When to move species in the face of climate change

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Managed relocation is a controversial climate adaptation strategy to combat negative climate change impacts on biodiversity. While the scientific community debates the merits of managed relocation [see 1-12], species are already being moved to new areas predicted to be more suitable under climate change [e.g. 13,14]. To inform these moves, we construct a quantitative decision framework to evaluate the timing of relocation in the face of climate change. We find that the optimal timing depends on many factors, including the size of the population, the demographic costs of translocation, and the

expected carrying capacities over time in the source and destination habitats. In some settings, such as when a small population would benefit from time to grow before risking translocation losses, haste is ill-advised. We also find that active adaptive management[15,16] is valuable when the effect of climate change on source habitat is uncertain, and leads to delayed movement.

Rapid climate change is leading to shifts in the distribution of many species [17-22] and will have economic and social consequences for human societies [23,24]. Predicting the impact of different climate change scenarios on biodiversity has been the overwhelming focus of research effort to date [e.g. 21,25]; far less attention has been devoted to developing and choosing between adaptation actions for biodiversity management.

Managed relocation is a controversial adaptation action for combating the impacts of climate change on biodiversity [1-12] and has recently been identified as a key priority for conservation research [26]. Managed relocation involves physically moving species from habitat predicted to become unsuitable under climate change, to locations where the habitat is predicted to become suitable, but where they have never occurred before. At present, debate is focused on whether to undertake managed relocation, in light of its potential risks and benefits [e.g. 2,5,9,11] . While this debate continues, species are being moved in anticipation of the risks of climate change [e.g. 13,14]. There is now an urgent need for a framework to underpin decisions about when to implement managed relocation, a framework that recognizes the potential for learning to reduce uncertainty and improve future decisions.

A decision framework for managed relocation

We propose a decision framework for managed relocation that includes learning. We focus on a situation where the risk of species extinction as a result of not undertaking managed relocation is considered greater than the risks to the recipient ecological community of undertaking managed relocation [see 9]. In this case, the manager is left with the decision about when, if ever, to implement managed relocation. We articulate several key elements of this decision framework: the objectives, the alternative actions, the assumptions about the system dynamics, the key uncertainties, and the role of monitoring.

Managed relocation will be invoked as an adaptation strategy to conserve species threatened by climatic changes, so a likely objective for managed relocation is to maximize the persistence of the species. We assume that probability of persistence is a monotonically increasing function of population size, so our explicit objective is to maximize population size at some point in the future, T. Other objectives, such as maximizing growth rate, are of course possible. (For a discussion of the effect of risk tolerance, see Supplementary text and Supplementary Fig. 1 and 2).

The actions that the decision-maker needs to evaluate regarding managed relocation include whether and where to move individuals, which kinds of individuals to move, how many to move, whether to move all-at-once or in staggered cohorts, what methods to use for release, and whether a period of temporary captivity is required. We examine what we believe to be the primary consideration with respect to our uncertainty about the impacts of climatic shifts; at what time to move. To illustrate our framework, we assume that the relocation involves moving every individual all-at-once. This strategy is applicable in situations where species wild populations are perilously small (*e.g. California Condor, Gymnogyps californianus, and Orange-bellied Parrot, Neophema chrysogaster,* [27]). Our framework however could easily be extended to consider more complex methods of implementation such as staggered movement.

Predicting the consequences of alternative management strategies in terms of their ability to achieve objectives requires making explicit assumptions about the system dynamics. There are a number of assumptions that have been implicit in past discussions of managed relocation. First, the motivation for managed relocation is that the suitability of the current (source) habitat, for example population growth rate or carrying capacity, is going to decline over time due to climate change ($K_S(t)$, Fig. 1). Second, the notion of managed relocation assumes that there is somewhere else that will be better for the species at some point in the future ($K_D(t)$, Fig. 1). Third, for managed relocation to be effective, at least one of the source and destination sites must be suitable at any one time (unless temporary captivity is being considered). Fourth, there is a demographic cost to moving individuals and only a fraction, ϕ, will survive and become established at the destination (Fig. 1). Fifth, the quality of the habitat in the destination needs to be sufficiently high so that recovery of the population is feasible within the desired time period, T; this habitat quality could be expressed as the expected intrinsic growth rate in the destination.

The success of a managed relocation program hinges on these assumptions; the difficulty is that there is likely to be considerable uncertainty about many of these. How much and how quickly will the source habitat decline? How much and how quickly will the destination habitat improve? What fraction of the population might die during relocation? What will be the intrinsic growth rate of the species in the destination? Three tools are valuable in the face of this uncertainty: predictive habitat modeling with explicit articulation of uncertainty, for example, by coupling general circulation models with species-specific habitat suitability models [e.g. 28], monitoring of key response variables; and Bayesian updating of the predictions in light of emerging monitoring data. In the face of uncertainty, a full-fledged decision framework should include explicit articulation of critical uncertainties and an on-going monitoring program designed to resolve that uncertainty, both key components of adaptive management [15,16,29].

Decision-making without uncertainty

We discovered that when we are certain about how the system will change in the future, the optimal timing of relocation is strongly affected by the suitability of the destination site, K_D, relative to the source site, K_S, the relocation survival rate, ϕ (Fig. 2), and the intrinsic growth rate of the population in both the destination and source sites. If the relocation survival rate is high ($\phi = 0.95$), then regardless of the number of individuals in the population, N, we should *not move* our threatened species until the carrying capacity in the source population, K_S, is less than that in the destination, K_D (Fig. 2a, e, h). A small difference in the maximum carrying capacities leads to an early crossing point of the two habitat models (Fig. 2a, t = 7.2 yr) and a correspondingly early optimal relocation time (Fig. 2b). An increase in this difference (Fig. 2d) increases the time at which the source carrying capacity falls below that of the destination (t = 11.7 yr), and therefore also increases the optimal time of relocation (Fig. 2e, also compare Figs. 2g, h).

When there is a large demographic cost to the relocation (that is, a low relocation survival rate, $\phi = 0.3$), the optimal timing of relocation is driven not only by habitat dynamics but also by the number of individuals in the source population (Figs. 2c, f, i). When the carrying capacity in the destination, K_D^{max}, is high (Fig. 2a), the timing depends largely on the population size in the source: if the population is large, the optimal strategy calls for immediate relocation, which allows recovery from the move to start sooner; if the population size is small, there is an advantage in leaving the population in the source to allow some recovery towards the carrying capacity before incurring the relocation cost (Fig. 2c). When the carrying capacity in the destination is much lower than the source (Fig. 2d), there is no point introducing more individuals than the destination can hold (Fig. 2f). Still, relative to the case when the relocation survival rate is high (Fig. 2e), the timing of relocation is earlier, to allow more time to recover from the demographic costs of relocation. Under all habitat suitability scenarios, below a certain population size we should never implement managed relocation as a result of the relatively high demographic costs of relocation.

Decision-making with uncertainty

Decision-makers are invariably uncertain about the response of species to climate change. Incorporating uncertainty about how the system will respond to changes in climate alters both what drives our actions and when we should act. We capture this uncertainty with a belief state, w. In our illustration w describes our belief that there will be no impact of climate change on the carrying capacity of the source population. We consider two cases: a static case, in which the belief state is fixed and does not change over time; and an active adaptive case, in which the belief state is dynamic and updated with ongoing monitoring data. The static case represents a likely scenario where insufficient resources are in hand to proceed with active adaptive management[15] and instead the best available knowledge regarding the impact of climate change is used to inform managed relocation.

In the static case, we assume the future population size is determined by the long-term carrying capacity in the final location of the population, which is a function of both the decision ("stay" or "move") and the reality about the effects of climate change. We find that the expected long-term value of keeping the population in the source ("staying") is greater than the expected long-term value of moving when our belief in the no impact model is above a critical threshold: $w > w_c$, where $w_c = \frac{K_D^{\max} - K_S^{\min}}{K_S^{\max} - K_S^{\min}}$. In other words, if our initial belief in the no impact model is greater than w_c then we do not move the species and no further decision is made. Conversely, if our initial belief in the no impact model is less than w_c, we move the species.

If we adopt an active adaptive management approach [15], for each year the population remains in the source habitat, our belief about the impact of climate change will change in response to monitoring data, specifically, to observed changes in the population size, N. Now, because we are implementing active adaptive management, our decisions are guided by the number of individuals in the population, as well as our belief, w, in whether climate change is having an impact on the carrying capacity of the source population (Fig. 3). When the belief in the no impact model is above the critical threshold, w_c, the optimal decision is to keep the population in the source, no matter the population size. When managed relocation is warranted, the optimal timing of movement is driven by our expectations about how the system will change and how rapidly the alternative models of system change can be distinguished from each other via learning (Fig. 3). When the rate of decline in the source habitat impact model (K_S model 2) is high (Figs. 3a, c), the optimal timing of relocation is between 13 and 18 years, depending on population size (Figs. 3b, d). This is later than in the corresponding case of known dynamics (Figs. 2c, f) for two reasons: first, as a bet-hedging strategy, we leave the population in the source longer, in case the source is not being affected by climate change; and second, we can only distinguish the alternative models if individuals remain in the source; leaving animals in the source population is the only way to monitor and learn in that population. Intriguingly, the value of learning does not last forever; if 16 or 17 years have gone by, and there is not enough evidence for the climate having no impact, it is best to move the population and avoid the risk of population collapse. When the rate of decline in the impact model (K_S model 2) is slower (Fig. 3e), the optimal timing of managed relocation is later, between 15 and 28 years (Fig. 3f). As a result of the slower loss of habitat in the impact model, more time is required to distinguish between the no impact (K_S model 1) and impact (K_S model 2) models through monitoring.

Using simulation, we compare the performance of our managed relocation strategies (Table 2). Allowing for learning through our active adaptive strategy (time-state-belief-dependent strategy) outperforms our strategy where the belief is fixed (belief- dependent strategy) and our strategy where we assume the dynamics about climate change impacts are known (time-state dependent strategy). See Supplementary Online Information for more detail on the simulation results.

Moving the debate from whether to when

The decision to move a species to a new area given the impact of climatic change is far from simple. Indeed, predictions and uncertainty about the effect of climate change on the source and the destination populations, the demographic cost of relocation, and the growth rate of the population in both areas, all influence the optimal timing of managed relocation. Alternative program objectives (e.g. maximize growth rate) and the consideration of a different suite of actions (e.g. allowing staggered movement) also may alter the optimal timing of relocation. The counterintuitive nature of some results and the sensitivity of the decision to these different factors highlight the need for an explicit structure that considers the anticipated system dynamics, uncertainty about those dynamics, and the benefits of active learning. The framework we present provides the scaffolding for careful analysis of managed relocation decisions.

There are additional factors that managers may want to consider. For example, first, the destination habitat is also likely to be changing with time; in fact, the suitability of this habitat may improve with time, affecting the best time to move a species (e.g., Fig. 1). In an extreme case, where the destination habitat may not become viable until after the source population is lost, the establishment of an insurance captive population may need to be considered as an interim strategy. Second, how the destination habitat is changing with time may be uncertain, requiring learning about the destination before making a decision to move the species. Third, environmental stochasticity may be an important dynamic to include in the population model, particularly for highly threatened species at low numbers. The framework we have provided could be expanded to incorporate all these intricacies and others, and we would expect this expansion to give rise to further novel patterns in the optimal strategies.

Our decision science framework provides a platform to increase our understanding of decision making in the face of climate change. There are two key components of climate change that are particularly challenging: management in the face of system changes; and management in the face of uncertainty surrounding these changes. Regarding the first challenge, we have shown that by using time-dependent dynamic optimization methods we can make informed decisions in the face of system change. The second challenge has paralyzed the ability of agencies to make decisions in a changing world, and caused some to advocate broad-based monitoring to reduce uncertainty without any link to what should actually be done if the systems are found to be in decline. Instead, we have shown here that by explicitly articulating uncertainty in the form of alternative models of system change, and evaluating the evidence for these different models with information gained about the system, we can make informed decisions regarding adaptation in the face of uncertain climate change.

Methods - Optimal managed relocation

Once the broader risks and benefits of implementing managed relocation have been considered, the question becomes one of optimal timing. We frame this problem as a time-dependent Markov decision process [30], and use stochastic dynamic programming to find the optimal time to implement managed relocation, conditional on full knowledge about the system dynamics, which in this case is the impact of climate change on the carrying capacity of the species. We also consider the case when we are uncertain about the system dynamics. Here, a tension may arise between actions that are optimal given uncertainty and actions that are most informative about uncertainty [15,16]; are the short-term costs of learning offset by their long-term benefits?

To illustrate the complexity of the decision for when to relocate a species and thus the value of a framework to aid this decision, we present the optimal timing of relocation given our objective is to maximize population size, the action is to move all-at-once, and the impact of climate change is modeled as carrying capacity changing through time. Further we present the changes in this optimal strategy that occur when we vary the specified parameters within the framework (e.g. the parameters within the models of carrying capacity and demographic cost of relocation). A detailed description of the methods can be found in the Supplementary Online Information.

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Figure Legends

Figure 1. System model for managed relocation. Carrying capacities in the source (K_S, solid) and destination (K_D, dashed) are shown with bold lines; the population size, N, is shown with a fine line. Population size represents the state of the system by which decisions are specified. Note, N can decline with K_S or increase towards K_S, depending on the starting population size. The premise of managed relocation is that the suitability of the source habitat will decline with climate change and a destination habitat will become suitable. The demographic cost of moving a population is expressed as the relocation survival rate, ϕ.

Figure 2. Optimal timing of managed relocation, as a function of population size in the source, when the change in the carrying capacity under climate change is known. (a, d, g) Known habitat carrying capacity over time in the source (K_S, solid line) and destination (K_D, dashed line), for three scenarios. (b, e, h) Optimal state- and time-dependent decision strategy for the corresponding habitat scenario when the relocation survival rate is high (ϕ = 0.95), and (c, f, i) when the relocation survival rate is low (ϕ = 0.3).

Figure 3. Optimal timing of managed relocation in the face of uncertainty about the impact of climate change. (a, c, e) For each scenario, there are two potential models for the carrying capacity in the source, one in which there is no impact of climate change (K_S model 1), and one in which carrying capacity declines with time (K_S model 2). The three

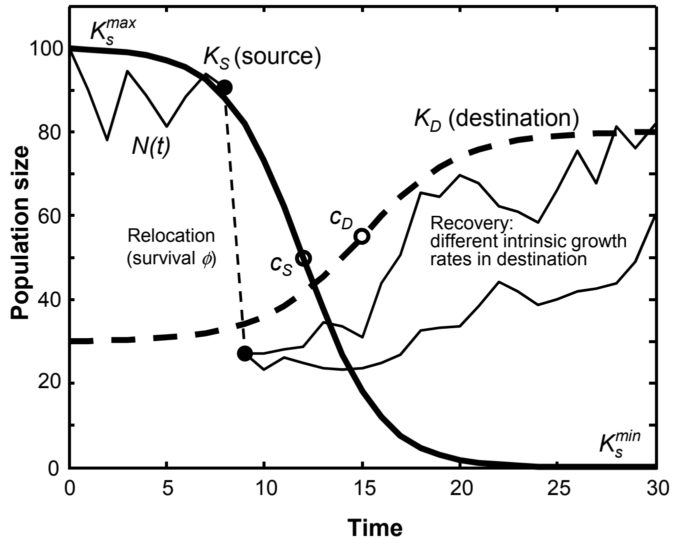
scenarios of decline correspond to the scenarios in Figure 2. (b, d, f) Optimal state-, time-, and belief-dependent decision strategy for the corresponding habitat scenario, when the relocation success rate is low ($\phi = 0.3$).

Table 1. Tradeoff table for a decision to move a population when belief about impact of climate change is static. The uncertainty concerns whether the source carrying capacity will, in fact, decrease (Impact) or not (No Impact). The consequences of taking a particular action, as a function of the true system dynamics, are expressed as the expected long-term population size. The Expected Value of each action is the belief-weighted average across the two system models – there is impact and there is no impact of a changing climate. Here K_S is the carrying capacity in the source area, K_S^{max} is the maximum carrying capacity in the source area, K_D^{max} is the maximum carrying capacity in the destination area, and w is our belief that there is no impact of climate change on the carrying capacity of the source population.

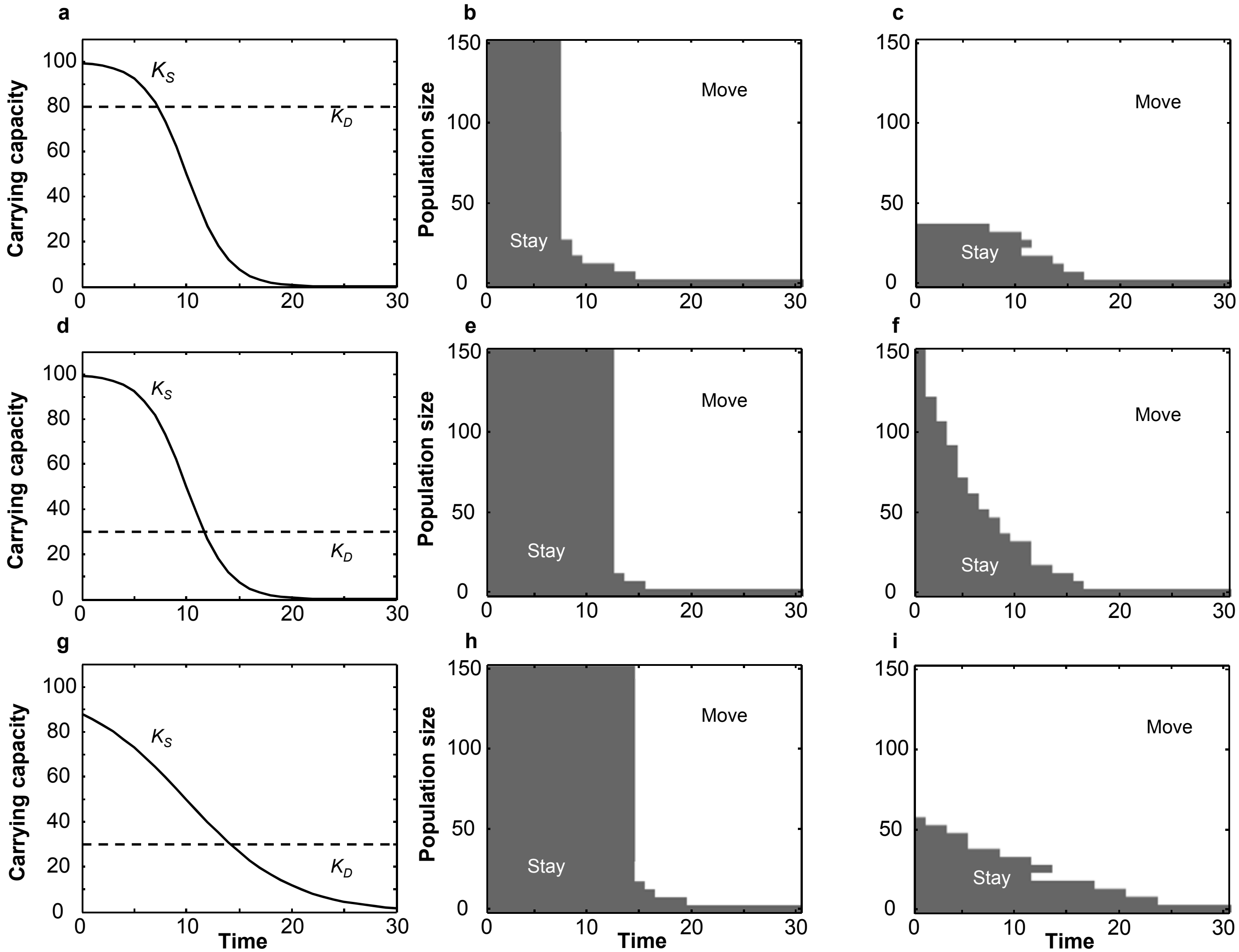
		Truth		**Expected Value**
	Model	**No Impact** (**K_S model 1**)	**Impact** (**K_S model 2**)	
	Belief	w	$1 - w$	
Action	**Stay**	K_S^{max}	K_S^{min}	$wK_S^{max} + (1-w)\,K_S^{min}$
	Move	K_D^{max}	K_D^{max}	K_D^{max}

Table 2. Performance of three managed relocation approaches under climate change. Case 1 is the time- and state-dependent strategy of Fig. 2f; Case 2 is the belief-dependent strategy of Table 1; Case 3 is the active adaptive strategy of Fig. 3d. Three performance metrics are shown, the probability of extinction after 100 years, *P*(extinction); the mean population size at 100 years for populations that did not go extinct, Terminal *N*; and the frequency with which managed relocation occurred, Freq. relocation. Parallel simulations were run for scenarios in which the underlying probability of the no impact of climate change model (Prob. model 1) was 0.8, 0.4, and 0.2, and in which the initial belief in that probability was 0.8, 0.4, and 0.2.

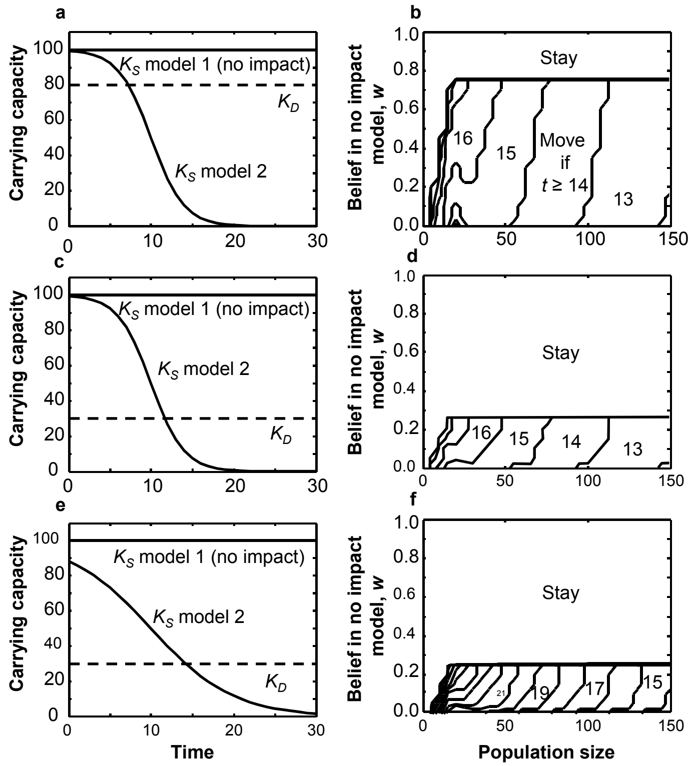
			Initial belief in Model 1 0.8		Initial belief in Model 1 0.4		Initial belief in Model 1 0.2	
Prob. Model 1	Performance metrics	Case 1	Case 2	Case 3	Case 2	Case 3	Case 2	Case 3
0.8	*P*(extinction)	0.00	0.22	0.00	0.22	0.00	0.00	0.00
	Terminal *N*	29.7	99.1	80.5	99.1	80.5	29.7	80.4
	Freq. relocation	1.000	0.000	0.266	0.000	0.266	1.000	0.268
0.4	*P*(extinction)	0.00	0.63	0.00	0.63	0.00	0.00	0.00
	Terminal *N*	29.7	99.2	53.1	99.2	53.1	29.7	53.0
	Freq. relocation	1.000	0.000	0.662	0.000	0.662	1.000	0.664
0.2	*P*(extinction)	0.00	0.81	0.00	0.81	0.00	0.00	0.00
	Terminal *N*	29.7	100.3	42.2	100.3	42.2	29.7	42.1
	Freq. relocation	1.000	0.000	0.822	0.000	0.822	1.000	0.824



K_s^{max}
K_S (source)
K_D (destination)
$N(t)$
Relocation
(survival ϕ)
c_D
c_S
Recovery:
different intrinsic growth
rates in destination
K_s^{min}
Population size
Time
0
20
40
60
80
100
0
5
10
15
20
25
30



a
b
c
d
e
f
g
h
i
Carrying capacity
Population size
Time
K_S
K_D
Move
Stay
0
10
20
30
40
50
60
80
100
150



a
b
c
d
e
f
Carrying capacity
Belief in no impact model, w
K_S model 1 (no impact)
K_D
K_S model 2
Stay
16
15
Move if $t \geq 14$
13
14
21
19
17
Time
Population size