181
Total:		100.00%	6,700

Figure 24. An example summary provided to cooperators shows frequencies of 10 plant cover types grouped by U.S. state.

The DST provides interactive features for methodical data-quality review. The coordinator performs custom validation of flagged records that meet specific criteria. For example, the DST flags management-action records for prescribed graze if grass utilization is "Slight (1-20%)." In this example, the coordinator could reclassify the management action from prescribed graze to "rest," if the management action taken is deemed insufficient to qualify as prescribed graze. The NPAM development team determined that flagging and reviewing could not be automated because, although based on defined criteria, potential interactions among multiple triggers for flagging mean reclassification must be determined under coordinator discretion.

3. **Step 3: evaluation of competing models**

NPAM's primary objective is to increase the proportion of native plant species on USFWS-owned prairies. To this end, cooperators receive situation-specific management-action recommendations. Generation of these recommendations entails using monitoring data to update model belief weights, which describe the relative influence of each model on the current management-action recommendation.

The coordinator launches an executable script to compute model-specific likelihoods (i.e., probability of data given correctness of the model) based on observed state transitions. Likelihoods inform Bayesian updating of model belief weights. Static optimal decision-policy tables generated externally by an adaptive stochastic dynamic-programming algorithm prior to DST development (Gannon et al. 2013) are searched using updated model belief weights. From decision-policy tables, optimal state-specific management-action recommendations for each management unit in the subsequent cycle are identified (Figure 30).

Management Recommendations in 2015						August 28, 2014 10:55:57 AM	
Management Unit	Year	NP Proportion	SB Proportion	KB Proportion	RM Proportion	Vegetation State	Recommended Management Action
G14 Pasture 1	2014	0.30	0.27	0.40	0.04	{0-30, Co}	GRAZE
G14 Pasture 2	2014	0.39	0.19	0.25	0.18	{30-45, Co}	BURN/GRAZE
G26 Paddock 1	2014	0.16	0.06	0.68	0.10	{0-30, KB}	BURN
G26 Paddock 2	2014	0.36	0.08	0.52	0.03	{30-45, KB}	REST
G26 Paddock 3	2014	0.11	0.06	0.60	0.22	{0-30, KB}	BURN
G26 Paddock 4	2014	0.12	0.18	0.48	0.22	{0-30, KB}	BURN

Figure 30. Management-action recommendations (far right) for each management unit (far left). Vegetation states and components (NP: native prairie, SB: smooth brome, KB: Kentucky bluegrass, and RM: remainder) are listed. This report is abbreviated for the purposes of presentation; the full version contains management-history state attributes that, in combination with vegetation state, determine management-action recommendations.

4. **Step 4: dissemination**

The coordinator uploads a table of management-action recommendations to the data entry website. The management action expected to provide the optimal outcome, factoring in cost, is reported per management unit. Cooperators retrieve management-action recommendations from the same website used for data entry, completing an iteration of the adaptive-management cycle.

E. **Results**

The DST has been used and incrementally improved over three management cycles in 2012 - 2014. Features described in preceding sections became fully operational in 2014, allowing the complete replacement of the original process. Here, we describe quantitative and qualitative measures of success.

1. **Cross-organizational data sharing**

In 2014, 20 refuge complexes representing 120 management units used this DST. Thus, the DST has the distinction of being adopted successfully for adaptive management, which is relatively rare (Stankey et al., 2005). It facilitates data sharing across widespread refuges that have no history of formalized information sharing prior to enrollment in NPAM.

The application of adaptive management in distributed decision-making environments, as are often found in conservation, requires sharing data. In adaptive management, learning is more efficient with replication of management actions and monitoring (Moore et al., 2013). The DST facilitates the annual entry of vegetation monitoring data collected along approximately 2,000 transects (about 100,000 observations), and details of management actions implemented.

2. **Perform analyses efficiently to improve conservation delivery**

Improving the understanding of biological systems through the evaluation of competing models is the hallmark of adaptive management and the foundation of NPAM. In NPAM, iterative reallocation of weight among competing models reflects learning over time, as models with consistently better predictive performance acquire weight at the expense of other models. Gannon et al. (2013) report model weights through three cycles of updating. The DST efficiently integrates what had previously been a disconnected, standalone process, and facilitates the improvement of conservation outcomes for native prairie brought about by knowledge-guided management.

A key feature of the DST, absent in the original process, is its facility to allow the coordinator to methodically review and resolve flagged records. This feature eliminates cumbersome steps that involved three people, streamlines flagging and reviewing, and more quickly brings about the generation of management-action recommendations. This improvement enables a complete data review within NPAM's deadlines, while requiring less personnel effort.

3. **No technical expertise or specialized software needed**

The development team realized early on that the initiative's success would hinge on the ability of the USFWS to implement sustained adaptive-management cycles without external technical support from the USGS. Therefore, we designed the DST such that it could be administered indefinitely by a coordinator who does not have specialized technical expertise. DST administration requires MS Access which, as part of the Microsoft Office Professional Suite, is frequently available institutionally. MS Access licenses cost approximately \$140 at the time of this writing. We run computationally

intensive analyses via a standalone executable module written in Python, an open-source platform. Analyses in Microsoft's Structured Query Language (SQL) and Visual Basic for Applications are implemented using button clicks. Therefore, the coordinator does not need to interact with code to perform analyses.

Cooperators interact with the Web-based portion of the DST via a Web browser of their choosing. SharePoint is institutionally available for the USFWS, and the U.S. Department of the Interior grants access to the data entry portal to non-USFWS partners. SharePoint costs vary by usage; the small business (fewer than 250 computers) package costs about \$6,300.

We developed a cost-effective DST by avoiding the use of expensive proprietary software. For example, a business license for the database platform Microsoft SQL server 2012 costs approximately \$9,000 per server. The realized cost is higher when the associated cost of a professional database manager is included. SQL server requires expertise to maintain and develop; the average SQL database manager's salary is \$91,000 (Indeed.com, 2013). In future applications, we will explore open-source options to replace SharePoint, for example, MySQL paired with Python.

F. **Conclusion**

The DST we describe performs as a comprehensive application supporting collection, management, analysis, and interpretation of data for broadscale conservation. The system helps NPAM meet program objectives in a coordinated and sustainable manner. Adaptive management requires the technical marriage of field observation and model prediction, often across long periods of time and large areas; our tool facilitates this integration and promotes cross-organizational data sharing. The

potential impact of the DST, which could serve as a template for other conservation efforts, extends beyond the scope of the specific application we describe.

One clear opportunity for further application of the DST is in other adaptive-management projects led by the USFWS. Under the leadership of its parent agency, the U.S. Department of the Interior, the USFWS, which manages 150 million acres in National Wildlife refuges, is increasingly using adaptive management (U.S. Fish and Wildlife Service, 2014). Other U.S. agencies, such as the U.S. Department of Agriculture, apply adaptive management, as do private and government organizations around the world, including in Australia, Canada, Europe, and South Africa (Stankey et al. 2005). By facilitating all aspects of adaptive management, we believe this DST could serve as a template for other programs, and result in more optimal decision support and conservation delivery.

G. **Acknowledgments**

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Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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VII. AN ECOLOGICAL CROWDSOURCING APPROACH TO STUDY MANAGEMENT OF COMMON REED IN NORTH AMERICA

A. Abstract

Ongoing invasive species management represents a largely untapped wealth of information on the ecology of invaded habitats. We use crowdsourcing to collect monitoring data, soil, and leaf samples from 50 stewards of 209 stands of invasive and native common reed (*Phragmites australis*) in 16 US states and Ontario, Canada. Soil moisture was $11.9 \pm 3.6\%$ SE higher and salinity was $404.4 \pm 284.5 \mu\text{S/cm}$ higher in invasive stands than in native stands. This supports the hypothesis that broader environmental tolerance to moisture and salinity contribute to the invasive success of common reed. Nitrate and phosphorous concentrations were $12.4 \pm 4.1 \mu\text{g/l}$ SE and $4.0 \pm 2.0 \mu\text{g/l}$ SE higher respectively in native stands than in invasive stands, which does not support the hypothesis that eutrophication facilitates invasion. Invasive stands were larger than native stands and were dominated by common reed; 57% of invasive stands had >90% common reed cover vs. 31% of native stands. Among invasive stands, 58% were actively managed, compared to 14% of native stands. The proof-of-concept analyses herein show that crowdsourcing managers using a standardized monitoring protocol can be an efficient way to gather large-scale ecological samples and management data. We conclude by describing how this approach could be expanded into an adaptive management framework, connecting managers and researchers in a mutually beneficial long-term partnership.

B. **Background**

Invasive species collectively represent one of the five main sources of human-caused extinctions, second only to habitat loss (Wilcove et al., 1998). There is a great deal of ongoing management to control invasive species. For example, the US federal government spent \$2.3 billion on invasive species management in 2014 (US NISC, 2014). Ongoing control efforts against invasive species represent a tremendous, but thus far largely untapped, opportunity to learn about the ecology of invasive species-impacted habitats.

Technological advances in recent decades facilitate incorporation of crowdsourcing into scientific research (Theobald et al., 2015). Crowdsourcing entails leveraging the internet to solicit information from a large pool of individuals to answer a targeted question or perform a task. Applied in a research context, crowdsourcing could narrow the divide between academics and practitioners in efforts aiming to improve natural resource management and conservation outcomes. Broad-scale, collaborative natural resource management and conservation efforts can use crowdsourced data to identify general drivers of ecological phenomenon such as invasion of non-native species. When managers share common challenges, improved conservation outcomes can be achieved by learning from one another (Wondolleck and Yaffee, 2000). Projects that employ crowdsourcing facilitate such collaboration.

Invasive common reed (*Phragmites australis* [Cav.] Trin. ex Steud.) is a promising candidate for study via crowdsourcing because (1) there is a great deal of ongoing management and (2) managers are motivated to collaborate to reduce uncertainties that complicate control of invasive common reed. For example, there is uncertainty regarding the best management practices (Hazelton et al., 2014; Martin and

Blossey, 2013) and the roles of environmental drivers in invasions. Another benefit of crowdsourcing is that it can be used to amalgamate data from many organizations and over a large spatial area; managers control common reed in a variety of management contexts (federal, state, municipal, academic, and private land owners), which may otherwise lack efficient mechanisms for sharing information (Martin and Blossey, 2013).

Common reed is a "cryptic invader," meaning that it cannot be easily classified as native or introduced due to the coexistence of native and invasive subspecies that look similar (Saltonstall, 2002). Invasive common reed grows in dense stands that displace native plants (Minchinton et al., 2006) and reduce habitat quality for wildlife (Benoit and Askins, 1999; Fell et al., 2003). The invasive subspecies exhibits more aggressive growth characteristics than the native subspecies, e.g., earlier emergence of new shoots and greater above ground biomass (League et al., 2006). However, the native and invasive subspecies can behave similarly under facilitative environmental conditions and the native subspecies has rapidly expanded in range in recent decades (Lynch and Saltonstall, 2002). Although there are physical differences between subspecies (Swearingen and Saltonstall, 2010), many managers cannot confidently differentiate subspecies solely based on outward indicators.

Further complicating management of common reed, the role of environmental determinism in invasion is unclear (Hazelton et al., 2014; Martin and Blossey, 2013). Two non-mutually exclusive hypotheses regarding the environment's role in common reed invasion are the "eutrophication hypothesis" and the "broader tolerance hypothesis" (Hobbs and Huenneke, 1992; Price et al., 2013; Zedler and Kercher, 2004). In support of the eutrophication hypothesis, invasive common reed benefits from anthropogenic disturbance (Brisson et al., 2010; Eallonardo and Leopold, 2014; Jodoin

et al., 2007) which contributes to nitrogen eutrophication of wetlands and shorelines (Bertness et al., 2002). Increased availability of soil nutrients, including dissolved organic nitrogen, yields a competitive advantage to invasive common reed over the native subspecies (Holdredge et al., 2010; Mozdzer et al., 2010). Mozdzer et al. (2010) dubbed the native subspecies a "low-nutrient specialist" compared to the invasive subspecies. In northeastern Illinois and northwestern Indiana, invasive common reed showed stronger responses to increased nitrogen and phosphorous in soils, relative to the native subspecies (Price et al., 2013). In support of the broader tolerance hypothesis, invasive common reed invades habitats characterized by a wide range of salinities (Vasquez et al., 2005) and water depths (Burdick and Konisky, 2003).

We address key uncertainties affecting control of invasive common reed by framing the problem at the spatial and temporal scales most relevant to managers. Common reed invasion operates over large areas, e.g., the Great Lakes Basin (Carlson et al., 2014), but much research on environmental drivers of invasion has been conducted on small scales under artificial conditions (Hazelton et al., 2014; Martin and Blossey, 2013). For example, management-focused research has been conducted in greenhouses (Ailstock et al., 2001) and on experimental plots (Moreira et al., 1999). Research on efficacy of management is typically conducted over a short period of time and focuses on eradication. Restoration of a diverse native plant community is often a primary management objective, but it is not directly assessed (Hazelton et al., 2014). There is a dearth of research on the prevalence and effectiveness of management approaches for common reed (Martin and Blossey, 2013, but see Hazelton et al. 2014 for a recent review on this topic). Additionally, much research has been carried out on the Atlantic coast of the United States where invasion began and where the invasive

subspecies now predominates (Saltonstall, 2003). Findings from the Atlantic coast may not be applicable where native and invasive subspecies coexist, e.g., in the Midwest and western US (Saltonstall, 2003).

We sought to determine if the invasive subspecies of common reed preferentially invaded nutrient-rich soil compared to the surrounding uninvaded area, and compared to the native subspecies. To this end, we crowdsourced monitoring data from managers to determine environmental drivers of common reed invasion that were not limited to specific geographic areas or wetland types. We also characterize what types of organizations manage common reed in North America, and what methods they use. This study demonstrates successful implementation of a standardized monitoring protocol coupled with crowdsourcing. We conclude with a discussion of how the approach described herein could be expanded into a long-term adaptive management framework.

C. **Methods**

1. **Transect-based monitoring protocol**

Managers monitored wetlands invaded by common reed using a transect-based protocol (Figure 31). The scalable protocol could be applied in common reed stands of varying sizes, and was accessible to managers with limited technical knowledge and prior monitoring experience.

The number of transects used to sample a common reed stand depended on the stand's area: one transect for stands of less than or approximately 1 ha, two transects for stands of 1-2 ha, and three transects for stands 2-5 ha. For common reed stands greater than 5 ha, we determined how many transects would be feasible on a case-by-case basis, taking into account logistical constraints.

To follow the protocol, the manager selected an arbitrary point on the edge of the common reed stand and recorded the latitude and longitude using a GPS-enabled device. The manager collected leaves from three common reed stems several paces apart and put the leaves into a re-sealable zippered plastic storage bag which we supplied. We requested leaves that were as green as possible to facilitate genetic analysis.

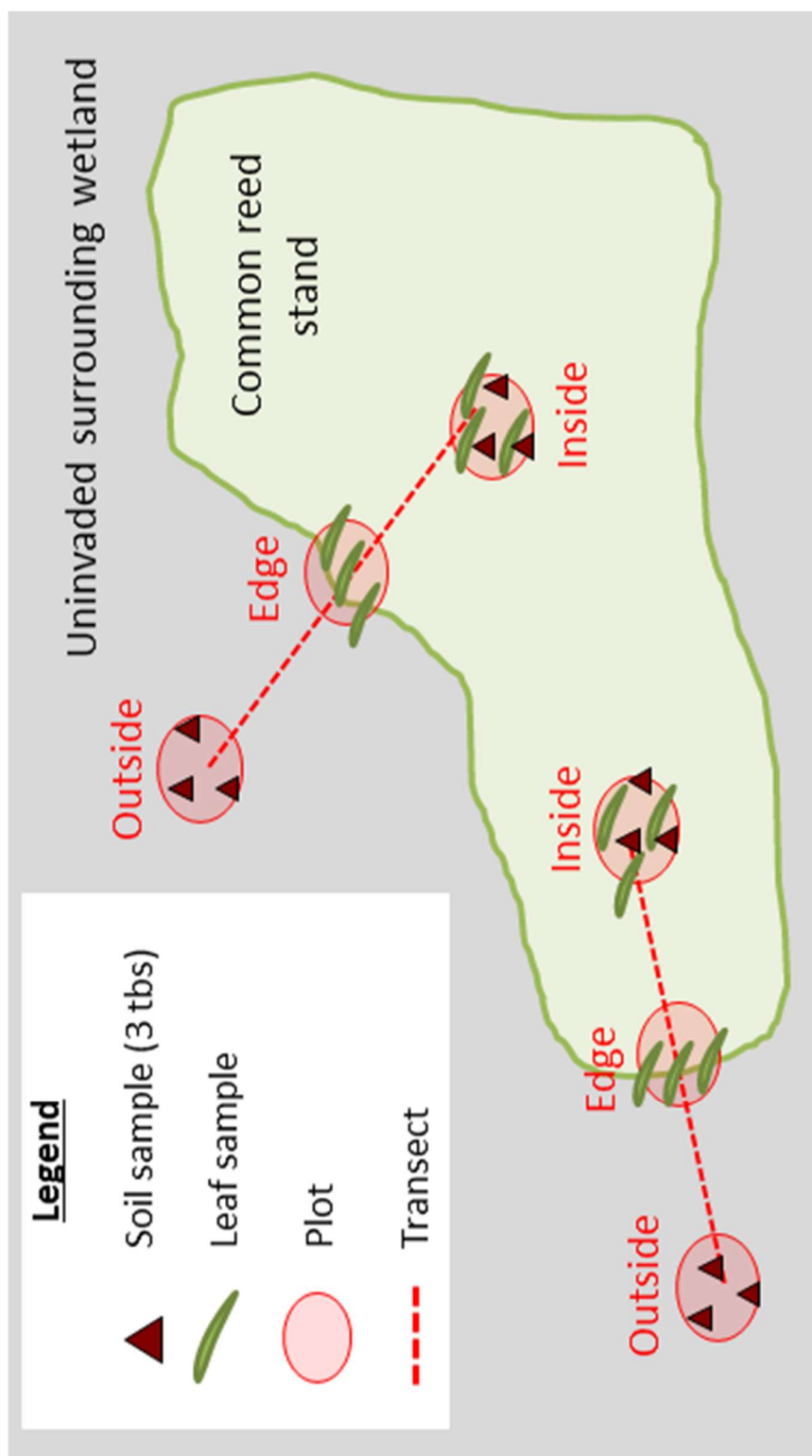


Figure 31. Illustration depicting transect arrangement used to sample a common reed stand, from the sampling protocol.

From the location on the edge of the common reed stand, the manager then walked in a straight line approximately 15 m into the interior of the stand. There the manager again recorded the location's coordinates, and collected soil and leaf samples. To sample soil, the manager collected approximately 45 ml samples from three locations located several paces apart, from a depth of approximately 10 cm. Soil samples were consolidated into a pre-labeled plastic bag. The manager followed the same procedure for leaf sampling used at the edge of the common reed stand, placing leaves from three common reed stems located several paces apart into a plastic bag. To assess community composition, the manager performed a visual assessment of vegetation cover in the interior of the common reed stand. Percent cover classes for common reed, other invasive species, and native species were recorded. Percent cover was categorized as one of five classes: none (0%), low ($>0\%$ and $\leq 10\%$), medium-low ($>10\%$ and $\leq 50\%$), medium-high ($>50\%$ and $\leq 90\%$), or high ($>90\%$). The manager also performed a visual assessment of hydrology in the interior of the common reed stand, ranking it as dry, muddy, or "water" (submerged).

The manager walked back to the location on the stand's edge where sampling began, and continued to walk in a straight line 15 m outside of the common reed stand into the uninvaded adjacent area. At this final point on the transect, the manager recorded the location's coordinates and identified the three dominant species of vegetation. For each of the three dominant plant species, the manager assessed percent cover. The manager also visually assessed hydrology, and collected soil following the same procedure used in the stand interior.

Data sheets, soil samples, and common reed leaf samples were sent to the Chicago Botanic Garden via the US Postal Service. Soil samples were analyzed for

nutrients that potentially play a role in invasion. Samples were extracted with potassium chloride (KCl) and gravimetric percent soil moisture, inorganic nitrogen (ammonium $[\text{NH}_3]$ and nitrate $[\text{NO}_3^-]$), and phosphorous (PO_4) concentrations were assessed following standard EPA methods with a SEAL AQ2+ Discrete Analyzer (Seal Analytical Inc., Mequon, WI). An EC (electrical conductivity) meter was used to determine salinity. DNA was extracted from viable leaf samples and was used to genotype the samples as the native or the invasive subspecies, following the CR-RFLP technique for genotyping common reed chloroplasts (Saltonstall 2003). Preparation of soil samples and laboratory procedures followed methods in Price et al. (2013).

We used linear mixed effects models in R (R Development Core Team, 2009) with package lme4 (Bates et al., 2015) to model soil attributes as a function of genotype and transect-position. The latter factor specified whether the soil sample was collected from the stand interior or from the area adjacent to the stand. Soil attributes considered were percent moisture, salinity, and concentrations of ammonium (NH_3), nitrate (NO_3^-), and phosphorous (PO_4). The linear mixed effects models allowed for a different random intercept for each stand. The best model was determined by comparison of AIC values (Akaike, 1974), a method for choosing between competing statistical models which is based on maximizing goodness of fit and minimizing the number of parameters required. We performed an analysis of variance (ANOVA) in R (R Development Core Team, 2009) to compare the best parameterized model to the null model, from which we derived $\text{Pr}(> \chi^2)$ values (Table XI).

TABLE XI
CANDIDATE LINEAR MIXED EFFECTS MODELS OF SOIL ATTRIBUTES AS FUNCTIONS OF
COMMON REED GENOTYPE AND TRANSECT-POSITION

Model ^a	ΔAIC	DF	Pr(>X ²)
%moisture ~ (1 stand)	34.3	3	
%moisture ~ genotype + (1 stand)	25.2	4	
%moisture ~ transect-position + (1 stand)	8.9	4	
%moisture ~ genotype + transect-position + (1 stand)	0	5	<0.001
nitrate ~ (1 stand)	6.9	3	
nitrate ~ genotype + (1 stand)	0	4	0.003
nitrate ~ transect-position + (1 stand)	8.8	4	
nitrate ~ genotype + transect-position + (1 stand)	2.0	5	
phosphorous ~ (1 stand)	3.4	3	
phosphorous ~ genotype + (1 stand)	0	4	0.02
phosphorous ~ transect-position + (1 stand)	5.2	4	
phosphorous ~ genotype + transect-position + (1 stand)	1.8	5	
EC ~ (1 stand)	1.6	3	
EC ~ genotype + (1 stand)	1.5	4	
EC ~ transect-position + (1 stand)	0.01	4	
EC ~ genotype + transect-position + (1 stand)	0	5	0.06
ammonium ~ (1 stand)	0.4	3	
ammonium ~ genotype + (1 stand)	2.2	4	
ammonium ~ transect-position + (1 stand)	0	4	0.12
ammonium ~ genotype + transect-position + (1 stand)	1.9	5	

^a The best models for each soil attribute are determined by comparison of AIC values and are listed in bold.

2. **Crowdsourcing**

We developed a network of 50 managers engaged in control of common reed. The managers characterized ongoing management efforts and provided data which we used to determine environmental drivers of invasion common across a range of ecotypes. To solicit interest in our research, we created a website, planned an introductory webinar, and disseminated invitations to attend the webinar and view the website via email-listservs including the Great Lakes Phragmites Collaborative, Plant Conservation Alliance, Northeast Illinois Invasive Plant Partnership, Invasive Plants Association of Wisconsin, and Midwest Invasive Plant Network. Some individuals forwarded the invitation to other networks, e.g., U.S. Air Force personnel and Colorado county weed managers.

We conducted online webinars on 14 September, 2012 and 20 September, 2013. In the webinars, we described our research objectives and the role of managers in the project. We also explained how managers could expect to benefit from participating; the principle incentive was free common reed genotyping services. Another potential benefit was contribution to a long-term effort to identify which management actions are most effective for controlling common reed and reestablishing desired plant communities.

To expand our network after the pilot year in 2012, in 2013 we sent managers packages containing all of the equipment they needed to monitor and submit samples and data. The packages contained copies of data entry forms, protocols for data and sample collection, pre-labeled sample bags, answers to frequently asked questions ("FAQs"), and pre-paid flat-rate boxes for shipping samples back to us for analysis.

For each common reed stand, managers reported which management action was being used or was planned: herbicide, mowing, burning (fire), seeding, resting (no treatment), or other. We focused on actively managed common reed stands in our outreach efforts. However, we did not exclude “resting” stands that were not actively managed. This inclusion was particularly important in the case of stands for which management was contingent on identification of subspecies.

D. **Results**

1. **Environment and genotype**

Managers contributed common reed leaf samples that were viable for genotyping from 168 transects in 140 stands. Of these stands, 88 were determined to be the invasive genotype (63%). Samples from the interior of common reed stands had higher percent soil moisture and higher electrical conductivity. The invasive genotype was associated with higher percent soil moisture and higher salinity. The native genotype occurred in soils with higher concentrations of nitrate and phosphorous. Results from the linear mixed effects models for soil attributes are shown in Table XII.

TABLE XII
COVARIATES FOR SOIL ATTRIBUTES OF COMMON REED STANDS AS FUNCTIONS OF
GENOTYPE AND TRANSECT-POSITION, FROM LINEAR MIXED EFFECTS MODELS

Predicted variable	Fixed effect	Estimate \pm SE
% moisture	Transect position: interior	9.3 \pm 1.7%
% moisture	Genotype: native	-11.9 \pm 3.6%
nitrate	Genotype: native	12.4 \pm 4.1 $\mu\text{g/l}$
phosphorous	Genotype: native	4.0 \pm 2.01 $\mu\text{g/l}$
EC (salinity)	Transect position: interior	379.4 \pm 201.3 $\mu\text{S/cm}$
EC (salinity)	Genotype: native	-404.4 \pm 284.5 $\mu\text{S/cm}$

Figure 32 depicts the difference between the percent soil moisture in the interior of the stand and the adjacent uninvaded area, for stands of the native and invasive genotypes. Differences are more variable in the invasive genotype. Mean differences for both genotypes occur at approximately 0. We also compared visual assessments of hydrology to percent soil moisture of soil samples (Figure 33). There was a great deal of overlap in all three categories. Managers could best distinguish between dry soils and soils that were either muddy or submerged ("water"). Soils that were identified as muddy or submerged in water according to visual assessment are indistinguishable in terms of percent soil moisture.

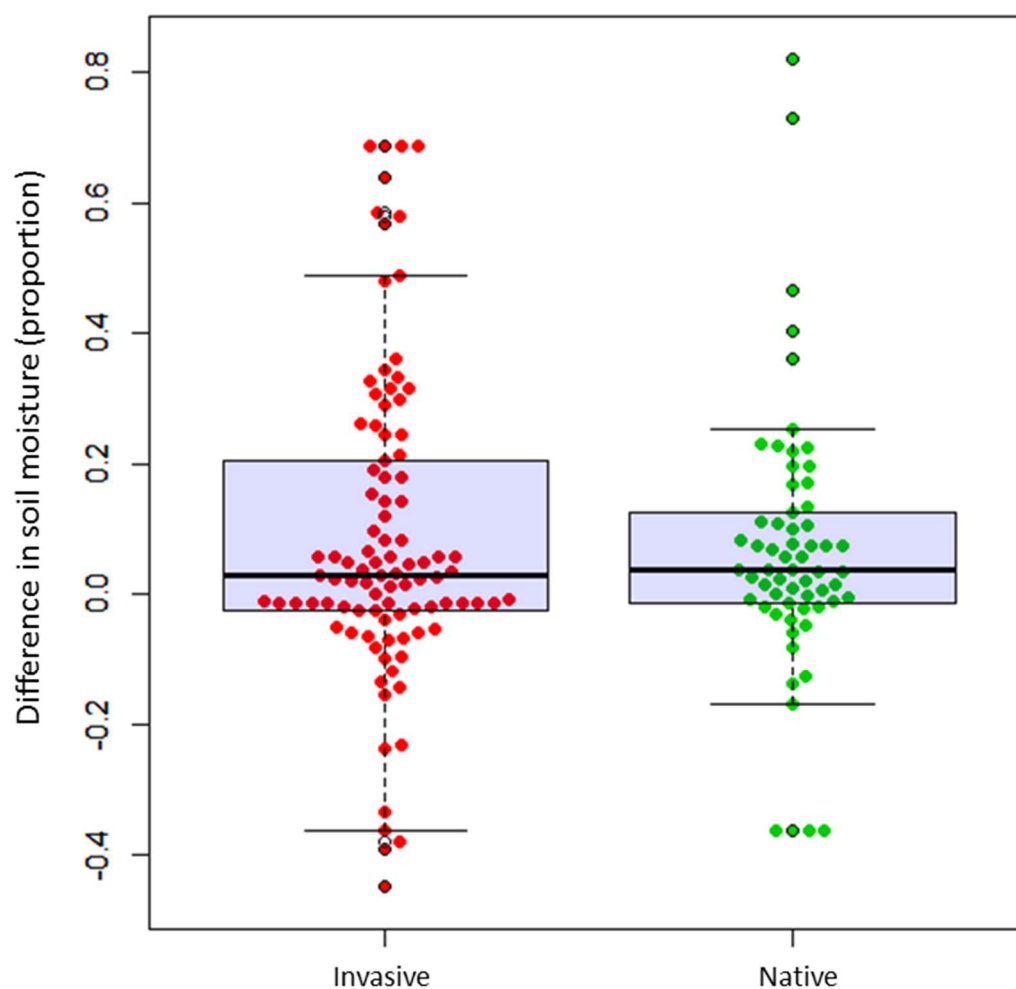


Figure 32. Boxplot (quartiles and median) of differences in soil moisture between paired plots inside and outside stands of common reed, grouped by genotype. Difference was determined as soil moisture within the stand minus soil moisture in the adjacent area. Red dots indicate samples of the invasive genotype. Green dots indicate samples of the native genotype.

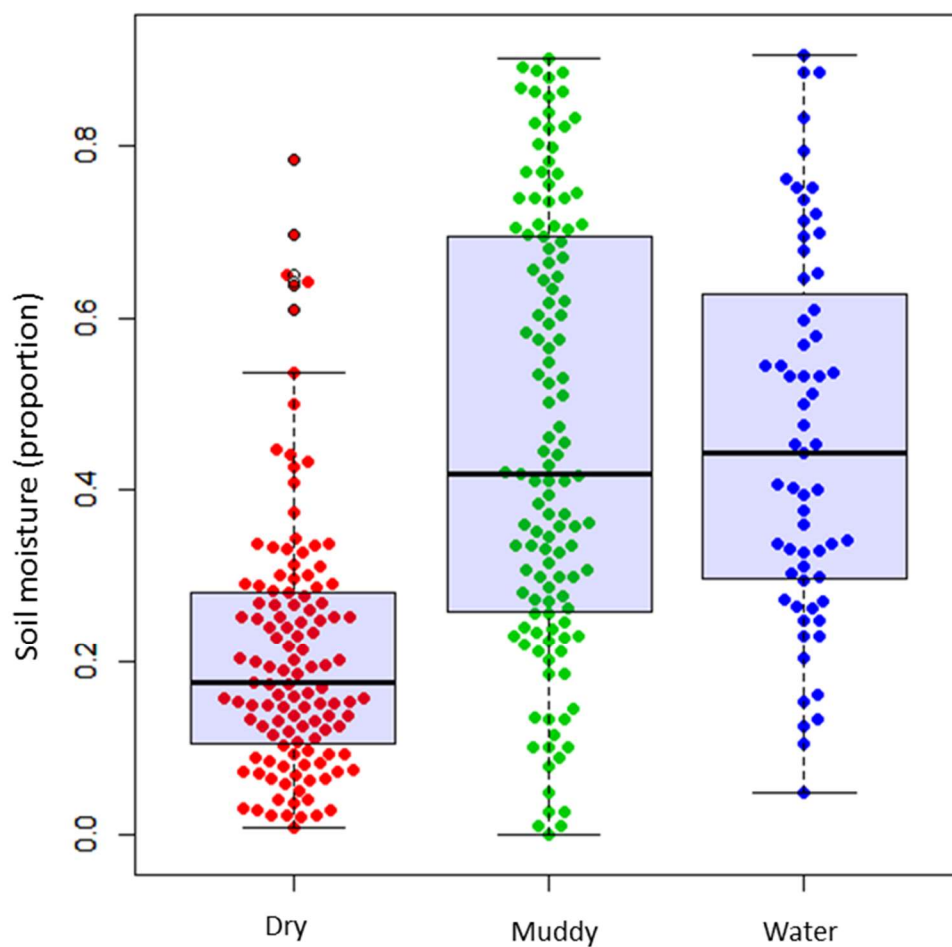


Figure 33. Boxplot (quartiles and median) of proportion soil moisture in common reed stands and the surrounding area, grouped by category recorded from visual assessment. Red dots indicate samples that were categorized as dry. Green dots indicate samples that were categorized as muddy. Blue dots indicate samples that were categorized as "water" (submerged).

2. **Management and genotype**

Eight management techniques for control of common reed were reported. Under "other" treatment, managers added disking (a mechanical control technique entailing use of a tractor-driven disc harrow) and hand pulling or cutting stems. Resting (no treatment) was employed on more common reed stands than any other management action (58%, $n = 106$), followed by herbicide (34%, $n = 63$). Infrequently applied actions included mowing (7%, $n = 12$), burning (4%, $n = 8$), grazing (4%, $n = 8$), and hand pulling or cutting of stems (2%, $n = 3$). Seeding and disking were applied on only one stand each.

The percentage of stands where resting, herbicide, or other treatments were applied depended on the affiliation of the manager and the common reed genotype (Figure 34). For example, state governments and private landowners applied herbicide to all of the invasive stands that they managed. Most native stands (86%) were not actively managed (rested), compared to 42% of invasive stands.

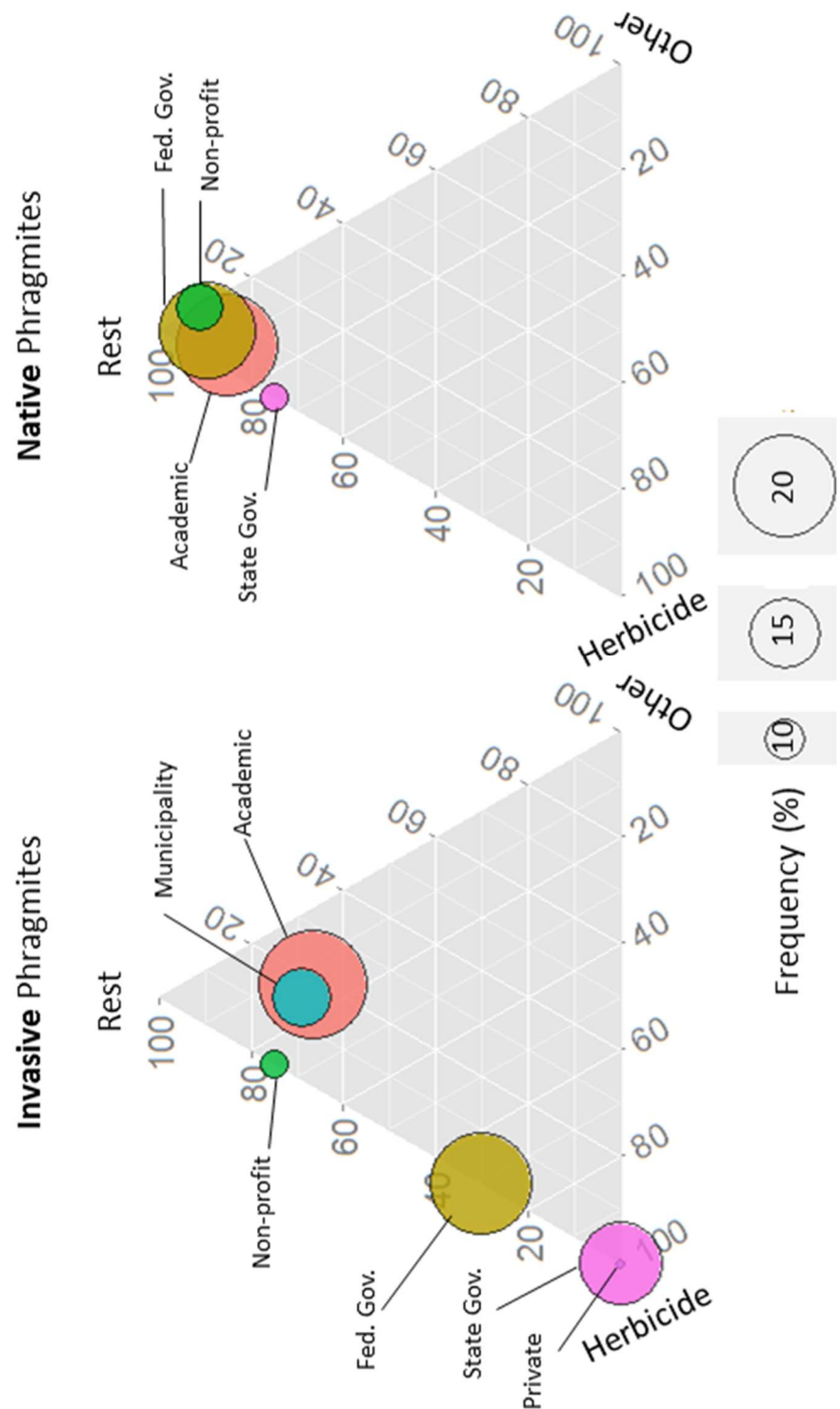


Figure 34. Ternary plots showing the frequency of three main treatment methods (rest, herbicide, and other) for invasive (left) and native (right) common reed, grouped by manager affiliation. Size of circles indicates the proportion of all stands of that genotype.

3. **Community composition and spatial area**

In stands of the invasive subspecies, common reed dominated (Figure 35). In 57% of the invasive stands for which percent vegetation cover was recorded ($n = 78$), the percent cover class for common reed was recorded as "high," indicating greater than 90% common reed cover. In contrast, 31% of stands of native common reed had greater than 90% common reed cover ($n = 51$). Additionally, 50% of stands of the invasive genotype contained no native species, whereas this was the case for only 31% of stands of the native genotype.

Excluding stands of unknown area, invasive stands were larger (mean 2.416 ± 3.6 ha SD; $n = 92$ invasive stands vs. mean 1.06 ± 3.13 ha SD; $n = 46$ native stands). Of native stands, 87% were less than 1 ha, and only 73% of invasive stands were less than 1 ha.

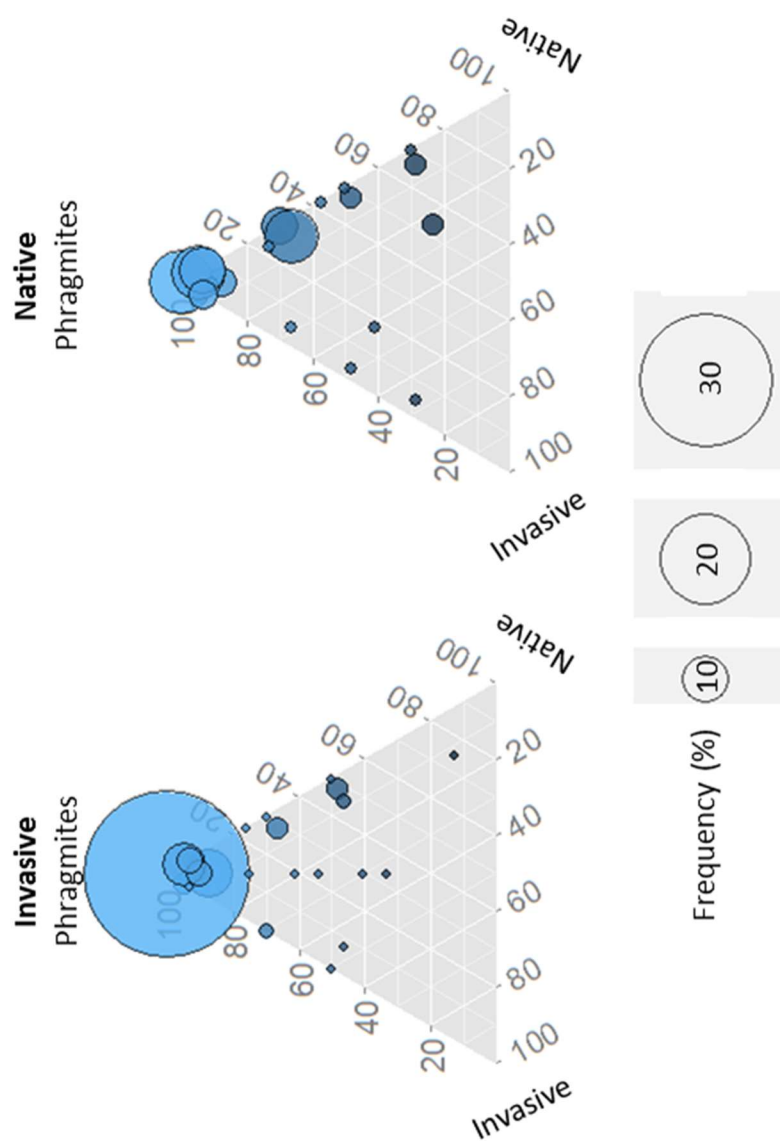


Figure 35. Ternary plots showing the community composition of invasive (left) and native (right) stands of common reed. Percent cover for common reed, (other) invasive, and (other) native species was recorded as one of five percent cover classes along transects: none (0%), low ($>0\%$ and $\leq 10\%$), medium-low ($>10\%$ and $\leq 50\%$), medium-high ($>50\%$ and $\leq 90\%$), or high ($>90\%$). For each stand, the midpoints of the recorded cover classes are averaged. Frequency (corresponding to size of points) refers to the proportion of invasive or native common reed stands of a specific community composition.

4. **Crowdsourcing**

The number of managers that contributed data and samples to this research effort increased from 6 to 50 between 2012 and 2013, likely as a result of distributing sampling materials in 2013. In 2013, we distributed 56 packages by mail, and received back 44 packages (80% response rate). Returned packages contained data sheets, soil, and common reed leaves for all monitored stands. One package was lost in the return mail. The response rate could not be determined in 2012 because we did not send packages that year.

Total spatial area sampled was ~282 ha (excluding stands of unknown area), comprising 209 common reed stands. Common reed stands were sampled in 16 U.S. states and in Ontario, Canada (Table XIII). Soil and common reed leaf samples, with associated monitoring data, were collected along 248 transects in the stands. Participants contributed data for up to 15 common reed stands each (mean 4.2 ± 3.3 stands SD). The area of stands ranged from less than 0.001 ha to 40.5 ha (mean 1.5 ± 4.7 ha SD). The Midwestern US, where we initially focused our outreach, were especially well represented. For example, 19 stands were sampled in Illinois, 17 in Michigan, and 35 in Wisconsin (see map in Figure 36). Colorado sampled the most common reed stands (39).

TABLE XIII**NUMBER OF COMMON REED STANDS AND SPATIAL AREA SAMPLED BY LOCATION**

State or Province	Stands	Stands of known	Mean area in	Total area in
	(n)	area (n)	hectares \pm SD	hectares
CA: California	5	5	2.2 \pm 1.2	10.9
CO: Colorado	39	37	0.6 \pm 0.9	22.1
FL: Florida	8	7	0.6 \pm 0.7	3.9
IL: Illinois	19	16	1.4 \pm 2.1	22.1
IN: Indiana	4	4	20.4 \pm 23.1	81.7
MA: Massachusetts	5	3	0.03 \pm 2.5	0.1
MD: Maryland	14	13	1.4 \pm 3.6	18.8
MI: Michigan	17	14	0.3 \pm 0.2	4.3
MT: Montana	14	12	0.1 \pm 0.2	1.9
NE: Nebraska	8	8	0.9 \pm 0.3	7.1
NJ: New Jersey	1	0	-	-
NY: New York	2	2	0.2 \pm 0.0	0.4
OH: Ohio	6	6	6.6 \pm 8.1	39.6
SD: South Dakota	11	11	0.6 \pm 0.6	6.1
VA: Virginia	12	12	3.9 \pm 3.9	46.4
WI: Wisconsin	35	32	0.3 \pm 0.4	10.7
Ontario, Canada	9	9	0.6 \pm 0.5	5.6

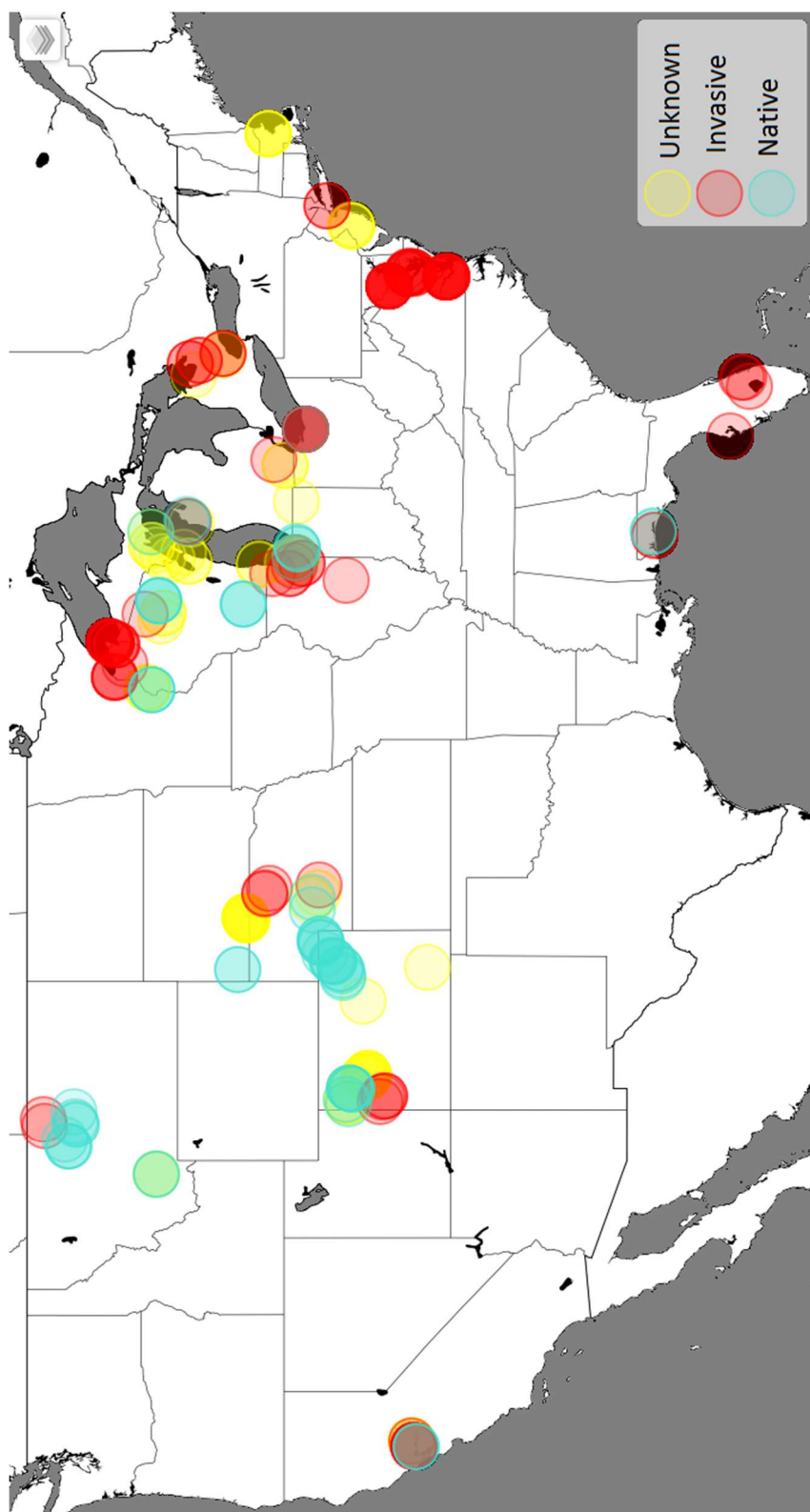


Figure 36. Map of sampled common reed stands. Circle color indicates genotype of samples: red is invasive, green is native, and yellow is unknown.

Contributing managers included land owners, volunteer stewards, professional natural resource management practitioners, and academics. Common reed-invaded wetlands were located within private, municipal, state, federal, and military lands. Common reed stands sampled by federal government agencies were largest (mean 2.9 ± 7.9 ha SD) (Table XIV). Federal government agencies represented 25% of participants, followed by municipalities such as city governments (21%), non-profit (21%), academic (13%), state government (12%) and private landowners or companies (8%). Managers associated with the federal government monitored a majority of the total spatial area (56%).

TABLE XIV

NUMBER OF COMMON REED STANDS AND SPATIAL AREA BY ORGANIZATION TYPE

Organization type	Number agencies (n)	Total area (ha)	Mean area (ha) \pm SD	Stands (n)	Stands of known area (n)
Academic	7	25.7	0.7 ± 1.0	40	39
Fed. Gov.	13	158.8	2.9 ± 7.9	62	54
Municipality	11	23.1	0.9 ± 0.9	29	27
Non-Profit	11	13.3	0.4 ± 1.1	41	37
Private	4	1.5	0.2 ± 0.3	9	6
State Gov.	6	60.0	2.1 ± 4.3	28	28

E. **Discussion**

1. **Environment and genotype**

We did not find evidence for the eutrophication hypothesis (Davis et al., 2009; Hobbs and Huenneke, 1992) which proposes that invasive plant species thrive in areas with elevated nutrients. In fact, we found the opposite, as nitrate and phosphorous concentrations were higher in common reed stands of the native genotype relative to the invasive genotype. This could be due to increased rates of sequestration of these nutrients by invasive common reed (Windham and Meyerson, 2003). In observational studies, the response of an invasive plant species to soil attributes and the influence of the invader on soil attributes are indistinguishable phenomenon and may co-occur (Price et al., 2013). Therefore in addition to responding to soil nutrients, common reed may itself alter soil characteristics including nutrient concentrations (Windham and Meyerson, 2003). For example, common reed often sequesters more nitrogen from soil relative to the tidal marsh plant communities it replaces in invaded wetland systems (Windham and Meyerson and Cronin, 2003). Price et al. (2013) also found that invasive common reed was not associated with more eutrophic conditions relative to the native genotype.

Our results support the conclusion that the likelihood of a wetland becoming invaded by common reed is far too complex to be assessed using a single variable (Ramseur, 2012). However, fine scale differences in soil moisture and salinity in the interior and area adjacent to common reed stands may be useful for managers engaged in control of common reed. Soil moisture in particular may be an important limiting feature that contributes to the delineation of common reed stands. In wetlands around

the St. Lawrence river in Canada, changes in water level have led to expansion of common reed into previously uninvaded habitats (Hudon, 2004).

From our comparison of visual assessment of hydrology to percent soil moisture, we conclude that visual assessment alone is inadequate to determine whether soil would be vulnerable to common reed invasion, based on the fine-scale differences found with the linear mixed effects model. Having percent soil moisture determined in a laboratory setting may be useful for managers to determine areas that may be vulnerable to invasion.

If soil moisture contributes to delineation of common reed stands, this also has implications for management techniques that involve manipulation of water levels. Flooding common reed is sometimes used in combination with other control techniques (Hazelton et al. 2014). However, these results suggest that increasing the percent soil moisture may increase the area vulnerable to common reed invasion. Comparing the difference between soil moisture inside and outside of common reed stands, we determined that differences were more variable in stands of the invasive genotype. This outcome is in agreement with experimental findings that invasive common reed is tolerant to a range of hydrologic conditions and flooding stress (Burdick and Konisky, 2003) and supports the broader tolerance hypothesis.

2. **Management**

We determined that invasive common reed is actively targeted for management to a greater degree than native common reed. The majority of sampled stands were invasive, likely because the behavior of invasive common reed is problematic compared to that of the native genotype (Price et al., 2013). Our analysis of community composition in common reed stands of invasive and native genotypes are in

agreement with Minchinton et al. (2006) and others who have found that invasive common reed necessitates management because it outcompetes native species and grows in monocultures.

3. **Crowdsourcing**

Crowdsourcing data, soil and leaves allowed us to sample geographically widespread common reed-invaded wetlands that were actively managed or were being considered for future management. Often such future management was contingent on genetic identification of subspecies, which motivated managers to participate. The outcomes from this crowd-sourcing effort provide insights into the conditions under which common reed is actively managed in the field. We also glean insights into the types of organizations controlling common reed and characterize their ongoing management practices.

The 80% response rate we observed refers to individuals that were effectively pre-screened by a series of conversations conducted beforehand. To receive a sampling package, the manager first had to answer several questions via email. For example, we asked potential participants how many stands they intended to sample, so that we could provide adequate data sheets and pre-labeled sample bags. Fifty-one individuals expressed interest in the project in 2012, and 105 individuals expressed interest in 2013. Most individuals that expressed interest did not follow-up with information necessary to receive sampling packages. We found that using conversations to screen applicants and sending sampling materials greatly increased the number of managers that participated in this research.

Many managers that participated in this research communicated to us that genetic analysis of common reed leaf samples, i.e., free testing of whether they had native or

invasive common reed, was their primary motivation for participating. Thus, offering genotyping services could be an effective incentive in projects that collect data and samples via crowdsourcing for cryptic invaders. However, we caution that managers should be carefully advised about how to collect viable samples. We requested that managers collect green leaf samples to facilitate genetic analysis, but in many cases this was not possible. We were unable to determine the genotype of many leaf samples that were dry and brittle. Some mucky and wet leaf samples were also impossible to genotype. We had a 74% success rate extracting DNA from and genotyping leaf samples.

The data we collected via crowdsourcing is a nonrandom sample. Data is essentially filtered because we only received samples from managers that (1) we contacted, either directly or indirectly, via outreach efforts during the timespan in which the project was active, and (2) were interested in and able to participate in this research. For example, extensive representation of Colorado in our dataset is likely the result of voluntary mass distribution of our contact information amongst weed managers throughout that state. Another potential bias stems from allowing managers to set up transects at a starting point of their choosing on the edge of the common reed stand. This made the protocol easier to follow than if we had required a random starting point. However, managers likely selected parts of the stand that were easiest to access, avoiding wet areas or areas with thick vegetation. Ultimately, we relied on managers to follow our protocol and we had no oversight over the process.

F. **Conclusions and future work**

Partnerships between the public and scientists have flourished in recent decades, in part to citizen science efforts that make use of new technologies that facilitate

massive collaborations (Theobald et al., 2015). However, many projects that use a crowd-sourcing approach to data and sample collection do not ultimately contribute to peer-reviewed literature. For example, only approximately 12% of biodiversity-focused citizen science projects contributed to scientific peer-reviewed articles according to a recent review of such projects (Theobald et al., 2015). Herein, we harness the power of ongoing management efforts to control common reed by crowd-sourcing ecological observations and samples from managers.

The protocol we developed would facilitate several analyses that we had planned on but ultimately did not have the resources to perform. We had hoped to assess the genetic structure, diversity, and relatedness of common reed stands using microsatellites, hence collection of leaf samples from the interior and edge of stands. There is evidence that clonal reproduction is dominant in the interior of large common reed stands, whereas sexual reproduction contributes to expansion at the edge of stands (Keller, 2000). Therefore, we hypothesized that genetic diversity would be lower in the interior of common reed stands relative to the edge. However, we were ultimately unable to perform microsatellite analysis due to funding constraints and difficulty extracting adequate DNA for subspecies identification in many samples. We included an assessment of the plant community outside of the common reed stand because we hypothesized that over the long-term, the adjacent plant community would recolonize cleared areas. Monitoring the return of a native plant community after eradication of common reed would be an important next step in terms of quantifying the success of common reed management.

In the long term, we sought to develop a monitoring protocol and network that could serve as a platform for future adaptive management efforts to improve

management outcomes for common reed control. Development of a network is a critical first step in harnessing the power of ongoing management to accelerate learning regarding how to most effectively control common reed and restore impacted habitats. We present a method for implementing such a network. Ultimately, we envision expanding this approach to strengthen the collective learning process over time by involving more managers. Standardized data and sample collection, coupled with a centralized online database, could facilitate sustainable, long-term monitoring. Such long-term monitoring is necessary to characterize the efficacy of treatment techniques over meaningful timeframes, rather than documenting only fleeting, short-term results under artificial conditions.

G. **Acknowledgments**

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I express my sincere thanks to all of the managers that participated in this research. Participants spent time and effort to learn about our project and to submit data and samples; without these individuals this work would not have been possible. Additionally, many individuals passed along information about our project to others, which facilitated our development of a large network of managers. The Great Lakes

Phragmites Collaborative posted a summary of our research effort on their website.

Clément Kouyoumdjian and Laura Steger performed genetic laboratory work including extracting DNA and running samples on gels to determine genotypes. Anna Braum organized and scanned in paper data forms. Joel Brown provided advice regarding the presentation of the context of this work. This work was funded by an Illinois-Indiana Sea Grant.

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A Decision Support Tool for Adaptive Management of Native Prairie Ecosystems

by

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