DECISION MAKING IN ECOLOGY AND ITS APPLICATIONS TO ANIMAL

CONSERVATION

by

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ABSTRACT OF THE DISSERTATION

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Ecology is the study of interactions between organisms and their environment. These interactions are shaped by the decisions made by both humans and non-human animals. From the human perspective our decisions to develop or preserve land have had and continue to have far reaching impacts on non-human animals. In light of the decisions we make, non-human animals must then make decisions on when/where to move, where to feed and where to breed. Understanding how animals make decisions is a difficult and complex endeavor, but one that can provide a vast amount of ecological knowledge. Knowledge related to animal decision making and other ecological processes can then be used to inform our own decision making processes in terms of when, where and how to invest scarce monetary resources intended for animal conservation.

In this dissertation I use simulation models to examine animal movement decisions and how these decisions can affect species persistence and ultimately species conservation. Additionally, I make use of optimization techniques to study how the different ways in which we choose to quantify the costs of conservation management can affect monetary expenditures. From the simulation models I found that evolved behaviors that dictate patterns of animal movement in the early breeding season can have profound

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effects on species persistence, in some cases leading to declines in expected annual growth rates of 25-50% when cues are altered by anthropogenic change. Additionally, the simulation models show that differences in animal behavior at the level of the individual affects the relative costs and benefits of animal movement which in turn help us to understand how animal decision making interacts with and responds to anthropogenic habitat changes. Finally, the use of optimization techniques allowed us to determine that using detailed tax records to quantify the costs of conservation management allows for a cost-savings of 70-75% over other, more traditional metrics used to quantify costs within the conservation planning literature.

The results obtained here have important implications for how we approach conservation management. The results of our simulation models provide a bridge between the seemingly unrelated fields of animal behavior and conservation.

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Introduction

Decisions about the management of threatened and endangered species are often made in the face of considerable uncertainty (McDonald-Madden et al. 2008). This uncertainty can take on many forms ranging from uncertainty of the population dynamics of a species, to how much money is available for conservation or how changing environmental conditions may affect our approach to conservation. Ignoring these uncertainties can lead to poor decision-making in regards to species conservation and management (Regan et al. 2005). In order to address some of these uncertainties we must attempt to synthesize information from multiple fields of study and question existing paradigms so that we can reevaluate how we think about species conservation in light of new information. This dissertation attempts to do this by first bridging the disparate fields of animal behavior and conservation biology by examining animal decision making processes and evaluating how this information can be applied to real conservation issues. Additionally, we then examine how the decisions we make in regards to reserve site selection and the monetary metrics by which we do so affect conservation expenditures in human dominated landscapes.

Anytime that an animal chooses one particular behavior from a set of alternatives a 'decision' has been made (Dill 1987). Decision-making as it applies to questions such as where to breed, who to mate with, and where/what to eat is a central determinant of an organism's fitness (i.e. the product of its survival and fitness) (Kao & Couzin 2014). As such, decision-making in animals has been the subject of many studies and is still an active area of research within the field of behavioral ecology (Lima 1998; Sih 1980; Stahlschmidt et al. 2014). The incorporation of this important behavioral knowledge into

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the field of conservation biology has been championed by many researchers, but the linkage between the two fields remains weak at best (Berger-Tal et al. 2011; Caro 1999). This weak linkage stems from the fact that many conservation biologists believe behavioral studies operate at scales irrelevant to protecting entire landscapes, the mostcost effective means of conservation (Buchholz 2007). Regardless of whether this assertion is actually true or not, it is important that we harness all available sources of information to better inform conservation management given the ever-present influence of anthropogenic change that all organisms are subject to.

The anthropogenic change that virtually all organisms experience is especially important from both a behavioral and conservation standpoint because behavior mediates the interactions of an organism with its environment (Sih et al. 2011). This statement leads to a few hypotheses concerning the effect of anthropogenic change on behavior: 1) an organism could alter its behavior such that it adapts to its new surroundings and continues to persist in human dominated landscapes, 2) an organism does not change its behavior in any way, in which case the result for species persistence is not always readily apparent, 3) or the organism changes its behavior, but it does so maladaptively and potentially expedites its own decline. It is this final point about altered decision making under anthropogenic change that is especially troubling and thus requires that we begin to examine decision making in animals more closely so that we can better inform conservation management decisions.

Maladaptive decision-making is a product of a mismatch between the cues that individuals use to make decisions and the fitness associated with those choices (Robertson et al. 2013). Cues that result in an individual showing preference for low quality habitat have been termed ecological traps (Robertson & Hutto 2006; Schlaepfer et al. 2002). Related is the possibility that cues become reversed so that individuals mistake high quality habitat for low; called perceptual traps (Patten & Kelly 2010). For many years it seemed that traps were a seemingly rare and unimportant ecological phenomenon (Robertson & Hutto 2006). More recent research though has shown that the incidence of traps is indeed quite ubiquitous and widespread across many animal groups (Jaquemet et al. 2011; Leighton et al. 2008; Semeniuk et al. 2009).

Species whose annual fitness depends on accurate and reliable cues appear to be very susceptible to traps (Robertson et al. 2013). It is for this reason that I chose to examine prospecting behavior and its potential for acting as a trap in human modified landscapes. Prospecting has been documented in a number of animal groups and thus a greater understanding of potential changes in prospecting behavior could have farreaching implications (Ponchon et al. 2012; Ward 2005). Prospecting individuals actively search their local landscape assessing the quality of nearby habitats in advance of breeding (Reed et al. 1999). Prospecting individuals will enjoy higher fitness (as compared to when they do not prospect)(Baker 1978; Boulinier & Danchin 1997; Ponchon et al. 2012), and thus higher annual growth rates (Schjorring et al. 1999). If the cues that prospecting individuals use to identify high quality habitat become unreliable, these individuals will become trapped. By explicitly modeling traps as maladaptive prospecting decisions we can determine when evolved behaviors are particularly detrimental to population persistence. Further insights into prospecting behavior provided by an examination of individual personality traits may alter how we view the prospecting process and ultimately what it means for species under changing environmental

conditions. Recent studies have shown that aggressiveness, boldness and sociality often differs between individuals of a species and these differences could have direct impacts on ecological process and thus alter our approach to animal conservation (Cote et al. 2010; Duckworth 2008).

While it is imperative that we try to consider all aspects of a species biology and ecology when considering conservation management, it is also true that species conservation is often limited by the availability of money (Joseph et al. 2009). In light of this it is important that we make smart decisions and use limited conservation funds in an efficient and cost-effective manner. Typical conservation efforts focus on setting aside land in reserve sites and there has been a large amount of money that has been spent on trying to do this (Szabo 2007). In spite of these large expenditures there are landscapes that have been largely ignored by the conservation community, specifically those are rapidly urbanizing landscapes (Rouget et al. 2003). Modern urban landscapes are complex mosaics of land uses with associated high heterogeneity in land values (Seto & Shepherd 2009). Recent research shows that optimal planning tools that explicitly incorporate costs of land acquisition tend to result in large total savings while also realizing all conservation targets (Armsworth 2014; Naidoo et al. 2006). This provides a modicum of optimism that, if such tools were utilized in future land acquisitions, it may be possible to acquire land in these urbanizing landscapes in a more cost-effective manner. However, this supposition is often based upon the use of land values that either take into account only land area or the value of agricultural land (Jantke et al. 2013; Margules et al. 1988). The validity of using these metrics of cost should be reexamined in urban landscapes due to the fact that these measures may do a poor job at capturing the high heterogeneity of costs typical of these areas.

My work will contribute to the field of conservation biology by showing the value of incorporating decision making behavior into how we approach animal conservation and additionally by reevaluating how we make decisions concerning the incorporation of costs in landscape_-level conservation planning in human dominated landscapes. The objectives of my dissertation are the following:

- Examine how evolved behaviors such as prospecting can serve as traps within rapidly changing environments and propose how this may affect species conservation efforts
- Investigate the influence of individual personality traits in animal decision making and examine how this decision making may change in the face of increased anthropogenic change
- Compare traditional conservation cost metrics to another more detailed cost metric to evaluate how this affects spatial conservation planning in highly urbanized landscapes

Evolved behaviors and traps

Human-altered environments are increasingly common. In many instances these alterations lead to maladaptive decision-making via a mismatch between the cues that individuals use to make decisions and the fitness associated with those choices. The dissociation of cues can result in individuals showing preference for low quality habitat or mistaking high quality habitat for low; called ecological and perceptual traps respectively. We suggest that species that prospect for breeding habitat are particularly susceptible to being trapped. Prospecting allows individuals to actively search and assess their local landscape prior to breeding, and has been documented across a variety of animals. We show that when prospecting takes place within the context of ecological and perceptual traps there are reductions of 25-50% in annual population growth rates; albeit the effects of ecological traps are not as severe as those of perceptual traps. Furthermore, our results show interactive effects between strength of cues and landscape change under both trap scenarios. Because there is very rarely any information on the perception of organisms and how they integrate cues into their decision making, this final result argues that our current interpretations of how traps affect organisms are inadequate, which in turn severely complicates our attempts to conserve animal populations.

This chapter is formatted for *Conservation Biology* and will be submitted there (Burkhalter and Lockwood, *in prep*).

Individual personality and its role in evolved behavior

Personality can play a large role in dispersal decisions, influencing how each individual estimates and values expected costs versus benefits of venturing out to explore the unknown. We contrast the impact of persistence on fitness using statistical decision theory to examine the relative success of prospecting movement (which is a widespread behavior used by animals to explore available breeding habitat before determining where to settle) in different landscapes among individuals with different personalities. We provide a quantifiable measure of the impacts of relative tenacity in prospecting behavior on fitness gains/losses. Our results indicate that, regardless of landscape composition,

individuals with greater tenacity in prospecting strategy have reduced fitness gains relative to individuals who are more willing to both initiate novel strategies, but then also abandon the new strategy rapidly if initial search does not seem fruitful. We show that fitness gains from choosing an appropriate prospecting strategy (i.e. abandoning poor habitat or staying in rich habitat) can be very high, indicating a potentially large influence from personality on fitness. Importantly, we show that relative fitness gains are highly dependent on the availability of high quality habitat in the landscape, even if the difference under varying fitness outcomes between poor and rich habitat was substantial. We further provide some insight into the impact climate-related change in habitat quality/availability may have on the success of different personality types.

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Conservation planning decisions in urban landscapes

Habitat loss is one of the most common causes of species endangerment, and thus conservation groups have invested heavily in building networks of protected areas. However, the costs of acquiring protected areas can be quite high. In spite of these large conservation expenditures these networks do not sufficiently represent the full variety of terrestrial ecoregions within its boundaries. The ecoregions that appear to be largely ignored from a conservation perspective and are under-represented in existing protected areas often lie within urbanizing landscapes which consist of complex mosaics of land uses with associated high heterogeneity in land values. Our work illustrates the importance of accurately defining cost metrics in reserve design planning. Relative to

relying on cost surrogates or average land values across our study area, we were able to achieve the same conservation goals for approximately 1/4 of the cost by using tax assessed values of individual land parcels. This results demonstrates that in urban landscapes we must reconsider the usage of agricultural land and land area as cost proxy for evaluating the costs of conservation. There is further need to evaluate whether our results in terms of the conservation efficiencies obtained using tax assessed land values hold in other urban landscapes, but as of yet systematic conservation planning studies have largely ignored a more detailed analysis of landscapes that have a large urban component.

This chapter is formatted for *Conservation Biology* and will be submitted there

(Burkhalter, Lockwood, Maslo, Leu, and Fenn, in prep).

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Chapter 1:When prospecting behavior turns into a trap

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Running title: Incorporating behavior into management

Abstract

Human-altered environments are increasingly common. In many instances these alterations lead to maladaptive decision-making via a mismatch between the cues that individuals use to make decisions and the fitness associated with those choices. The dissociation of cues can result in individuals showing preference for low quality habitat or mistaking high quality habitat for low; called ecological and perceptual traps respectively. We suggest that species that prospect for breeding habitat are particularly susceptible to being trapped. Prospecting allows individuals to actively search and assess their local landscape prior to breeding, and has been documented across a variety of animals. We show that when prospecting takes place within the context of ecological and perceptual traps there are reductions of 25-50% in annual population growth rates; although the effects of ecological traps are not as severe as those of perceptual traps. Furthermore, our results show interactive effects between strength of cues and landscape change under both trap scenarios. Because there is very rarely any information on the perception of organisms and how they integrate cues into their decision making, this final result argues that our current interpretations of how traps affect organisms are inadequate, which in turn severely complicates our attempts to conserve animal populations.

Key words: population model, prospecting, behavior, ecological traps, perceptual trap, conservation

1. Introduction

Virtually all species on Earth live in environments that have to some extent been altered by humans (Sih et al. 2011). In some cases, such alterations will lead to individuals making maladaptive behavioral decisions in regards to where to breed, who to mate with, and where and what to eat (Robertson et al. 2013). Maladaptive decision-making is a product of a mismatch between the cues that individuals use to make decisions and the fitness associated with those choices (Robertson et al. 2013). Cues that result in an individual showing preference for low quality habitat have been termed ecological traps (Robertson & Hutto 2006; Schlaepfer et al. 2002). Related is the possibility that cues become reversed so that individuals mistake high quality habitat for low; called perceptual traps (Patten & Kelly 2010). Species whose annual fitness depends on accurate and reliable cues appear to be very susceptible to traps (Robertson et al. 2013). We suggest that species that prospect for breeding habitat fall into this susceptible category. Prospecting individuals actively search their local landscape assessing the quality of nearby habitats in advance of breeding (Reed (1999). Prospecting individuals will enjoy higher fitness (as compared to when they do not prospect) (Baker 1978; Boulinier & Danchin 1997; Ponchon et al. 2012), and thus higher annual growth rates (Schjorring et al. 1999). If the cues that prospecting individuals use to identify high quality habitat become unreliable, these individuals will become trapped. We seek to gain insight into the effect of traps on population growth by explicitly modeling traps as maladaptive prospecting decisions. Our results provide insight into when traps are particularly detrimental to population persistence.

There has been extensive documentation of prospecting across a variety of animals; principally among birds, but also in groups as disparate as mammals and insects (Aragón et al. 2006; Canonge et al. 2011; Reed et al. 1999; Ward & Schlossberg 2004; Young et al. 2005). Prospecting behavior can occur within any age class and across a wide range of life history strategies (e.g., long-lived vs. short lived, colonial vs. territorial, etc., see Dittmann et al. 2005; Kesler et al. 2007; Reed et al. 1999; Serrano et al. 2004; Zicus & Hennes 1989). Furthermore, prospecting can occur either prior to, or after, a breeding season. All prospecting individuals respond to site-specific social and physical cues, which together provide reliable indicators of the quality of resources and/or mates at that site (Cox & Kesler 2012; Doligez et al. 2003). The proximal mechanisms for how prospecting individuals distinguish habitat quality are thought to include factors like conspecific reproductive success, but the topic remains unclear and is under active investigation (Mares et al. 2014). Human-related activities can change the quality of a habitat (i.e. convert habitat quality from high to low) without altering the cues that prospecting individuals use to determine that quality (Ahlering et al. 2010; Ward 2005). When these cues are no longer reliable due to anthropogenic change, we should expect maladaptive decisions to reduce fitness (Battin 2004).

There are a handful of published population models that seek to represent prospecting behavior (Delgado et al. 2014; Reed et al. 1999), but none have linked prospecting to traps. Existing models of prospecting have primarily been concerned with predicting the optimal amount of time to spend prospecting (Baker 1978; Johnson 1989). Although these models provide relevant insights, they do not represent prospecting decisions in a manner that allows them to be easily modified to include traps. Existing models do not

explicitly include a term which dictates how movement is related to the quality of habitat an individual is assessing in any given time step. These models instead assume that individuals will randomly search until they encounter high quality habitat, and related, that those individuals that spend more time moving are more likely to find high quality habitat. In the context of prospecting, we suggest that traps can be modeled by including a term that defines how individuals respond to the cues they encounter as they move across a landscape at each time step, and what effect altering those cues have on population growth rates. If we set cues to be reliable indicators of low and high quality habitat, and we have individuals respond to these cues by either settling (high) or moving on (low), then this model will depict reliable prospecting and it can be used to judge under what circumstances such behavior provides a substantial boost in annual growth rate. If we set the cues to be unreliable, individuals will respond by settling in low quality habitat (ecological trap) or moving out of high quality habitat (perceptual trap). Incorporation of such dynamics within population models will thus allow us to realistically depict the consequences of traps via prospecting and the factors that moderate their effects on annual population growth rates.

Here we develop a simple model framework to compare annual population growth rates produced by individuals that randomly search for breeding habitat, prospect for high quality habitat using reliable cues, and prospect for breeding habitat using unreliable cues (traps). Furthermore, we examine how a change in the prevalence of high and low quality habitat within a landscape (composition) modifies the effects of prospecting on annual growth rates. We identify when reliable prospecting provides the needed boost in fitness to push annual population growth rates above replacement levels. We expect that the benefit of prospecting will be higher than random searching when high quality habitat is relatively scarce in the landscape, but only when cues are reliable. We explore these relationships at two ends of the life history spectrum; species that exhibit high annual reproduction and low survival (fast life history) and those that exhibit the reverse (slow life history). Although species falling on either end of this spectrum have shown empirical evidence of prospecting (Reed 1999), existing models have not considered the degree to which their growth rates may increase via prospecting, what effect traps have on growth rates, and under what circumstances either of these outcomes is likely. We use bird populations as our empirical support for this model, in large part because prospecting and traps are well-documented within this group but also because there is considerable published information on bird life history.

2. Materials and Methods

We built a spatially-implicit model to quantitatively compare annual growth rates that result from three possible pre-breeding within-season dispersal actions; random movement, prospecting using reliable cues, and prospecting using unreliable cues (traps). We set annual growth rates (λ) to be a product of habitat-specific survival and fecundity, where λ is calculated independently for populations that prospect (*p*) and those that randomly search available habitat (*rs*);

$$(\lambda_{rs}) = \sum_{z=1}^{z=2} \{ (s_z \times m_z) \times \theta_z \}$$

$$(1a)$$

$$(\lambda_p) = \sum_{z=1}^{z=2} \{ (s_z \times (m_z - we^{bt})) \times \theta_z \}$$
(1b)

where s and m are the survival and fecundity of an average individual respectively, and θ represents the amount of habitat of type z within the landscape (where z is either high or low quality). We use a time-dependent sub-routine to determine the length of a search, whether a search is random or involves prospecting using reliable or unreliable cues. We use this sub-routine to determine the habitat in which an average individual settles to breed, and thus the values of s and m in equation 1a,b. This sub-routine is described below in more detail. When individuals prospect we include a cost of movement function, we^{bt} , that serves to subtract from the fecundity experienced in the settlement location. Here w serves as the intercept term of an exponential function, e is the base of the natural log and b is a constant that determines the steepness of the exponential curve; while t represents duration of search. We use an exponential function to represent this movement cost to ensure that prospecting behaviors that are relatively short in duration will not incur much loss in fecundity, while behaviors that delay settlement have significant effects on final reproductive output. We refined our exponential function to reflect greater levels of realism by determining a value for our b parameter that reflects breeding bird phenology (Battin 2004). The exponential cost function is commonly assumed in dispersal literature (Pettersson & Hedenström 2000; Phillips et al. 2008).

We represent movement before settling to breed (within-season) using a timedependent search sub-routine where the probability of settling in habitat of low or high quality is calculated as the proportion of a given habitat type within the landscape (θ_z), the probability of initiating a search given the type of habitat (*d*), and the probability of staying in the given type of habitat (*q*, where *q* =1-*d*). The values of *d* and *q* are set for each run of the model according to the scenario under consideration (Figure 1; see

below). Within each run, habitat type is chosen at each time step according to its prevalence in the landscape. To determine how prospecting occurs during each run of the model, an exhaustive set of possible prospecting strategies is constructed, with each strategy differing in the number of time steps spent prospecting and the sequence of habitat types visited by a prospecting individual. A single prospecting strategy is chosen for each run of the model based upon the cumulative probability that results from the individual probabilities of finding a habitat type (i.e. θ_z), the probability of settling in the chosen habitat (q), and the probability of leaving a particular habitat (d). Thus, for example, if high quality habitat is common in the landscape (θ_1 is high and thus is likely to be found) and there is a high probability of settling in that habitat type (q is high), and the probability of initiating a search is low in high quality habitat (d is low), the cumulative probability of continuing to search (advancing another time step) is low. If another time step is not initiated, settlement has occurred and the values of m and s that correspond to that habitat type are used in equation 1b. Alternatively, if low quality habitat is common (θ_2 is high and thus is likely to be found), and the probability of initiating a search is high in low quality habitat (d is high), the probability of continuing to another time step is high; that is, searching continues. This process continues until the search is terminated (settlement), or three time steps have passed. In such cases, we assume that the individual is a 'floater' and never breeds (m = 0). Each time that an individual leaves a particular habitat type it is assumed that the search phase lasts three days, and we reference this duration in the cost of movement function as t in we^{bt} . Because our model is spatially implicit we assume that the probability with which a particular habitat is chosen in each time step remains constant.

We use the above model to explore three search scenarios; random search, prospecting with reliable cues, prospecting with unreliable cues (i.e. traps). These scenarios are defined by the values of d and q used. For random searching, these variables are both set to 0. This ensures that for each model run, a habitat type is chosen according to its prevalence in the landscape and the survival and fecundity associated with that habitat are used in equation 1a. Functionally, annual growth rate is then the sum of habitat specific survival and fecundity values weighted by the prevalence of each habitat type in the landscape (equation 1a).

For scenarios where prospecting occurs, d (and by default, q) are varied systematically to represent strength of cues and their reliability. To depict prospecting using reliable cues we set d to be high within low quality habitat, and low in high quality habitat (Table 2). If the strength of cues is low, then the difference in the probabilities of moving between the two types of habitat will be small. We are thus assuming that individuals may use reliable cues to judge habitat quality, but their response is muted so that they do not show a strong aversion to low quality habitat or great affinity to high quality habitat (low cue strength). We represent heightened response to cues by simultaneously increasing the value of d in low quality habitat and reducing it in high (high cue strength; Table 2). To represent traps we changed the value of d so that an individual would show either a preference for settling within low quality habitat (ecological trap), or a high probability of moving out of high quality habitat (perceptual trap). For the perceptual trap scenario, we simply reversed the probabilities of prospecting used for reliable prospecting, across all strengths (Table 2). For ecological traps, we used a constant, low value of d for high quality habitat, but successively

lowered d within low quality habitat (Table 2). This change had the effect of reducing the strength of the cue to move on in low quality habitat, and thus increased the likelihood that individuals would settle there to breed.

To create landscapes with differing amounts of the two habitat types (high and low quality), we generated a sequence of numbers ranging from zero to one, moving along this range in steps differing by 0.005 (i.e. $0 \rightarrow 1$, by 0.005). This effort produced a total of 201 unique landscape compositions. To define survival and fecundity across habitat qualities (high and low) we used empirically-derived average survival and fecundity (defined as the number of fledglings to successfully leave the nest) data for seven bird species that we know exhibit within-season prospecting. The data were sourced from published research and from life history tables within Bennett and Owens (2002) (see Table 1, Brown & Brown 1998; Clark & Martin 2007; Mills & Ryan 2005; Niel & Lebreton 2005; Nolan Jr 1978; Robertson 1993; Rolland et al. 2010). The seven bird species were binned into either slow or fast life history categories, which we defined based upon annual survival and egg production values within Bennett and Owens (2002). For two of the seven species we could not find a survival value for low quality habitat. When this occurred, we calculated the percentage difference in fecundity between high and low quality habitat in this species and reduced the survival rate in the high quality habitat by this amount to derive survival value for low quality habitat. For each life history group we then calculated the average survival and fecundity measurements in both habitat types and used these as the model input parameters for the different life history groups.

Within each search scenario (prospecting or random), a model run represents a single calculation of annual population growth rate (λ) according to equation 1a or 1b. For each unique landscape composition we conducted 1000 model runs. We then computed an average λ value across all of these runs. Thus, each model run can be thought of as independent realization of either random settlement or prospecting, and the average λ value calculated can be thought of as the population-level consequence of either action. The entire process was repeated for both life history types. All simulations and subsequent analysis were performed in program R v.3.1.0.

3. Results

In the random movement scenarios, annual population growth rate (λ) always declines in a monotonic fashion as the prevalence of low quality habitat increases in the landscape (Fig. 2 and 3). For slow life history species, prospecting, whether reliable or not, always results in a lower value of λ as compared to random movement on average (Fig 2a–c). When prospecting is reliable (Fig. 2a), there is an interaction between the strength of the cue and the amount of low quality habitat in the landscape. When we assume individuals react strongly to reliable cues, population growth rates stay relatively high (hovering around $\lambda = 1$) until the landscape is composed of >40% low quality habitat; after which growth declines sharply (Fig. 2a). This threshold response occurs because individuals strongly respond to low quality habitat by continuing to search, and searching has a cost in the form of reduced fecundity. As the landscape becomes dominated by low quality habitat, the probability of long prospecting searches increases. Because we set the cost of searching to be exponential through time, longer searches result in much higher costs, and thus larger reductions in λ . For slow life history species, this threshold response is muted when the strength of the cue is lessened so that individuals are less likely to either move out of low quality habitat or stay in high quality habitat.

For slow life history species, unreliable cues consistently result in annual population growth rates that are lower than either random or reliable prospecting (Fig. 2b, c). When we set cues so that they mimic ecological traps (i.e. individuals are unlikely to move out of low quality habitat), population growth for slow life history species steadily declines as low quality habitat becomes more common in the landscape (Fig. 2c). The differences in strength of cues are negligible in this scenario although there is an interaction with cue strength and prevalence of low quality habitat (Fig. 2c). Note however that when low quality habitat is common (nearly 100% of the landscape) annual population growth rates remain higher than when prospecting occurs using reliable and strong cues (comparing Figs. 2a and c). Finally, in the perceptual trap scenario annual population growth rates for slow life history species increase as the prevalence of low quality habitat increases; especially when the strength of cues is high (Fig. 2b). The influence of cue strength diminishes on growth rate as low quality habitat becomes common. The decreased values of λ when there are large amounts of high quality habitat are the result of increased searching due to the perception of lower attractiveness of the high quality habitat.

For the fast life history species we see very different results when prospecting uses reliable cues (Fig. 3a). When cue strength is at its highest level (i.e. the attractiveness of high and low quality habitat are at their respective maximum and minimum) reliable prospecting produces a positive population growth rate ($\lambda > 1$) as long as the landscape
consists of at least 60% of high quality habitat. Additionally, reliable prospecting with moderate to strong cues produces a higher annual population growth rate than random movement up to the point at which there is approximately 70% low quality habitat in the landscape (Fig. 3a). When we evaluate the effect of perceptual traps on annual growth rates for fast life history species we again see reductions in λ when there is very little low quality habitat in the landscape (Fig. 3b). However, unlike the slow life history species we do not see an attenuation in these reductions as more low quality habitat is added to the landscape. Additionally, as the strength of cues increases we see that λ remains consistently low across all landscape configurations indicating that if cues are strong, the population will decline drastically regardless of landscape configuration (Fig. 3b). When we evaluate annual growth rates under the ecological trap scenario we again see a decrease in λ as low quality habitat increases in prevalence, but this reduction is nowhere near as severe as under the perceptual trap scenario (Fig. 3c). Finally, under the ecological trap scenario for fast life history species, we do not observe an interaction between strength of motivation and increases in low quality habitat as is the case in every other scenario regardless of life history. As more low quality habitat is added to the landscape we see almost identical rates of population decline regardless of strength of cues (Fig. 3c).

4. Discussion

Attempts to conserve animal populations, especially within changing environments, may be severely complicated by ecological traps (Robertson et al. 2013). However populations models routinely used within conservation biology direct us away from considering ecological traps by not explicitly accounting for habitat selection (Battin 2004). In doing so these models will produce overly optimistic estimates of population persistence when traps are present. We show that perceptual traps in particular will profoundly reduce population growth rates. For both slow and fast life history species we show reductions of 25-50% in annual population growth rates in the presence of perceptual traps. The effects of ecological traps also reduce annual population growth rates, but these reductions are not as severe. Furthermore, our results point to the fact for both slow and fast life history species there are interactive effects between strength of cues and landscape change under both trap scenarios. Because there is very rarely any information on the perception of organisms and how they integrate cues into their decision making, this final result argues that our current interpretations of how traps affect organisms are inadequate.

Both types of traps lead to lower population growth rates when compared to random settlement irrespective of the strength of cues or the landscape composition. This suggests that prospecting can lead to rapid population declines if the cues organisms use to select habitat are altered in some way. Perceptual traps are considerably worse than ecological traps due to their effect of driving down population growth rates (λ) when the landscape is composed mostly of high quality habitat. When there is a mostly high quality habitat perceptual traps lead to reductions in growth rates of up to 50%, while ecological traps lead to declines of 10%. The low population growth rates observed when high quality habitat is common are the result of avoidance of high quality habitat and thus increased time spent prospecting. In order to counteract traps it has been suggested that you simply have to restore degraded habitat or preserve more high quality habitat (Robertson et al. 2013). In addition to performing these actions, our results suggest that if the cues are not there or are incorrect, the population will suffer severe declines.

Conservation biologists often lack sufficient knowledge of animal decision making behaviors to implement successful behavioral manipulations (Greggor et al. 2014). This gap may have severe consequences because the degree to which prospecting individuals rely on cues to make decisions determines the drop in growth rate they experience when traps occur. When cues are strong, individuals respond sharply to this information and either stay put or move on. When cues are reliable and strong we can see benefits to population growth rates, but these benefits drop off very quickly as low quality habitat increases in prevalence. Interestingly, when cues are strong but incorrect, as in perceptual traps, it does not matter what the landscape looks like; population growth rates drop precipitously. Animal behavior has been shown to be an important determinant of a species ability to cope with anthropogenic change (Sih 2013); and our results strengthen this assertion. We suggest that understanding not only the cues themselves, but how much species rely on these cues to make breeding decisions will determine the severity of traps.

It is imperative for any species to select the best quality habitat for breeding, but for a fast life history species this need is even more pressing because one bad breeding season can greatly affect lifetime reproductive success. Our results indicate that for fast life history species prospecting leads to positive population growth rates when strength of cues is high (i.e. individuals can accurately assess habitat quality), even when there is a moderate amount of low quality habitat within the landscape. We know that prospecting is common in these species (Reed et al. 1999), which would also lead us to presume that

traps may be very common for these species in areas that have experienced significant anthropogenic change. Our results also suggest that prospecting may not be as important in long-lived species due to the fact that prospecting does not increase expected annual population growth rates above those observed for random settlement. Interestingly in both cases, when cues are accurate, the prevalence of low quality habitat has a marked effect on growth rates. This effect can be thought of as a behavioral sink, whereby population growth drops at a very rapid rate when large amounts of low quality habitat are around due to the effects of evolved behaviors. This behavioral sink is so severe that it eclipses the effects of ecological traps (regardless of cue strength) and approaches that of strong perceptual traps. To some extent this arises due to the way we penalized for continued searching, but even if a less severe penalty is imposed the effect will remain. This result raises the question of what empirical evidence exists for assessing the penalty of continuing to prospect. There is some indication that individuals that do not settle to breed within a timely fashion ultimately become 'floaters', which allows them to remain in a population, but results in their not breeding in a given year (Reed et al. 1999).

Our model provides an initial attempt at incorporating prospecting behavior into a conservation model, while also providing a bridge between the fields of animal behavior and conservation management. Behavioral ecology is increasingly recognized as a part of species conservation, yet there is continued debate over its relevance to conservation biology (Moore et al. 2008). Much of this debate stems from the fact that many conservation ecologists believe behavioral studies operate at scales irrelevant to protecting entire landscapes, the most-cost effective means of conservation (Buchholz 2007). Understanding how prospecting and traps operate in different species and how

changes in landscape composition in turn affects these processes allows for more informed management. The identification of traps is crucial and there are many places that have been identified as potential locations of traps such as, agricultural fields, airports, artificial wetlands and most commonly habitat edges (Best 1986; Flaspohler et al. 2001; Gates & Gysel 1978; Kershner & Bollinger 1996; Tilton 1995).

Our model can accommodate a wide variety of species, any range of habitat values or number of habitat types, and is thus easily parameterized using basic field-derived information on survival, fecundity and movement. Although our model is spatially implicit, we suggest this is appropriate due to the complexity associated with incorporating different life histories and habitat specific probabilities of prospecting. Additionally, spatially implicit models such as ours possess an inherent strength in that they allow modelers to combine all existing quantitative knowledge in a straightforward manner, providing a more transparent view of how dispersal behaviors influence conservation outcomes (Bode & Brennan 2011). Detailed dispersal data is sparse for many large, free-ranging species, and thus our modeling approach provides an avenue by which researchers can begin to investigate how behavior influences conservation planning without having to wait for detailed behavioral information.

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Table 1. List of species that exhibit early season prospecting behavior. Life history classifications based upon annual adult survival and annual egg production values found in Bennett and Owens (2002). Species specific demographic parameters (survival (s) and fecundity (m) sourced from 7 other studies (see Methods). HQ denotes high quality estimate and LQ denotes low quality estimate

Species	<u>S</u> HQ	<u>S</u> LO	$\underline{\mathbf{m}}_{\underline{\mathbf{H}}\underline{\mathbf{O}}}$	m _{LQ}
Slow life history species				
Roval Albatross	0.95	0.89	1.05	0.96
Wandering Albatross	0.94	0.86	1.07	0.98
Sooty Albatross	0.94	0.91	1.05	1.02
Northern Fulmar	0.95	0.85	1.11	1.00
Mean	0.945	0.88	1.07	0.99
Fast life history species		0.20	2.79	1.00
Cliff Swallow	0.45	0.29	2.78	1.80
Prairie Warbler	0.5	0.33	3.13	2.03
Orange-crowned Warbler	0.5	0.33	2.34	1.52
Mean	0.48	0.22	2.75	1 79

Table 2. Conceptual framework of how cues relate to traps and prospecting behaviors. (+) indicates that organisms exhibit attraction towards a certain habitat type based upon perceived habitat quality. (-) indicates that organisms are not attracted towards a certain habitat type based upon perceived habitat quality. (•) indicates no preference towards a certain habitat type based upon perceived habitat quality. (•) indicates no preference towards a certain habitat type based upon perceived habitat quality. Range of parameter values used to characterize strength of cues to leave a given habitat type for the reliable cue scenario, perceptual traps scenario and the traditional ecological trap scenario. Higher parameter values indicate that an organism is more likely to leave a given habitat type and lower parameter values indicate that an organism is less likely to leave a given habitat type. HQ denotes high quality habitat and LQ denotes low quality habitat.



FIG. 1. A graphical representation of the basic inputs of our modeling framework. Θ_z represents the proportion of the landscape made up of high and low quality habitat, *d* is the probability of leaving a habitat type once it is found, *q* is the probability of staying in habitat type once it is found, m_z is the fecundity of a given habitat type, s_z is the survival of a given habitat type and λ_n is the expected annual population growth rate of the two actions.

FIG. 2a-c. Line graph showing how expected annual population growth rates for slow life history species change in response to the proportion of the landscape composed of low quality habitat and the strength of cues. Moving from left to right, the first panel depicts the results of random movement and prospecting using reliable cues (Fig. 2a), the second panel depicts the results of random movement and prospecting under perceptual traps (Fig. 2b), and the third panel depicts the results of random movement and prospecting under perceptual traps (rig. 2b), and the third panel depicts the results of random movement and prospecting under perceptual traps traditional ecological traps (Fig. 2c). The solid line black line(—) corresponds to the expected annual population growth rate across all model runs for random movement. The solid red line (—), the solid blue line (—), and the solid green line(—) lines correspond to the expected annual population growth rate across all model runs for prospecting associated with cue strength scenarios 1, 2 and 3 respectively.

FIG. 3a-c. Line graph showing how expected annual population growth rates for fast life history species change in response to the proportion of the landscape composed of low quality habitat and the strength of cues. Moving from left to right, the first panel depicts the results of random movement and prospecting using reliable cues (Fig. 3a), the second panel depicts the results of random movement and prospecting under perceptual traps (Fig. 3b), and the third panel depicts the results of random movement and prospecting under perceptual traps traditional ecological traps (Fig. 3c). The solid line black line (—) corresponds to the expected annual population growth rate across all model runs for random movement. The solid red line (—), the solid blue line (—), and the solid green line (—) correspond to the expected annual population growth rate across all model runs for runs for prospecting associated with cue strength scenarios 1, 2 and 3 respectively.



Figure 1



Figure 2



Figure 3

Chapter 2: The impact of personality on the success of prospecting behavior in changing landscapes

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Abstract

Personality can play a large role in dispersal decisions, influencing how each individual estimates and values expected costs versus benefits of venturing out to explore the unknown. We contrast the impact of persistence on fitness using decision theory to examine the relative success of prospecting movement (which is a widespread behavior used by animals to explore available breeding habitat before determining where to settle) in different landscapes among individuals with different personalities. We provide a quantifiable measure of the impacts of relative tenacity in prospecting behavior on fitness gains/losses. Our results indicate that, regardless of landscape composition, individuals with greater tenacity in prospecting strategy have reduced fitness gains relative to individuals who are more willing to both initiate novel strategies, but then also abandon the new strategy rapidly if initial search does not seem fruitful. We show that fitness gains from choosing an appropriate prospecting strategy (i.e. abandoning poor habitat or staying in rich habitat) can be very high, indicating a potentially large influence from personality on fitness. Importantly, we show that relative fitness gains are highly dependent on the availability of high quality habitat in the landscape, even if the difference under varying fitness outcomes between poor and rich habitat was substantial. We further provide some insight into the impact climate-related change in habitat quality/availability may have on the success of different personality types.

Introduction

One of the least understood but more common components of dispersal is prospecting behavior (Ponchon et al. 2012, Morales et al. 2010). Prospecting movements are exploratory in nature and aid an individual in finding, assessing and settling within high quality habitat. It occurs at either the start or end of the breeding season, and involves individuals moving within their local landscape, assessing available information about the quality of the various habitats present. If prospecting occurs at the begin of the breeding season it is used to choose where to settle and breed in the current breeding season. If prospecting occurs at the end of the breeding season it is used to choose where to breed in the following breeding season (Reed, 1999). The ability of an individual to find, recognize, and settle within the highest quality habitat available provides fitness payoffs in the form of higher fecundity and survival, and thus has direct implications for population persistence (Morales et al. 2010). While the degree to which fitness is increased by moving into a new habitat (i.e. differences in the demographic rates between available habitats relative to each other) and the energetic and opportunity costs associated with engaging in searches (cost of moving) can be considered objective metrics, both tenacity in prospecting strategy (i.e. how long one persists in one's current behavior) and individual estimation, or selectivity, of current habitat quality seem highly susceptible to influence from individual personality. We explore how varying these factors influences fitness gains associated with prospecting movements, and evaluate these fitness gains across a variety of landscape compositions. We thereby provide a more mechanistic understanding of how individual personality can affect the evolutionary success of prospecting behavior, especially as habitat patch quality might be expected to change over time.

While individual dispersal events seemingly only have fitness consequences for that individual, numerous studies have shown that dispersal has important implications for population dynamics and species' distributions (Bowler and Benton, 2005). In contrast to this statement, a simplifying assumption made in many studies of dispersal is that all individuals of a population behave identically. While helping to reduce complexity, this assumption prohibits exploration of the ways in which individual personality can affect the dispersal process. Recent studies have shown that aggressiveness, boldness and sociality often differs between individuals of a species and these differences could have direct impacts on the dispersal process (Cote, Clobert, Brodin, Fogarty and Sih 2010, Duckworth 2008). These studies provide the impetus to try and provide a more mechanistic understanding of how personality affects prospecting movements.

Prior to dispersing and settling in a new breeding site organisms will often prospect for more favorable conditions in neighboring areas (Matthysen 2012), and prospecting has been documented in a variety of animals (Ponchon, Gremillet, Doligez, Chambert, Tveraa, González-Solís and Boulinier 2012, Reed, Boulinier, Danchin and Oring 1999, Ward 2005). For prospecting behavior to provide a consistent net fitness payoff to an individual, three things must be true. First, there must be enough high quality habitat within a landscape for an individual to have a reasonable chance of finding it, and the boost in survival and fecundity that comes with moving to and settling within these habitats must be relatively high (Fahrig 2007). Second, the costs of searching for high quality habitat must be small due to there being some combination of (a) low energetic requirements of movement or (b) a lack of a fecundity penalty associated with delaying the onset of breeding while searching (Bonte, Van Dyck, Bullock, Coulon, Delgado, Gibbs, Lehouck, Matthysen, Mustin and Saastamoinen 2012). Third, an individual must be able to gather reliable information on the quality of the various habitats they encounter while prospecting, and then be able to transfer this information behaviorally into a motivation to either move or stay put (Dall, Giraldeau, Olsson, McNamara and Stephens 2005).

There have been a variety of theoretical and field investigations into each of these three factors as they relate to dispersal patterns more broadly (Burgess, Bode and Marshall 2013, Caswell, Lensink and Neubert 2003, Lidicker Jr and Stenseth 1992). These studies highlight the context-dependent nature of when dispersal should be favored, and provides relevant mechanistic details about each factor in isolation (Cote and Clobert 2012, Matthysen 2012). In regards to prospecting there have been a variety of field experiments that document prospecting behavior (e.g., Calabuig, Ortego, Aparicio and Cordero 2010, Mares 2012), but little exploration of its mechanistic underpinnings other than as a way to gather public information (Blanchet, Clobert and Danchin 2010, Danchin, Giraldeau, Valone and Wagner 2004). More interestingly the impact of individual personality on estimations of the two subjective factors (i.e. tenacity and selectivity), and thus on the relative fitness of personality types within the same suite of external environmental factors, has gone unexplored.

Mathematical and simulation models have a long history of producing basic insights into dispersal more generally (Kisdi, Utz and Gyllenberg 2012). The output from such models provide insight into understanding the evolution of dispersal, and how to devise conservation actions while explicitly considering dispersal dynamics (Lookingbill, Gardner, Ferrari and Keller 2010). We use a population-level, spatially implicit simulation model to evaluate the impact on the costs and benefits of prospecting over a variety of landscape compositions from two major facets of personality: *tenacity* in prospecting strategy and *selectivity* about habitat quality. We also explore the resultant effects on the net fitness gains (or losses) for individuals with those personality traits living in these landscapes.

Methods

Our model describes early-season prospecting behavior only (as opposed to late-season; Reed, 1999). Thus, the fitness consequences of an individual's prospecting decisions are realized within that year's breeding season and not in the following season. This decision simplified the conceptualization of fitness components (survival in particular); but we note that our model structure can be modified to represent late-season prospecting behaviors as well.

Our modeling framework is based on decision theory (DT), which was developed within a biological context as a conceptual framework to evaluate optimality of behavior under uncertain conditions (McNamara 1980). DT models have at their core a mathematical formulation of the costs and benefits of a suite of possible actions. Here we utilize the essential structure of DT models (i.e. formalizing costs and benefits associated with actions), but we do not assume the need for an optimal decision. Instead, we quantitatively compare net fitness payoffs associated with the impact of personality type on the success of resulting prospecting behavior given three mechanistic rules about how costs and benefits accrue to individuals. DT provides a way to study complex outcomes associated with behavioral decisions that can in some cases be solved without the use of complicated mathematical formulations (Possingham, Andelman, Noon, Trombulak and Pulliam 2001). This aspect of DT models is ideal for our goals here as it provides a relatively simple and transparent way of calculating costs and benefits over a range of often-complex inter-relationships. We collate our results in such a way so as to create a framework for future study, indicating under what circumstances each cost-benefit mechanism plays a dominant role in the fitness payoffs of prospecting under different personality types.

We designed our model so that individuals either settle in the breeding habitat first encountered and never use prospecting to assess other habitat types ('Not Prospecting'), or they can engage in prospecting behaviors that allow them to move across a landscape seeking other habitat states ('Prospecting'). If they do not prospect, we defined them to select a settlement site at random based strictly upon the proportional amount of each habitat type available. If they are prospecting, we defined them to disperse using prospecting behavior in which each individual has the option to search among all available habitats or a subset of all habitat types. We define θ to describe the habitat options available to a prospecting individual. This variable is often referred to as a 'state of nature' in SDT parlance (McNamara 1980). We define the first state of nature, θ_{1} , as the proportion of habitat available that could be considered objectively high quality breeding habitat. The remaining states of nature, θ_2 and θ_3 , are defined as the proportion of the landscape that consists of objectively mid-quality breeding habitat and unsuitable breeding habitat, respectively. (These proportions are designated as external reality, rather than reflecting the estimation of the quality from the perspective of the individual; influence of individual personality on habitat estimation is captured solely in whether or not the individual is highly selective in their habitat preferences.)

These two basic inputs to the SDT framework (actions and states of nature) are organized into a payoff matrix (i.e. a graphical structure that allows us to determine the fitness outcomes associated with each behavior), and for each unique action by state of nature combination there is a resultant fitness payoff value, $P_{x,n}$ (e.g., $P_{\text{pros},2}$ is the payoff associated with prospecting and the state of nature represented by θ_2 ; see Figure 1), calculated as;

Eq.1
$$(P_{x,n}) = [(f_t - K(d)) * s_t)] - [(f_i * s_i)],$$

where f_i and s_i are the fecundity and survival of an individual in its initial location, f_t and s_t are the fecundity/survival of an individual in its location of settlement (terminal location), K(d) represents the cost of movement as a function of search duration.

By moving to a habitat of lower quality relative to the initial location, an individual can be expected to lower their survival and fecundity. The losses that result from moving into lower quality habitat can be thought of as opportunity costs. The cost of movement is the energetic costs associated with engaging in search behaviors. For purposes of our exploration into the impact of personality, we assume that the energetic cost is linear in time, but that individual personality manifests by estimation of that cost and we therefore explored three functional forms: linear, exponential, and logarithmic functions of search duration (Figure 2; Table 1). As assumed, a linear function represents an "accurate" estimate of monotonically increasing costs with increased time searching across the landscape. In this case, the individual's personality can be considered as moderate: willing to begin prospecting should it seem appropriate, but also willing to abandon prospecting should the first few days of effort fail to yield a more promising option_(hereafter referred to as a 'realistic' personality). In comparison, the exponential function captures a less tenacious personality type, easily willing to engage in short duration movements but hesitant to prospect for longer durations_(hereafter referred to as a 'fickle' personality). Lastly, the logarithmic function captures a very 'tenacious' personality type, in which there is a large individual preference for continuing in whichever is the current strategy. For individuals with this personality, initiating even short duration searches is very unlikely, but once initiated, it is also unlikely that they would abandon prospecting until an acceptable quality habitat is found.

To capture these personality types mathematically, we set the cost of movement in Equation 1 as (1) md+b for the linear function (where *m* is the slope; *b* is the intercept; and *d* represents the duration of search) (2) be^{md} for the exponential function personality type (where *b* is the intercept term of the exponential function, *e* is the base of the natural log; *m* is a constant that determines the steepness of the exponential curve; and *d* represents duration of search), and (3) as $b(log_{base10}(md))$ for the logarithmic function (where *b* is the intercept term; *m* is a constant that determines the shape of the logarithmic curve; and *d* once again represents duration of search). A value of 0.1 was used to define *b* for the linear and exponential functions and a value of 0.6 was used to define *b* for the logarithmic function. The values of the slope term were 0.10, 0.14 and 2.3 for the linear, exponential and logarithmic cost functions respectively. While the exact values and quantitative predictions made by our models are, of course, dependent on the choices of these values, they were chosen to provide insight into general outcomes and interpretations gained by comparison of the qualitative representation of the curves as we attempted to capture broad personality types. We also assume that mortality is uniform across personality types and therefore due no include a direct mortality penalty term within the model. Our model is built to explore only the relative impact of personality type and its impact on prospecting success. To determine whether or not prospecting under each personality type results in a net fitness gain or loss given a particular landscape composition, we took the sum over all states of nature for each action such that

Eq. 2 (NP_x) =
$$\sum_{n=1}^{n=3} \{P_{x,n} \times \theta n\},\$$

is the net payoff associated with either not engaging in prospecting behavior (NP_{Not}), or engaging in prospecting behavior (NP_{Pros}). The value of θn is the proportion of the landscape composed of each habitat type, and $P_{x,n}$ is the prospecting cost/benefit of each action (*Prospect* or *Not Prospect*) as calculated in Eq. 1. Because 'not prospecting' does not include any searching, $P_{x,n}$ for that case does not any include opportunity or energetic costs.

Our goal was to explore how NP_x varies according to personality type under different mechanistic rules (some reflecting objective states of reality, and others reflecting subjective states of personality). Our rules are therefore: the objective differences in survival and fecundity across habitat types (demographic difference relative to each other), the subjective estimations of energetic and opportunity costs from initiation and continuation of searching (tenacity as measured by cost of moving), and the selectivity of an individual determining their propensity to move out of one habitat type and into another (motivation for moving). Our focal metric for relative fitness payoffs among the personality types, and within different objective environmental scenarios, becomes the NP_{Pros}/NP_{Not} , hereafter referred to as the NP ratio (NP_r). When this fraction is above 1, prospecting movements resulted in a higher net fitness payoff than not prospecting. When this fraction is below 1, not engaging in prospecting behavior provided a better net fitness payoff. The exact value of this fraction provides a continuous measure of how much more (or less) prospecting pays in terms of net fitness benefits. In this way, we can consider this the measure of when the environment will selectively favor which personality type, and by how much. We set three levels of each mechanistic rule, and by changing these rules independently we derived 9 scenarios (Table 1). We have only 9 scenarios because we examined changes in each mechanistic rule independently and without interactions. When changing the demographic rule we held tenacity constant at Level 2 (i.e. 'realistic' rule) and selectivity constant at Level 1. When changing the tenacity rule we held the demographics constant at Level 1 and again we held selectivity constant at Level 1. Finally, when changing the selectivity rule we held demographics constant at Level 1 and we held tenacity constant at Level 2 (i.e. 'realistic' rule). We then calculated NP_r across all landscape compositions (see below) for each scenario.

To then determine which mechanistic rule, when changed, had the greatest effect on the expected fitness costs/benefits associated with moving, we calculated the cumulative absolute difference (CAD) in fitness between each scenario (Eq.3);

Eq. 3:
$$CAD_n = \sum_{x=1}^{x=3} |(NP_{x,n} - NP_{y,n})|$$

where n denotes the mechanistic rule under scrutiny, and x and y are place holders for the different levels associated with that mechanistic rule. For example, equation 3 formulated to estimate the cumulative absolute differences in fitness associated with the three more or less tenacious personality types assigned to cost of moving is:

$$CAD_{cost} = |(NP_{log} - NP_{exp})| + |(NP_{log} - NP_{lin})| + |(NP_{lin} - NP_{exp})|$$

where *log* represents a logarithmic cost function, *exp* an exponential function and *lin* a linear function. Because CAD is a scalar quantity with an associated magnitude, but lacking any directionality (i.e. the differences between the various levels of a mechanistic rule could be positive or negative) we also recorded the direction of change. Due to the fact that we evaluated CAD over a large number of landscape compositions (see below), it would be impossible to report all the component differences that comprise all CAD values for each scenario. Thus we report the component differences in CAD when the values were at their maximum and minimum absolute differences within each scenario.

Based on first principles and from a variety of existing research (Jauker, Diekötter, Schwarzbach and Wolters 2009), we know that net fitness payoffs will vary according to the availability of habitats of different qualities across the landscape (i.e. landscape composition). Thus, we generated a set of landscape compositions that ranged in a standardized way from being dominated by low, to medium, to high quality habitat. To do this, we generated a sequence of numbers ranging from zero to one, moving along this range in steps differing by 0.05, to create landscapes that varied systematically in the proportion of high quality and mid-quality habitat available (θ_1 and θ_2). The proportion of unsuitable habitat (θ_3) was then created by simply subtracting the sum of each sequential pairing of θ_1 and θ_2 from one (i.e. $\theta_3 = 1 - (\theta_1 + \theta_2)$). This effort produced a total of 231 different landscape compositions after we removed those combinations of θ_1 and θ_2 that greater than one . We used this set of landscape compositions for all scenarios (see above, Table 1) thereby allowing composition to change (and thus alter the trade-offs explored within each scenario) but in a standardized manner.

A fundamental mechanistic determinant of expected fitness payoffs associated with prospecting is the range of survival and fecundity rates (with the product being represented as λ) experienced by individuals in each of available habitat types (see equation 1). We set λ for each habitat type initially at 0.5, 1.0 and 1.5 for low quality, mid- and high quality habitat respectively. We then created two alternative demographic scenarios by increasing and then decreasing in tandem the survival and fecundity of midquality habitat by 15%. These changes had the effect of creating three levels of demographic payoff associated with moving from lower to higher quality habitat types (Table 1).

The costs of engaging in prospecting movement are also heavily influenced by the willingness of individuals to incur those costs (i.e. their motivation to move). There are a variety of factors that can influence this motivation (Christe, de Lope, González, Saino and Møller 2001, Travis, Murrell and Dytham 1999), but here we focus on 'selectivity': how habitat quality influences motivation. To characterize an individual's selectivity about habitat type (i.e. how motivated they were to move from poor to rich habitat) we assigned probabilities of engaging in search behaviors that were specific to each habitat type (γ). We set the probability of searching to be greatest for individuals residing within

low quality habitat, allowing it to decrease in mid-quality habitat, and reach its lowest value in high quality habitat (Table 1). To explore how varying the selectivity of the individual influenced net fitness payoffs, we twice increased the selectivity (i.e. propensity to move) by 10% increments in low quality habitat while at the same time we decreased the selectivity by 10 % increments in high quality habitat (Table 1). This effort created three levels for how selective an individual was in discriminating between habitat of various qualities, and then in responding to this information by dispersing out of low quality habitat or remaining in high quality habitat (Table 1). The values contained within in Table 1 were not informed by empirical data, but rather were simulated to investigate the shape of particular model inputs as opposed to being concerned with particular numerical results.

We allowed for an individual to visit all habitat types, a subset of the different habitat types, or continue to search without ever settling to simulate instances in which an individual searches for so long all available mates or breeding territories become unavailable . The probability of any particular search strategy occurring is a stochastic process and is determined based upon its cumulative probability resulting from the product of 3 variables: 1) the proportion of a given habitat type within the landscape (θ), 2) the probability of initiating a search (γ), and 3) the probability of the individual staying in a given habitat type once an it has initially arrived there (p_s , where $p_s=1-\gamma$.) Each time that an individual leaves a particular habitat type it is assumed that the search phase always lasts three days (as an arbitrary interval that allows uniform comparison), and we factor duration of search (d) into the relevant subjective cost function. For each combination of high, mid and low quality habitat (i.e. landscape composition) we conducted 100 model runs (100 realizations was determined to be computationally sufficient since there was no change in either outcome or variance of results from additional runs after this point). Each run consisted of the aforementioned steps where we combined the habitat specific estimates of survival and fecundity for each action per Eq. 1, allowing for the stochastic selection of a prospecting scenario to simulate the action of prospecting and its associated outcomes for each model run. We then computed the NP ratio and the cumulative CAD value to determine how the perceived costs and benefits of prospecting change when we change the mechanistic rules to reflect both changes in objective environment and subjective elements of individual personality from tenacity and selectivity. All simulations and subsequent analysis were performed in program R v.3.1.0.

Assumptions, limitations and future applications of model framework

Decision theory (DT) provides a concise and coherent framework with which to evaluate how various factors contribute to a complex ecological process, such as prospecting (Rousset and Gandon 2002). However, all models have their inherent limitations, tradeoffs and assumptions. We evaluated a subset of the factors we believe are important for the problem we addressed (McNamara 1980), and restricted ourselves to only the simplest cases (single factor influences; i.e. no interactive effects from more than one mechanistic rule being changed at once). This was done to ensure the clearest interpretation at this initial modeling step, but we anticipate that future models will want to explore these possibilities when applied to specific systems for which the shape of any interactive effects may be empirically determined. Similarly, the model is spatially implicit, which imposes limitations to interpretation such as lack of any connection or distance between different types of habitat. However, the use of a spatially explicit landscape computationally limits the number of distinct habitat patches that could feasibly be modeled, in addition to introducing limits on the number of distinct habitat compositions that could be constructed. We opted to err on the side of greater flexibility in exploring a wide range of landscape compositions. Finally, much like nearly all other theoretical work on dispersal and movement, we do not have the empirical data to verify specifics of our results (Bowler and Benton 2011). Our model, like many others, is meant to provide the conceptual framework from which specific, testable hypotheses may be generated rather than to test those hypotheses directly.

Results

Overall NP ratios (NP_r) and thus CAD values varied considerably across landscape compositions and as both the environmental and personality rules changed (Table 2).

Changes in NP_r across various landscape configurations

A primary pattern in *NP*_r is that prospecting generally resulted in a perceived net fitness payoff for the less tenacious (or 'fickle') personality types if at least 40% of the landscape was composed of some combination of mid- and high quality habitats. However, prospecting never provided a perceived net positive payoff for very tenacious individuals (Fig. 3). In addition, when habitat selectivity was high, prospecting provided a perceived net fitness payoff with a lower combination of high and mid-quality habitat (~35%). Finally, in cases where individuals had realistic (i.e. linear) perceptions of the costs of movement, prospecting did not provide a perceived net fitness payoff until there was a relatively high amount of either mid- or high quality habitat (~60% total).

<u>Changes in CAD values in response to varying landscape configuration and mechanistic</u> <u>rules</u>

To visualize how the cumulative absolute difference changes across all landscape configurations we constructed a series of 3-D surface plots. The cumulative absolute difference in NPr (CAD) associated with our demographic rule changes were consistently small across all landscape configurations, thus creating a flat, low elevation 3-D surface (Fig. 4a). This result indicates that changing the demographic payoffs associated with mid-quality habitat (either lowering or raising it) had very little influence on how often prospecting will pay off in higher net fitness, and that this result is unaffected by the prevalence of mid-quality habitat in the landscape. There was a somewhat flat 3-D surface plot depicting the effect on CAD from the different personality types as it relates to tenacity (Fig. 4b). There was a slight increase in CAD as high quality and/or midquality habitat increased in prevalence, reaching a maximum value of 1.44 when the landscape is 95% high quality habitat. In marked contrast to the results for changing demographic rules, however, CAD values associated with personality type were consistently high, hovering around 1 across all landscape compositions (i.e. creating a flat, high elevation 3-D surface, Fig. 4b). This indicates that perceived fitness levels are somewhat insensitive to changes in landscape composition, but that fitness differences across personality types (more or less tenacious) are nearly always high.

When looking at the surface plot showing how CAD responds to altering habitat selectivity, we see that CAD is zero when there was only low quality habitat in the landscape; but that there was an upswing in CAD as small amounts of mid-quality habitat were added (Fig 4c). As we approached greater availability of mid-quality habitat CAD values fell again, terminating in a value of zero when there was only mid-quality habitat in the landscape. Once high quality habitat reaches an availability of ~20% we began to see a gradual increases in the CAD values, approaching a maximum value of 1.14 when the landscape was composed of 90% high quality habitat. These results suggest that there is a strong interactive influence of landscape composition and individual habitat selectivity on the net payoffs expected when engaging in prospecting behavior.

Component differences in CAD values

The CAD values taken by themselves provide a magnitude of change, but do not indicate the directionality of change. Thus we examined the component differences when the CAD value attained its maximum and minimum value across all landscape compositions for each mechanistic rule change (Table 2). There was a large difference between very tenacious individuals as compared to either realistic or fickle individuals. When the CAD value reached its maximum value of 1.44 in Fig. 3b, the largest component of this value was comprised of the difference between the fickle and tenacious individuals (0.72). This difference indicates that, when high quality habitat is abundant, there is a relatively greater perceived payoff to prospecting for fickle individuals relative to tenacious individuals. The difference value of -0.54 between the tenacious and realistic individuals also implied a fairly large difference in terms of the fitness benefits of prospecting (much as with the fickle individuals) with greater benefits associated with prospecting when movement costs are closest to the realistic linear functions. The smaller difference in perceived payoff between the fickle and realistic personality types (0.18, Table 2) suggested that having either personality has similar effects on the fitness benefits of engaging in prospecting. When the CAD value is at its minimum we see similar patterns, but smaller magnitudes of change for each personality type. This result suggests that, even though the relative rewards of prospecting are not particularly high for fickle or realistic individuals, a tenacious individual can still be expected to do much worse in terms of perceived fitness outcomes.

The component differences between the three levels for selectivity showed more interesting patterns. There was a change of -0.25 when we simultaneously increased and decreased the probability of dispersal by 0.1 in low and high quality habitats respectively from the initial values of probability of dispersal (i.e. Level 1 for the selectivity rule). This result indicated that prospecting has a higher relative fitness payoff when individuals could recognize the quality of the habitat in which they currently resided, and act more strongly to either remain or move on. When we doubled the changes in probability of initiating a search to 0.2, thereby making individuals in high quality habitat even more likely to stay but those in low quality habitat more likely to move, we saw the relative benefit to prospecting more than double. This result indicates a non-linear dynamic whereby fitness gains associated with prospecting are the result of an interplay between landscape composition and individual selectivity in habitat evaluation. Much like when we changed the demographic rule, the differences between the various levels of selectivity were zero when the CAD value is at its minimum.

Discussion

Prospecting behavior has evolved within a variety of animal lineages and is seen as a common mechanism by which individuals can increase their annual and lifetime fitness through dispersal (Kesler, Haig and Brittingham 2007, Parejo, White, Clobert, Dreiss and Danchin 2007, Reed, Boulinier, Danchin and Oring 1999). We used a simple model scaffold to explore the complex interplay of one objective and two subjective, personality-based, mechanistic rules that underpin the fitness rewards associated with early-season prospecting behavior. Concomitantly, we also evaluated how the influence of these rules varies across a more or less heterogenous landscape. We found that when individuals have tenacious personality types, there is a marked drop in the expected fitness benefits of prospecting relative to the reality of the situation, meaning that individuals may fail to prospect in cases when their actual fitness benefits would be increased by prospecting behavior. There was, however, little difference between the perceived payoffs for fickle personality types versus realistic personality types, meaning that while tenacity may lead to missed opportunities, there is little to no realized fitness penalty for those individuals that are willing to initiate a search, but quickly abandon it if the search does not prove fruitful (i.e. fickleness). This result holds regardless of the range of habitats available in the landscape. We also show that an individual with strong selectivity about habitat, causing them to be more likely to leave poor habitat and remain in good habitat, will experience a non-linear rise in fitness payoffs as the amount of high quality habitat in the landscape comes to dominate. This result implies that if an individual can easily find high quality habitat (because it is common), recognize the quality of this habitat and thus move no further, prospecting will pay comparatively large fitness dividends. Finally, we found that as long as there was at least some elevation in
survival and fecundity from low to higher quality habitat, prospecting paid a net fitness dividend. This result pertains despite the fact that we altered the differentials in demographic payoffs associated with the various quality habitats that ranged from 0.5 to 1.5 (as measured by λ from low to high quality).

Predicting personality in relation to prospecting behavior across animal groups

While in our studied scenarios we assumed that the 'realistic' scenario was that captured by the linear cost function, this is, of course, not necessarily the case. Our results apply equally well to scenarios in which exponential or logarithmic functions are the 'reality', but then our interpretation of personality must be relative to that accepted reality. For example, if the exponential curve is the 'real cost function', then our results indicate that relatively more tenacious individuals (i.e. linear personality types) may actually not suffer any detriment in fitness payoffs, and it would not be until a personality type was so extreme as to perceive a 'real' exponential curve as a logarithmic outcome that fitness penalties would be incurred. This means we can make predictions about the variation in estimation of habitat quality and costs of movement for different species, depending on our external scientific estimates of the cost of movement function that best applies.

For example, within birds and mammals, Sutherland et al. (2000) show that smaller species tend to disperse shorter distances than larger species, in part because there is increased energy consumption per unit of weight in smaller species (Kleiber 1947). Because of this relationship, small species will consume energy at such a rate that maintaining enough energy to reproduce once settled becomes compromised rapidly. Therefore, a logarithmic cost function may be more appropriate for modeling deferred prospecting costs in smaller species while a linear or exponential cost function may be more appropriate for larger species that consume energy at a slower rate. If true, we would expect that larger species of birds and mammals should exhibit much greater variety of personality traits relevant to early-season prospecting behaviors as compared to their smaller counterparts.

Similarly, those species that have very short breeding seasons (e.g., high latitude species) have very little time to prospect over multiple breeding sites and still have sufficient time to successfully breed that year. In this instance prolonged early-season prospecting forays would result in increased opportunity costs, as opposed to increased energetic costs. These species may be more likely to experience a logarithmic cost structure, and thus be expected to exhibit very little variation across personality types relative to than their longer breeding-season (e.g., lower latitude) counter-parts.

Further eco-evolutionary insights

From an evolutionary perspective, our results suggest that there is a potentially strong selective advantage to individuals that collect accurate habitat quality information and use this information to guide their breeding decisions, a conclusion reinforced by past studies of the source-sink dynamics of metapopulations (Doligez, Cadet, Danchin and Boulinier 2003, Major and Jones 2011, McNeely and Singer 2001, Redmond, Murphy, Dolan and Sexton 2009). From a conservation perspective, the non-linear relationship between individual selectivity and landscape composition could have profound impacts on population persistence. For example, several species have evolved to use particular cues to locate high quality breeding habitat. When these cues become disassociated from the underlying demographic rates associated with a habitat, prospecting has the potential to create fitness sinks whereby populations decline faster than simple demographic rates or landscape quality would predict (Burkhalter and Lockwood, unpublished data).

The insensitivity of fitness rewards to alterations in the underlying differences in habitat qualities suggests that one or both of the following two statements must be true. First, the evolution of prospecting behavior is more constrained by mechanisms that govern the tenacity and selectivity of the individuals than it is the range of habitat qualities individuals encounter. All else being equal, we should therefore expect to find highly correlated matching between the two relevant personality traits affecting prospecting behaviors in a range of species, which together occupy a very wide array of natural landscape configurations, from highly heterogenous to nearly homogenous in habitat quality. Second, we did not capture within our model the full range of habitat quality differentials experienced in nature. It is possible that landscapes commonly provide a much more pronounced difference in expected demographic rates across habitats than we considered, and that if these differences are included, we would have seen a much higher sensitivity in terms of fitness rewards. Either of these outcomes can be explored either empirically or via simulation thus providing further insight into the conditions under which prospecting behavior is likely to be observed.

Implications for Personality Types under Habitat Alteration from Climate Change

Our findings demonstrate that there are scenarios in which personality traits can impact fitness more than differences in habitat quality. However, which traits are important may shift over time, meaning there should be selective maintenance of varied personality types to enable success under different ecological conditions. For example, previous research on the evolution of dispersal suggests that temporally stable landscapes decrease the importance of prospecting in individuals that can learn and remember the location of various habitat patches, and vice versa (Clobert, Danchin, Dhondt and Nichols 2001). Temporally stable environments would be expected to decrease the benefits from prospecting, favoring a decrease in tenacity and an increase in selectivity so that animals don't continually explore, but if they do prospect they still select the habitat that leads to the greatest fitness benefits. Conversely, under shifting landscape conditions (as with those that could be expected due to climate change), increased tenacity and decreased selectivity may be the more successful combination of personality traits due to the fact that animals would need to be willing to search for viable habitat (i.e. habitat that doesn't lead to declines in fitness), but not so discerning such that they only settle in the best habitat. Critically in the case of climate-driven landscape change, we may expect an interval of landscape shifting converging to a new stable pattern. In this scenario, the plasticity in behavior achieved by the influence of maintained diversity of personality traits within a population may be critical to the long-term success of the population. A natural next step from the work presented here would be to consider explicitly these types of time-dependent landscape scenarios.

Conclusions

By using DT to explore the impact of personality on the fitness implications from prospecting behavior, we can begin to make very general, testable hypotheses about a range of personality traits under different conditions. These hypotheses will be important in both validating the insights from the theoretical models (using correlations in habitat/landscape types and observed prospecting behaviors), and in making predictions about the viability of populations over time as landscapes may change. The models presented here have provided a general framework that can be easily tailored to reflect the specifics of a variety of systems and will enable cross-taxa exploration of hypotheses as they relate to personality and changing environmental conditions.

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Figure Legend

Figure 1. The payoff matrix is a graphical representation of the basic inputs of a decision theory problem. States of nature (θ_n) are listed across the horizontal axis, and actions (a_x) are listed on the vertical axis. The payoff values $(P_{x,n})$ for each respective state of nature x action combination are presented inside the table. The net payoff of each action (NPx) is calculated according to Equation 2.

Figure 2. Graph depicting the three time-dependent functions (i.e. exponential, logarithmic and linear) used to determine cost of movement used within Equation 1.

Figure 3. Line graph depicting how the NP ratio changes as more low quality habitat is added to the landscape. Each line represents the mean NP ratio at each landscape composition and the shaded region around the line is the 95% CI of the mean estimate calculated across all simulations at each landscape composition. The solid blue line () represents the simulations estimates obtained from Level 1 of the demographic rule. The dashed blue line () represents the simulation estimates obtained from Level 2 of the demographic rule. The dotted blue line

represents the simulation estimates obtained from Level 3 of the selectivity rule. When the NP ratio is above 1 it indicates that prospecting results in greater fitness rewards than not prospecting and when it is below 1 not prospecting results in greater fitness rewards than prospecting.

Figure 4a-c. Three-dimensional surface plots depicting how the costs/benefits of engaging in prospecting behavior are altered across various landscape compositions. Along the *x*- and *y*-axes is the proportion of the landscape composed of high quality habitat and mid-quality habitat, respectively. Along the *z*-axis (i.e. vertical axis) we show the cumulative absolute difference in the NP ratio (CAD) between each of the different levels for a given mechanistic rule (see text, Table 1). The NP ratio defines by how much prospecting results in a higher net fitness payoff as compared to the net fitness payoffs associated with not engaging in prospecting. Panels show CAD when we alter (a) the demographic parameters associated with mid-quality habitat, (b) the tenacity of individuals via the cost of movement, and (c) the selectivity exhibited in high and poor quality habitat . When CAD is high, an alteration in a mechanistic rule associated with engaging in this behavior.

	θ ₁ ; High quality habitat	θ ₂ ; Mid- quality habitat	θ_{3} ; Poor quality habitat	
Action 1 (a ₁); No Prospecting	Payoff (P ₁₁)	Payoff (P_{12})	Payoff (P_{13})	$NP_x = \sum_{\theta=1}^{\theta=3} P_{x,n} \ x \ \theta_n$
Action 2 (a ₂); Prospecting	Payoff (P_{21}	Payoff (P ₂₂)	Payoff (P_{23})	$NP_x = \sum_{\theta=1}^{\theta=3} P_{x,n} \ x \ \theta_n$

Figure 1



Figure 2



Figure 3



Figure 4a)



Figure 4b)



Figure 4c)

Table 1. Mechanistic rules used within the model and the various changes made to each one in order to determine its relative importance. λ = expected fitness (product of survival and fecundity), HQ=High quality habitat, M=Mid-quality habitat, P= Poor quality habitat, γ = Probability of initiating a search

<u>Demographic</u>	Tenacity rule	Selectivity rule
Level 1	Level 1	Level 1
λ of HQ: 1.5	Less tenacious or	γ in HQ: 0.3
λ of M: 1.0	'fickle'(Exponential Cost)	γ in M: 0.5
λ of P: 0.5 <u>Level 2</u>	Level 2	γ in P: 0.7 <u>Level 2</u>
λ of HQ: 1.5	Moderate or 'realistic'	γ in HQ: 0.2
λ of M: 1.15	in regards to tenacity	γ in M: 0.5
λ of P: 0.5	(Linear Cost)	γ in P: 0.8
Level 3	Level 3	Level 3
λ of HQ: 1.5	Very tenacious	γ in HQ: 0.1
λ of M: 0.85	(Logarithmic Cost)	γ in M: 0.5
λ of P: 0.5		γ in P: 0.9

Table 2. Average differences in costs/benefits of prospecting, measured using the NP ratio, when differences reached their maximum and minimum between various parameter scenarios. For the differing levels see Table 1.

Difference at

	Scenario	<u>Max. and</u>	Min.
Changes in tenacity	Level 1-Level 2	0.18	0.07
	Level1-Level 3	0.72	0.30
	Level 2-Level 3	0.54	0.23
Changes in demographic inputs	Level 1-Level 2 Level1-Level 3 Level 2-Level 3	-0.05 0.02 0.07	0.00 0.00 0.00
Changes in selectivity	Level 1-Level 2	-0.25	0.00
	Level1-Level 3	-0.57	0.00
	Level 2-Level 3	0.32	0.00

Chapter 3: Evaluating the role of cost surrogates when planning protected area networks within urban landscapes

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Abstract

Habitat loss is one of the most common causes of species endangerment, and thus conservation groups have invested heavily in building networks of protected areas. However, the costs of acquiring protected areas can be quite high. In spite of these large conservation expenditures these networks does not sufficiently represent the full variety of terrestrial ecoregions within its boundaries. The ecoregions that appear to be largely ignored from a conservation perspective and are under-represented in existing protected areas often lie within urbanizing landscapes which consist of complex mosaics of land uses with associated high heterogeneity in land values. Our work illustrates the importance of accurately defining cost metrics in reserve design planning. Relative to relying on cost surrogates or average land values across our study area, we were able to achieve the same conservation goals for approximately 1/4 of the cost by using tax assessed values of individual land parcels. This results demonstrates that in urban landscapes we must reconsider the usage of agricultural land and land area as cost surrogates for evaluating the costs of conservation. There is further need to evaluate whether our results, in terms of the conservation efficiencies obtained using tax assessed land values, hold in other urban landscapes. Systematic conservation planning studies have largely ignored a more detailed analysis of landscapes that have a large urban component.

Keywords: conservation, planning, cost, reserve design, optimization

2 Introduction

There has been substantial investment in creating conservation planning tools that seek to

- 4 maximize the biodiversity benefits of protected area networks, while also minimizing the costs associated with acquiring and managing these areas (Moilanen et al. 2009; Sarkar et al. 2006).
- 6 There are two spatially explicit inputs required by these planning tools: information on species' use of planning units (e.g., land parcels) and the costs associated with designating any given unit
- 8 as 'protected' (Wilson et al. 2009). There has been much more attention paid to the former than the latter (Armsworth 2014). However, what evidence we have shows that information that
- 10 reflects the real spatial heterogeneity of costs, as opposed to data that ignores this variation, tends to produce vastly cheaper (terrestrial) protected area networks while achieving the same
- 12 biological conservation goals (Armsworth 2014; Naidoo et al. 2006). These results suggest that the ability of cost data to capture the full heterogeneity in land values will profoundly affect how
- 14 one views the feasibility of implementing a protected area plan. Here we utilize three measures of land acquisition cost to explore how and why better cost data produces cheaper conservation
- 16 outcomes. We explore these issues in the context of protecting eastern deciduous forests within an urbanizing region. Conservation planning in urban areas presents a complex dilemma of
- 18 protecting valuable habitat that is simultaneously expensive to acquire and in eminent threat of destruction. Within this context, finding the cheapest solution to maximizing biodiversity
- 20 protection is paramount.

Temperate deciduous forests once covered a large swath of eastern North America, and despite over a century of logging and land conversion, remain the dominant habitat there (Ricketts 1999). These forests harbor a substantial number of rare and endangered species and are considered vital sources of global carbon (Askins et al. 1987; Turner et al. 1995), but they are

- vastly under-represented in existing networks of protected areas (Ricketts 1999; Scott et al.
 2001). As urban growth continues to exponentially expand outward from eastern coastal cities,
- 4 land that support these forests are subdivided and sold off as ever-smaller parcels and then often converted into residential housing (Davies et al. 2010). These factors create a vexing problem
- 6 for those interested in increasing the representation of eastern deciduous forests in networks of protected areas. These forests are under extreme threat of losing their ecological value while at
- 8 the same time their economic value is extraordinarily high and growing. Far from being an exception, the fate of eastern deciduous forests reflects a growing issue in conservation planning.

10 Globally half of all people now live in or near urban centers, and the trend toward higher concentration of human populations within cities is likely to continue into the near future

- 12 (McDonald et al. 2013). The ecoregions that house these urban centers are also of substantial conservation value, creating a high-risk situation whereby ecological valuable lands are under
- 14 intense development threat (McDonald et al. 2008; Rouget et al. 2003; Seto & Shepherd 2009)

Conservation planning algorithms were first introduced in the 1980s and have since grown in complexity and capacity to become a standard tool for building networks of protected areas (Pressey et al. 1997). Optimization algorithms require a measure of cost that can be

assigned to each parcel of land (or water) that is considered for incorporation into the network.Most often this costs has been represented by area, with the assumption that larger parcels will

20 cost more to acquire and manage than smaller parcels (Margules et al. 1988). Area, however, does not accurately represent the true economic value of a parcel and thus tends to greatly

22 suppress the heterogeneity in true costs between parcels (Armsworth 2014). In response to this issue, many recent global scale studies have relied upon gross revenue from agriculture and

nominal Gross Domestic Product (GDP) values to represent cost (Carwardine et al. 2008; Eklund

- 2 et al. 2011). Recent continental, national or regional scale studies have utilized as cost surrogates agricultural price indices, which reflect either gross production output value or simply the price
- 4 of agricultural land (Jantke et al. 2013; Lubowski et al. 2006; Polasky et al. 2008). Of the 27 conservation planning prioritization studies reviewed by Armsworth (2014), only one

6 incorporated a surrogate for cost related to urban land value (Visconti et al. 2010). None of these more recent cost surrogates seem to adequately capture the heterogeneity in true acquisition

costs, and in particular it is not clear if (or when) surrogates accurately reflect the spatial
 differences in cost across parcels (Davies et al. 2010). These spatial differences in costs create

10 the backdrop over which optimization algorithms 'run', essentially dictating if and when tradeoffs in acquisition costs can be made without sacrificing achievement of biodiversity goals.

- 12 Here we calculate the total cost of setting up a network of protected areas that will support 17 forest bird species of conservation concern within the northern counties of New
- Jersey, USA. This region is rapidly urbanizing due to the influx of people that want to live near or work in New York City. Our conservation goal is to design a protected area network that
 incorporates existing protected forested lands and adds more so that the total network provides sufficient breeding habitat for 17 forest-dependent bird species. We utilize Marxan to derive an

18 optimal solution whereby this biodiversity goal is satisfied while minimizing the total monetary cost of acquiring new lands. We use three measures of 'cost': area, value of agricultural land

- 20 (calculated by county), and property tax assessment records produced for each land parcel. The first two of these cost metrics have been used regularly within published conservation planning
- exercises, with the latter considered the more informative. We use tax assessed land value at the parcel level as a benchmark for 'true' acquisition costs, and the one that best captures spatial

variation in land value. We evaluate how these three costs metrics influence the total cost of the proposed optimal network, and the spatial configuration of this network.

4 Methods

2

Study Region and Species of Concern

- Our study area spans much of the northern half of New Jersey including the seven counties of
 Sussex, Warren, Hunterdon, Somerset, Morris, Passaic and Bergen (Supplemental Fig. 2-4; 6480
- 8 km²). The easterly counties of Passaic, Bergen and portions of Morris are predominantly urban/suburban as a result of their proximity to New York City; while the remaining counties
- 10 include a mix of suburban development, private agricultural farms, and large tracts of state and federally owned forested land. New Jersey, like many areas surrounding large metropolises,
- 12 requires a very complex approach to landscape level conservation planning due to the large number of small land parcels (898,029 in our study area) and the predominance of privately
- 14 owned lands (72% private vs. 28% public) (Hasse & Lathrop 2003).

As our biodiversity target we consider 17 forest bird species that have declined in population size by a minimum of 1.5% per year since 2001 both within New Jersey and across the northeastern US (Table 3,Sauer & Link 2011). Although all breed within deciduous forests,

- 18 they require distinct forest structures representative of the different forest successional stages (e.g., mature versus early-successional shrub forests). These species have been formally
- 20 recognized as in need of conservation action by the State of New Jersey or by national non-profit conservation organizations (Dettmers & Rosenberg 2000). Some species are of higher
- 22 conservation concern than others (Table 1). For example, the cerulean warblers (Setophaga

cerulea) is a rapidly declining Neotropical migrant species that is rare across its summer

- 2 breeding range and has a persistent but localized breeding population in the mature secondgrowth forests commonly found in the northwestern corner of our study area. In contrast, the
- 4 eastern towhee (*Pipilo erythrophthalmus*) is a small sparrow-like species that relies on the thick understories of early-successional forests, which are much more widespread in our study area.
- 6 The towhee has experienced large annual declines in abundance in recent years despite being somewhat widespread, which is why it is considered of conservation concern. Such differences
- 8 in species' habitat requirements and threat status require consideration when formulating conservation targets (see below).
- A principal requirement of conservation planning is to be able to designate planning units as habitat for the focal species. To do this we utilized previously published species distribution
 maps for each of our 17 birds (Maslo et al. In Press). These authors used maximum entropy software to predict the occurrence of each species across our study area (Maxent v3.3.3k,
- Phillips et al. 2006). Maslo et al. (In Press) used point-count data collected at over 2,000locations in 2002 across our study area to create distribution maps. All of their distribution
- 16 models provide a statistically reasonable depiction of the distribution of our focal species across our study area (see Maslo et al. In Press for more details). We utilized their maps depicting the
- 18 top 10 percentile of probability of occurrence to determine how much of each of our planning units were occupied by each species. The 17 species occupied from 4% to 56% of our study
- area, with a mean of prevalence of 34% (Table 1). Maslo et al. (In Press) show that the distribution of predicted habitat for our focal species is mostly split between publicly owned
- 22 forests and privately owned agricultural lands.

Analysis framework

- 2 To select planning units for inclusion in a reserve network we used the decision support tool Marxan (Possingham et al. 2000). Marxan relies upon a simulated annealing optimization
- 4 algorithm to identify planning units (the unit of analysis specified by the user) for inclusion in a reserve network to achieve conservation goals at the minimum cost. Our application of Marxan
- 6 requires information on the spatial distribution and size of potential planning units, and the amount of habitat that is occupied by each of our 17 focal species in each of these planning units.
- 8 Additionally, we had to set conservation targets for each of the focal species, define metrics that represent the costs of achieving the conservation targets, and define ways to measure the
- 10 differences in cost that arise from using various metrics so that they are on a common scale for comparison. We discuss each of these below.
- 12 We used tax assessed land parcels to define our planning units. There are a total of 898,029 land parcels within our study area ranging in size from <1 to 1,945 ha. We defined the
- boundaries of each parcel, and each parcel's ownership category, using the New Jersey MOD IV
 Tax Manual (Table 2). The MOD IV Tax Manual is maintained by the New Jersey Division of
 Taxation, which is a division of the New Jersey Department of the Treasury. The tax manual
- provides for the uniform preparation, maintenance, presentation and storage of local tax
- 18 information for the entire state (Treasury 2014). We determined the current protection status (i.e. whether or not a parcel is under current protection by a governmental body or NGO) of each
- 20 parcel using two of the most up-to-date protected areas databases available: the USGS Protected Areas Database of the United States, and the New Jersey Highlands Council Protected Areas
- 22 Database (Council 2014; USGS 2012). These two databases were last updated in 2012, and

include protected areas that are under permanent protected status as well as land parcels that are

2 enrolled in conservation easement programs.

Using both ownership and protection status, we assigned all parcels to one of three status
groups: 1) available for acquisition ; 2) already protected; or 3) not available for acquisition.
Any parcel that had an ownership category that indicated existing facilities or structures were

- 6 present were considered unavailable for acquisition (Table 1). These land parcels either were not likely purchasable (e.g., railroads), or had existing facilities or development on them that
- 8 substantially reduced their ecological value (e.g., apartment complexes). We considered parcels available for acquisition if they were not already protected and did not show evidence of
- substantial development (Table 1). We also deemed a land parcel as unavailable for acquisition if it was smaller than 2.5 hectares, because it was likely too small to support any of our focal
- 12 species (Blake & Karr 1987). To reduce computational complexity all unavailable land parcels that shared a common boundary were dissolved into one unit within ArcGIS, leaving all other
- 14 parcels unchanged, so that the final land parcel count for the remaining analysis was 65,711. A total of 15,881 land parcels were already protected, 41,639 were considered not available for
- 16 acquisition, leaving 8,181 as acquirable. The distribution of acquirable lands was heavily skewed toward smaller parcel sizes (Supplemental Figure 1).

18 To determine the conservation targets for each species we used the approach outlined in Wilson et al. (2010) that allows for equitable protection of each species by relying upon the their

- 20 particular life history characteristics. Previous studies have shown that the mean time to extinction (*M*) for a population of organisms subject to environmental stochasticity can be
- 22 determined using the following equation,

$$M = 2K^b / \sigma^2 b^2 \tag{1}$$

where K is the carrying capacity of the population, σ^2 is the variance in the growth rate of the

- 2 population, *b* is a constant and is calculated according to $([2r/\sigma^2] 1)$ (Lande 1993; McCarthy et al. 2005). Assuming that M = 100,000 years is an average time to extinction for every species
- 4 (per Wilson et al. 2010), then the target population size, *K*, can be found by rearranging Eq. 1 to,

$$K = (100\ 000\ \sigma^2 b^2 / 2)^{1/b} \tag{2}$$

6 Data on *r* and σ² are usually not available so approximations must be used to ultimately derive *K*. Wilson et al. (2010) used the following function to obtain estimates of the maximum
8 instantaneous rate of population growth (*r_m*) as a function of body mass, *r_m* = 1.375*W*^{0.315}, where

- W is the adult live body mass of females in kilograms (Sinclair 1996). The coefficients derived
- by Sinclair (1996) are not applicable to our focal species because they were derived for mammals. Therefore, we used the function described as $r_m = 0.025 W^{0.26}$, according to the
- 12 allometric relationship determined by Blueweiss (1978) for a range of taxonomic groups (including birds). From here the instantaneous rate of change between population censuses, r_t ,
- 14 can be approximated by r_m/T , with *T* (i.e. generation time) being calculated using the avian specific coefficients via $T = 53W^{0.27}$ (Millar & Zammuto 1983). We used the approximation for
- 16 r_t in place of σ^2 to calculate *b* and then substituted these values into Eq. 2 to derive *K*, which we use as our conservation target.
- Because *K* is measured in terms of the number of individuals, we then adjusted our conservation targets so that they are measured with the same metric and same scale as our
 planning units. We multiplied *K* by the average territory size for a pair of birds for each focal
- species to obtain the target area required for each species. Average territory size for each species
- 22 and average adult live weight for females of each species, *W*, were obtained from species descriptions in Birds of North America Online (Ornithology 2014).

Conservation weights

- 2 When designing a reserve network for multiple species it would be ideal to give equal importance to all species, but given that conservation managers work with monetary constraints
- 4 there is the need to prioritize species that may be limited in range/habitat type or are currently experiencing the greatest levels of decline. To address this concern within our study we
- 6 formulated a ranking of our 17 focal bird species by considering three factors: 1) their conservation status within New Jersey; 2) their regional rate of decline; and 3) how much of their
- 8 overall geographic distribution lies within our study area. To reflect this ranking within Marxan we adjusted what is termed the 'species penalty factor'. This factor is a multiplier applied to the
- 10 objective function calculated by the optimization algorithm when the conservation target for a given species is not met. A higher species penalty factor implies that a species is of higher
- 12 conservation concern (see Table 2). Following the recommendations laid out in the Marxan User Manual we were able to calibrate our species penalty factors so that we balanced the need to
- 14 meet our conservation targets, while also limiting any influence that our assigned values might have on Marxan optimization performance (Game & Grantham 2008).

16 *Cost Metric*

We derived an optimal protected area network using one of three different cost metrics; area,

- 18 agricultural value, and tax assessed value. Area is simple the size of each parcel (m²) as recorded in the NJ MOD IV database. We determined agricultural land value on a price per unit area
- 20 (2014 USD\$/m²) basis for each county in the study area (7) and then multiplied the total parcel area by its respective county agricultural land value. Finally, we used the tax assessed dollar
- 22 value attached to each land parcel taken from the NJ MOD IV database. New Jersey tax assessments are based on market value of land, and thus we consider these the most accurate

measure of true acquisition costs we have. In New Jersey assessment practices are standardized

- 2 across the state and assessment rates are uniformly 100% (Treasury, 2014). If there was no dollar value attached to a land parcel, which was rare (< 1% of all ~898k parcels), we calculated</p>
- 4 the average land price (2014 USD\$/m²) for each status group (i.e. status being either available for acquisition, already reserved or not available for acquisition) on a county-by-county basis and

6 multiplied this value by the total size of each parcel with an unspecified value to determine its acquisition cost.

8 We deduct the cost of each parcel included in the protected network from an overall acquisition 'budget', which is not capped but is to be minimized. Thus the cost of each parcel is a

- 10 form of a penalty, whereby more costly parcels penalize the overall budget more than less costly alternative. To visualize how this acquisition penalty is represented by each cost metric, we
- 12 plotted parcel size (ha) against the log-transformed cost metric. To represent each cost metric on the same axis, we had to convert them all into the same units. Tax assessed parcel value and
- agricultural land value are by default represented in 2014 USD. To convert area into the same units we imposed a 1:1 ratio between area and USD, so that $1m^2 =$ \$1. Logging the cost metric
- 16 (acquisition penalty) was necessary in order to better visualize the relationship with parcel size since the distribution of parcel sizes is heavily weighted toward smaller sizes.

To examine overall trends between parcel size and acquisition penalty we fit a lowess smoother using the 'lowess' package in program R v.3.0.1 for each cost-area relationship. We
derived a single function for the relationship between area and parcel size, and another single function for area and tax assessed value. For agricultural land value, we fit a function for each of
the seven counties since this value is county specific. A 'lowess' smoother can serve different

purposes, however, our purpose was to provide an exploratory graphical representation of the

relationship between parcel size and acquisition penalty (Cleveland & Devlin 1988). Lowess

- 2 smoothers are also very useful because they do not assume that the data fits any particular distribution or that any one function describes all of the data. Rather it subsets the data so that
- 4 neighboring values of the independent variable are used to fit a response curve to the dependent variable (Trexler & Travis 1993). To balance the need to best portray the relationship between
 6 the data while avoiding 'oversmoothing' the curve, we implemented an iterative procedure that

allowed us to refit the lowess curve multiple times until variability in fit no longer changed.

- 8 For each cost scenario, we determined the optimal reserve design by initiating Marxan using the guidelines set forth in the Marxan Good Practices Handbook (Ardron et al. 2008). We
- 10 performed 1000 runs, each run containing 1,000,000 simulated annealing iterations. We then selected the run that met the conservation goals for all 17 focal species at the lowest acquisition
- 12 budget and used this optimal scenario as the basis of comparison between the different cost scenarios. Because our study area has a substantial number of existing protected areas, and these
- 14 were always 'locked into' the final optimal network design (no matter the cost metric used), the total acquisition budget of each optimal network is calculated as the sum cost of all added land
- 16 parcels. When using the tax assessed NJ MOD IV value of each parcel as our cost metric, this simply required us to sum the tax value of all added parcels. For the scenarios where cost was
- 18 not based upon tax assessed land values (i.e. area as cost surrogate, agricultural land value), we looked up the tax assessed value of all added parcels in the NJ MOD IV database, and summed
- 20 these. We then directly compared the total acquisition budgets across final optimized protected area networks realized under each cost metric. To show how this total acquisition budget is
- 22 divvied up across all selected parcels, we plotted parcel cost against size for each cost metric scenario. We fit lowess functions to these data using the same methods as described above.

2 **Results**

Heterogeneity in acquisition costs

- 4 When we considered tax assessed land values as the acquisition penalty we observed a large heterogeneity costs ranging from 2014 USD\$0.33/m² to \$55.28/m² (Figure 1). Most between-
- 6 parcel variation in acquisition penalty as represented by tax-assessed value occurs within small parcels (Figure 1). Agricultural land values were calculated on a per county basis, and doing so
- 8 converted a substantial portion of this heterogeneity in parcel acquisition penalties into betweencounty differences (Figure 1). Representing acquisition penalties based on area alone collapsed
- 10 all heterogeneity in parcel costs into a single linear function (which when depicted in semi-log space appears as an increasing and then saturating curve; Figure 1). Agricultural land values
- 12 captured some of this heterogeneity in parcel acquisition costs at small parcel sizes, but in general imposed higher costs across all parcel sizes than either area or tax assessed value. For
- 14 some counties, using agricultural land value as the measure of acquisition penalty greatly inflates costs across all parcel sizes (Figure 1). Using area as the acquisition cost not only suppresses
- 16 parcel heterogeneity in cost, but also tends to impose higher costs across all parcel sizes as compared to tax assessed values due to the fact that area of parcel does not always reflect its
- 18 price. This imposition of higher acquisition penalties by agriculture land value is due to the intrinsic properties of averages. When calculating the mean of a given sample, the mean is
- 20 sensitive to extreme values and in our case this translates into small parcels of high cost inflating the average cost per unit area. When this inflated cost per unit area is then applied to all parcels it
- 22 can result in an increasingly unrealistic representation of acquisition costs.

Costs of Conservation

- 2 The minimum acquisition budget needed to achieve our conservation goals varied dramatically depending upon the cost metric used (Figure 2). When using the tax assessed land values as a
- 4 measure of acquisition cost there was a 73% and 78% cost savings in comparison to networks derived using area or agricultural land value as acquisition penalties respectively. Given that all
- 6 model parameters, except for cost metric were the same across all model scenarios we are confident that this result is due to the difference in how the costs are represented by the different
- 8 cost metrics and not due to some other constraints imposed by the model (i.e. species penalty factors, the conservation targets and the boundary length modifier (BLM), which controls overall
- compactness of the final reserve design) (for further explanation of BLM see Game & Grantham2008). Figure 3 depicts how total acquisition budget was spread across selected parcels of
- 12 various sizes, and thus it allows visualization of where efficiencies could be realized between cost metrics (i.e. what is the relative difference between the lines). Figure 3 shows that that the
- 14 low acquisition budget realized using tax assessed land values stems largely from the selection of much cheaper parcels that are <350ha as compared to what occurs using the other cost metrics</p>
- (Figure 3). Using area or agricultural land values as cost metrics resulted in largely the same acquisition costs for parcels <200ha. At larger parcel sizes, using area as a cost metric
- 18 continued to result in the selection of relatively expensive parcels for the network. However, the use agricultural land values resulted in the highest savings in acquisition costs when selecting
- 20 large (>400ha) parcels. Note that under no cost metric were the largest parcels selected in the optimal network (maximum parcel size of selected parcels was 551 ha, whereas the largest parcel
- 22 available for acquisition was 903 ha).

Spatial differences in parcel selection

- 2 To visualize the differences in the spatial distribution of parcels selected for inclusion an optimal network across cost metrics we created a series of spatial overlays of the final protected parcels
- 4 (Supplemental Figures 2-4). From overlaying the map of selected parcels when using tax assessed value and area as cost metrics, we can see that, when tax assessed land value is used as
- 6 the cost metric, most of the parcels added to the optimal network are located in the two westernmost counties (Sussex and Warren, Supplemental Fig. 2). These two counties had on
- 8 average the lowest tax assessed land values per unit area of all seven counties, and thus selecting parcels in these counties allowed conservation targets to be met while imposing the lowest
- 10 acquisition penalty. Furthermore, we see that when using area as the cost metric a few relatively large parcels were selected for inclusion in the network in the southeastern portion of the study
- 12 area (within Somerset county). Similar spatial patterns were observed when we compared the location of parcels selected using tax assessed land value as the cost metric as compared to
- 14 agricultural land value (Supplemental Fig. 3). Using agricultural land value led to inclusion of many more parcels in the southeastern portion of the study area, predominantly in Somerset
- 16 county. However, when comparing the agricultural land value scenario to area cost values we see a high degree of overlap in the parcels that were selected for inclusion in the network
- (Supplemental Fig. 4). It is also worth noting that when comparing these two optimal networks,both cost metrics selected parcels in the western portion of the study area, but these parcels
- 20 tended to not be the same ones.

22 Discussion

There is an ever-rising need to set aside land in protected status for biodiversity conservation,

- 2 while at the same time resources to meet this need are certain to remain limited. This situation places high importance on deriving the most cost-effective conservation strategies as possible
- 4 (Grantham et al. 2009; Wilson et al. 2007). We show that accurately representing acquisition costs when planning protected area networks has substantial effects on the efficiency with which

6 conservation goals can be met. Relative to relying on cost surrogates such as average agricultural land value or area, we show that the use of tax assessed land values allows the

- 8 achievement of the same conservation goals for approximately one-quarter of the cost. In addition, we show that such cost savings can be realized even within urbanizing landscapes
- where the ecological threats are high and the value of land is high. Perhaps most importantly relative to the conservation planning literature, we identify exactly where those cost savings
 acms from (*V*im et al. 2014)

12 come from (Kim et al. 2014).

It is well-known that using area as a surrogate for the cost of acquiring protected land suppresses all underlying heterogeneity in true costs (Armsworth 2014). In New Jersey's heavily urbanized landscape we see a large heterogeneity in land prices that varying from less than a dollar to over fifty dollars per square meter. We show that the use of agricultural land values not

- only also suppresses substantial heterogeneity in costs but also tends to over-estimate those
- 18 costs; sometimes severely. In our case, the vast majority of heterogeneity in costs occurred across parcels of small relative size. Following long-established conservation axioms, we forced
- 20 the optimization algorithm to favor larger parcels over smaller ones for acquisition. From this perspective, we may expect wide differences in costs of small parcels may not have that much
- 22 influence on the final acquisition budget. However, in our case this heterogeneity had a substantial influence because (1) the differences in costs across small parcels spanned orders of

magnitude and (2) the vast majority of acquirable lands were small. To achieve our conservation

- 2 goals, large numbers of small parcels had to be acquired and the ability of the algorithm to choose a parcel of land that was of equal quality for our target species but for substantially less
- 4 cost produced a huge net drop in total budget expenditures.

6

We also show that the heterogeneity in acquisition costs had a strong spatial signal in that parcels in the southern and eastern portion of our study area had 20 to 30X higher values than parcels in the western portion. This difference in land value was consistent across all parcel

- 8 sizes, thus indicating that large parcels were present across this spatial cost gradient (i.e. large parcels were not confined to low cost regions, or vice versa). This substantial price
- 10 heterogeneity is masked when using cost surrogates, and it significantly reduces the overall efficiency of allocating funds for conservation. Our cost gradient is a product of the proximity of
- land to New York City, where land closer to the city (or to commuter rail lines) has high value.This gradient in land values is common to nearly all urbanizing regions, and may be a common
- 14 feature of many ecological valuable landscapes. Our results suggest that in such situations accurately representing this spatial pattern in costs is vital to realizing the most cost efficient
- 16 protected area network design. Indeed, one reason why the use of agricultural land values as a cost metric failed to produce any cost savings (relative to the other metrics) is because it could
- 18 not accurately represent this spatial difference in costs. This effect was especially noticeable when evaluating the acquisition costs of land parcels that were relatively large.

20 Agricultural land values and area tended to estimate much higher acquisition costs relative to tax assessed value across all but the smallest sized parcels. This observation suggests that part of

22 the larger total acquisition budgets associated with using area and agricultural land value is because the estimated cost for all selected parcels was inflated. In our case, the fact that the final
networks produced under each cost metric included nearly the same number of parcels, and the

- 2 same total area, suggests that this inflation did not restrict the size of the network chosen.However, if any one of our species' habitat requirements dictated that only relatively expensive
- 4 or large parcels would satisfy their needs, the general inflation of costs could have imposed stronger constraints on the total network size; perhaps even disallowing an optimal outcome
- 6 altogether. The decreasing variance in acquisition costs from small to large parcels that we observe ensures that any method that extrapolates costs across all parcel sizes will badly mis-
- 8 estimate costs at the larger end of the distribution. The most obvious case of this is within Morris county (top white curve in Figure 1), where tax assessed land values can be very high for very
- 10 small parcels (including agricultural land). When this cost per unit area is extrapolated to even slightly larger parcels sizes, it greatly over-estimates costs.
- 12 We have relied upon highly detailed tax records to account for acquisition cost heterogeneity, but these data may not be available for many areas where conservation planning initiatives are
- 14 taking place. In such cases, cost surrogates are required. Our results suggest that any surrogate should not only capture the spatial structure in cost heterogeneity as suggested by Armsworth
- 16 (2014), but also how that heterogeneity manifests itself across the range of available parcel sizes.Additionally, we assume that acquisition costs are the only types of costs that determine overall
- conservation planning outcomes, although we know this to not be true (Naidoo et al. 2006).Transaction and management costs remain a vital, but badly under-documented element to
- 20 devising optimal protected area networks, and we would expect these costs to be equally heterogeneous (and likely high) in urbanizing landscapes such as ours. Finally, we suggest that
- 22 the need to conduct conservation planning within urban areas is urgent both in terms of the surprising ecological value these areas often have (Donnelly & Marzluff 2004; Pennington et al.

2008) and the extremely high risk that remaining land of ecological value will be lost to land

- 2 conversion. However, as of yet systematic conservation planning studies have largely ignored landscapes that have a large urban component (Armsworth 2014). There are many large cities
- 4 that sit within ecologically valuable landscapes and it would be informative to see if the patterns we observed here hold elsewhere.
- 6

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16

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Figure Legend

Figure 1. Scatterplot depicting (log) acquisition penalties (2014 USD\$) against size of parcels available for acquisition within our study area. Area is assigned a monetary costs of \$1/1m², and the other costs are directly measured in USD\$ (see text). The green squares and solid green line depict parcel acquisition penalties based on their tax assessed land value, the yellow circles and solid yellow line depict penalties based on area, and the white triangles and solid white lines depict penalties based agricultural land values. Because agricultural land values were derived per county (seven), we fit functions for each county (seven white lines). In semi-log plots, linear functions appear as increasing and then saturating functions. Note that many data points (parcel costs) may stack on top of one another making them visually indistinguisable, which is most often the case when depecting agricultural land value and area costs per parcel.

Figure 2. Total land acquisition budgets (2014 USD\$) required to achieve our conservation targets using tax assessed land value, area, and average agricultural land prices as acquisition cost metrics.

Figure 3. Scatterplot depicting (log) acquisition cost (2014 USD\$) by parcel size across all parcels selected for inclusing in the optimal preserved area network under each cost metric. The total acquitision budgets for each cost scenario correspond to Figure 2. The

solid green line represents the cost of selected parcels when using tax assessed land value as the cost metric, the solid yellow line depicts the cost of selected parcel when area is the cost metric, and the solid white line represent the cost of selected parcels when agricultural land values are used as the cost metric. The lower a line relative to the others, the less a selected parcel of that size penalized the total acquisition budget.

Supplemental Figure 1. A frequency histogram depicting the distribution of parcel sizes measured in hectares. This distribution applies only to those parcels that were available for acquisition.

Figure S2. Map showing the final reserve designs when using tax assessed values and parcel area as a proxy for acquisition cost. The areas highlighted in green are the existing reserve sites throughout the study area. The gray areas show sites that were not selected for inclusion in the final reserve design. The areas highlighted in red are the sites selected for inclusion in the final reserve design when using area as a acquisition cost surrogate. The areas highlighted in blue are the sites selected for inclusion in the final reserve design when using area as a acquisition cost surrogate. The areas highlighted in blue are the sites selected for inclusion in the final reserve design when using tax assessed land values for acquisition cost. The sites highlighted in purple designate the sites that were selected for inclusion in the final reserve design by both cost metrics

Figure S3. Map showing the final reserve designs when using tax assessed values and agricultural land values as acquisition cost metrics. The areas highlighted in green are the existing reserve sites throughout the study area. The gray areas show sites that were not selected for inclusion in the final reserve design. The areas highlighted in red are the sites selected for inclusion in the final reserve design when using agricultural land values as a

proxy for acquisition costs. The areas highlighted in blue are the sites selected for inclusion in the final reserve design when using tax assessed land values for acquisition cost. The sites highlighted in purple designate the sites that were selected for inclusion in the final reserve design by both cost metrics

Figure S4. Map showing the final reserve designs when using area and agricultural land values as proxies for acquisition cost. The areas highlighted in green are the existing reserve sites throughout the study area. The gray areas show sites that were not selected for inclusion in the final reserve design. The areas highlighted in red are the sites selected for inclusion in the final reserve design when using agricultural land values as a proxy for acquisition costs. The areas highlighted in blue are the sites selected for inclusion in the final reserve design when using agricultural land values as a proxy for acquisition costs. The areas highlighted in blue are the sites selected for inclusion in the final reserve design when using parcel area as proxy for acquisition cost. The sites highlighted in purple designate the sites that were selected for inclusion in the final reserve design by both cost metrics

Table 1. Basic landownership categories of all land parcels within the study area; If the landownership category is bolded this indicates that all parcels with this landowner designation were excluded for inclusion in the final reserve design, unless already under some form of protection.

Landowner categories

Churches and Charities	Roads
Cemeteries	Railroads
Commerical Tax Exempt	Schools
Federal Facilities (Armories, Post Offices, etc.)	State Facilities (Storage facilities, buildings, etc.)
Municipal Facilities (Firehouses, libraries, storage buildings, municipal	Telco and Utilities
bldgs., etc.)	Undifferentiated Protected lands
Municipal Open Space	Undifferentiated Unprotected lands
NonProfit Open Space	Vacant Church and Charity land
Private Commercial properties (non tax exempt)	Vacant Farms
Private Farms	Vacant Municipal land (both tax exempt and non-tax exempt)
Private Industry	Vacant NonProfit
Public Federal land holdings	Vacant Private Citizen land
Public Municipal land holdings	Vacant Residential Development lands
Public Non Profit land holdings	Vacant School land
Public State land holdings classified	Vacant Sate land
Residential	Vacant Unknown Owner
Residential apartment complex	Wildlife areas that are listed as 'nature reserves' or 'bird sanctuaries'.
Tax exempt residential (Disabled veteran housing, etc.)	

Table 2. Listing of the 17 avian species used as focal conservation targets. ¹ Significant declines from 2001-2010 in the NE US region
(Sauer, 2011); . 2Substantial portion of range restricted to NE US region (Dettmers and Rosenberg, 2000); . 3Listed as Special Concern by NJ
Endangered and Nongame Species Program.

Common Name	Scientific Name	% of Study Area	Significant Declines ¹	Regional Importance ²	Threatened in study area ²
Baltimore oriole	Icterus galbula	44	+	+	-
Black-and-white warbler	Mniotilta varia	38	+	+	-
Cerulean warbler	Setophaga cerulea	4	-	+	+
Least flycatcher	Empidonax minimus	13	+	+	+
Northern flicker	Colaptes auratus	53	+	-	-
Northern parula	Setophaga americana	10	-	+	+
Veery	Catharus fuscescens	39	+	+	+
Worm-eating warbler	Helmitheros vermivori	<i>um</i> 18	-	+	-
Wood thrush	Hylocichla mustelina	56	+	+	-
Blue-winged warbler	Vermivora cyanoptera	38	+	+	-
Brown thrasher	Toxostoma rufum	21	+	-	+
Common yellowthroat	Geothlypis trichas	51	+	+	-
Chestnut-sided warbler	Setophaga pensylvanic	a 35	+	+	-
Eastern kingbird	Tyrannus tyrannus	31	+	-	-
Eastern towhee	Pipilo erythrophthalma	<i>is</i> 45	+	-	-
Field sparrow	Spizella pusilla	40	+	+	-
Rose-breasted Grosbeak	Pheuticus luodvicianus	42	+	+	-



Figure 1



Figure 2











Figure S2



Figure S3



Figure S4

Conclusions

By providing a greater understanding of decision-making, from both the nonhuman and human perspective, we should be able to improve animal conservation and management strategies. By studying animal decision-making processes we gain a greater understanding into how animals respond to anthropogenic change and what this could mean for species persistence within human-modified landscapes. Additionally, studying animal decision-making can allow us to determine which species may be more vulnerable to anthropogenic change by evaluating how evolved decision-making behaviors can become suboptimal. Finally, by examining our own decision making and how it relates to conservation management we can determine when we may be making suboptimal decisions due to misguided information.

My results provide direct information on how animal behavior relates to animal conservation. When the cues that animals use to guide movement decisions become decoupled from fitness consequences related to those movement decisions we see dramatic declines in population growth rates. This decoupling of fitness consequences from decision making can then result in evolved behaviors become a detriment to long term species persistence in human modified landscapes. Additionally, we have found that the behaviors of individuals can have profound impacts on those same decision making processes in human modified landscapes. We observed interactions between individual selectivity and changes in landscape composition. Those individuals that are more selective often incur greater fitness costs as a result of movement when there is a large amount of poor quality habitat in the landscape and conversely can receive the greatest benefit when there is a large amount of high quality habitat within the landscape.

Furthermore, the tenacity of an individual greatly affects movement costs with those individuals displaying the highest levels of tenacity incurring the greatest fitness penalties.

By evaluating how we determine costs within conservation reserve site selection we have shown that different representations of costs can greatly impact the economic feasibility of conservation and thus our decisions in regards to how much we may be willing to invest in conservation. Commonly used metrics of cost, area and agricultural land values, are very poor indicators of the true cost of conservation in highly urbanized landscapes. This poor representation of costs in turn leads to conservation initiatives that would cost 3-4X as much when compared to a situation in which we used tax assessed land values. By showing that we can conserve the same number of species using significantly less money we provide the impetus to reevaluate current strategies for conservation on a landscape scale.