Population Viability Analysis (PVA) as a platform for predicting outcomes of management options for the Florida Scrub-Jay in Brevard County

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Summary

The Florida scrub-jay (FSJ) is a species in decline because of extinction debt caused by habitat fragmentation and degradation. Understanding and managing the species and its habitats is challenging due to the complex interactions among the social system, a dynamic mosaic of scrub habitat, and active management. To provide insights into the possible fates of the FSJ populations of mainland, cape, and island sections of Brevard County, we modeled the population dynamics using the Vortex population viability analysis (PVA) software. Vortex is an individual-based simulation that allowed us to include such factors as demographic rates dependent on habitat state, impact of helpers on breeding success, and helper to breeder transition probabilities responding to availability of nearby vacant optimal habitat and vacancies due to the death of breeders. Detailed modeling of the FSJ was possible only because a lot of data about the species and its habitats have been gathered over decades of intensive research.

We followed a phased approach to constructing population models that incorporated the best available science and data to address a variety of conservation actions. The first phase focused on constructing a model that incorporates sociobiology and source-sink habitat dynamics. This model allowed us to address some of the most important questions about population size and habitat quality. Once the model framework was in place, we considered the real landscapes and actual local populations, rather than just generic representations of typical FSJ dynamics. After examining the viability of the metapopulations under current conditions, we explored the likely consequences of various management actions that might slow or reverse population declines.

Determinants of population viability

Some of the findings from the first phase include:

- Habitat classified as Strong can support population growth (exponential growth rate r = 0.06). Habitat classified as Weak or Sink is not adequate to sustain the population: the demographic rates in those habitats would result in declines (r = -0.14 and r = -0.22, respectively).
- Sink habitat is currently more abundant than Strong or Weak habitat. Consequently, the PVA models predict that the overall FSJ population would be in continuing decline unless habitat is improved. This may represent accurately the expected fate of the population, or it might suggest that the population will be expected to contract until it occupies primarily the better-quality habitat.
- If we use common definitions of MVP and Endangered, such as less than 5% probability of extinction and retention of more than 90% of gene diversity over 100 years, then a Minimum Viable Population requires about 100 potential territories of high quality (Strong) habitat.
- Adding Weak habitat to a population otherwise occupying a fixed amount of Strong habitat can allow for increased population growth and decreased probability of extinction, but only if the jays preferentially access any available Strong habitat before using Weak habitat. Weak habitat can serve as a buffer when there are more breeding pairs than can use the available Strong habitat. However, the more important benefit of Weak or Sink habitat could be its potential to become more optimal habitat (if managed), rather than its current benefit as breeding habitat for the scrub-jays.
- Immigration of about 2 jays per year (whether via natural dispersal or managed translocations) adds considerable demographic stability to populations even as small as 25 potential territories.

- Sensitivity tests of uncertain PVA parameters indicates that for an isolated population with 100 potential territories, across the ranges of uncertainty in the parameter estimates, the most influential of the rates affecting population persistence were, in order: adult mortality, breeding success, impact of inbreeding, and juvenile mortality. However, more than half of the variance in population projections was due to intrinsic unpredictability of biological processes. Thus, even if we had perfect knowledge of demographic rates, there would be a lot of unpredictability in the fate of any given population.

Viability of the metapopulations under current conditions

In the second phase, we developed metapopulation models that represent the observed configuration of local populations on the landscape. We tested the validity of the simulation as a model of FSJ population dynamics by comparing observed to projected population structure (e.g., helpers per breeding group, distribution of breeding groups across Strong, Weak, and Sink habitat). The tests indicated that the current PVA model is a good model of the FSJ population dynamics, but it perhaps is biased toward projecting better population viability than is occurring with the current habitat quality and spatial distribution. Management plans should use a precautionary approach (with extra margin for error), and actual consequences of management actions should be monitored closely so that management can be adapted as needed. Some overall conclusions regarding each of the metapopulations were:

KSC/MINWR: The metapopulation at Kennedy Space Center and Merritt Island National Wildlife is large enough, and each of its four constituent populations are large enough, so that it is likely to avoid complete extinction for at least 80 years. However, the metapopulation is projected to decline to occupy mostly Strong habitat in the long term. Moreover, dispersal between local populations is currently much lower than what would allow for maximal metapopulation viability.

Cape Canaveral Space Force Station (CCSFS): If we assume that the demographic rates in comparable habitats are similar to what has been measured in KSC/MINWR, then only 13 out of 256 potential territories in Cape Canaveral Space Force Station populations would be classified as Strong, 6 are Weak, and the remaining 237 are Sink habitats. Consequently, the CCSFS populations are projected to decline rapidly, and the metapopulation is projected to go extinct in about 30 to 60 years.

SC Mainland: If the 14 relatively isolated populations in South and Central Mainland Brevard were to be fully interconnected (panmictic), the metapopulation is projected to decline to occupy mostly Strong habitat in the long term. However, the highly fragmented nature of the habitat leads to the metapopulation declining to extinction in about 40 to 70 years if nothing is done to increase optimal habitat and connectivity.

N Mainland: The North Mainland metapopulation has too few breeding groups, too little optimal habitat, and is scattered among too many very small fragments to persist as a functional metapopulation. Even under high rates of dispersal, the N Mainland metapopulation is projected to have a 50% probability of complete extinction within about 16 years. Extinction could be as soon as 10 years, or as late as about 30 years.

Management scenarios

The above projections for the metapopulations indicate that the Florida scrub-jays in Brevard County are not likely to recover under current conditions. The metapopulations are all expected to decline, with only the

KSC/MINWR metapopulation likely to persist for the long-term, although at a smaller size. Below are the findings for some of the scenarios we tested to evaluate management strategies that might reverse the declines, stabilize the metapopulations, or even achieve growth in numbers. The first question asked about each metapopulations was: *What would be required to keep the metapopulation persisting (probability of extinction < 5%), stable (N > 0.5·Kmax), and genetically healthy (inbreeding < 0.10)?*

KSC/MINWR metapopulation management scenarios

If the KSC/MINWR habitat is improved to be > 50% Strong (increased from the current 20%), the metapopulation would grow, be sustained, and be considered viable by all criteria. With an increase to >30% Strong, the population would be safe from extinction, but would maintain less than 50% occupancy of potential territories.

What would be the effect on the KSC/MINWR metapopulation if some or all Sink habitat was lost?

In the short-term, the loss of current Sink habitat would result in a faster reduction in population size, as Sink habitat would not be available for use by the more than 100 breeding groups currently in Sink. Removal of some Sink habitat might have little impact on the metapopulation, because jays seeking new breeding territories would use only Strong or Weak habitat. Weak habitat and most sink habitat in the focal landscape for jays can be converted to source or may serve as a stepping stone contributing to connectivity among areas of Strong habitat. The results imply that sink habitat outside the focal landscape for jays have little to no value for jays. In summary, results suggest that management efforts should focus on maintaining and developing enough source habitat and improving connectivity.

What if the Schwartz Road unit cannot be managed for scrub-jays and becomes all Sink habitat?

Loss of the Strong and Weak territories from Schwartz Road reduces the metapopulation size by about the number of breeding groups currently using Strong and Weak habitat (25 breeding groups), but it would have only a small negative effect on the persistence of the entire KSC/MINWR metapopulation. Additional scenarios could be conducted to what improvements might occur if the Schwartz Road landscape could be improved. However, given the low dispersal among cores and ability to enhance connectivity between cores, improving Schwartz Road might not have as much benefit as expanding and connecting the Shiloh and Happy Creek populations.

How much would it help if the Happy Creek and Shiloh populations were fully connected?

Connecting Happy Creek and Shiloh would moderately reduce the accumulation of inbreeding (shifting mean F from > 0.10 to < 0.10), resulting in improved population persistence. However, improvement of habitat (more Strong) has a much greater benefit.

Does the metapopulation remain viable if jays are removed from Weak and Sink habitat (for translocation to support other sites)?

If there is not habitat improvement, then harvesting more than about 1 pair from Weak and 1 pair from Sink per population each year would considerably accelerate the projected metapopulation decline. If the habitat is first improved to 70% Strong, then the numbers that could be removed from the KSC/MINWR metapopulation without causing decline is about 14 to 16 pairs per year.

CCSFS metapopulation management scenarios

The CCSFS population has too little Strong habitat to be expected to avoid a steady decline toward extinction. The metapopulation could be sustained by steady immigration (either natural dispersal or via managed translocations), but only at breeding population sizes that approximate the number of Strong habitat territories. If habitat could be improved to become 50% to 70% Strong (from the current 5% Strong), then the projected decline in population size could be temporarily halted for about 30 years. However, even with habitat improvement, in the long-term inbreeding would accumulate to levels that depress survival, and that would cause a significant possibility of extinction. If habitat is improved to 70% Strong and there is regular reinforcement via immigrants, then the CCSFS population could be largely stabilized and extinction would be avoided. Thus, the CCSFS metapopulation could be sustained and viable only if there is considerable habitat improvement and regular immigration from KSC or elsewhere. Few management scenarios were considered for the CCSFS population and results relied greatly on applying vital rates from KSC and the mainland to CCSFS.

South and Central Mainland metapopulation management scenarios

The SC Mainland population is currently projected to decline to extinction (with a median time of about 55 years) because the local populations are too small, too isolated, and have too little optimal habitat. Increased dispersal (up to 5x current estimates) would considerably slow the decline, but even with complete connectivity the population is projected to slowly decline because there are too few Strong potential territories (currently 80). Habitat improvement would slow the decline in numbers, but does not stop the decline nor prevent extinctions, because the limited dispersal among populations results in inbreeding accumulating to damaging levels. If habitat could be both improved and more connected, in the best case (70% Strong and complete panmixia) the metapopulation is projected to be viable – staying above 50% occupied, not at risk of extinction, and inbreeding kept low.

With supplementation of 2, 4, 8, or 12 jays added to the metapopulation each year, the population size initially decreases and then plateaus at progressively higher numbers of breeding pairs with more immigration. If habitat is first improved to be 70% Strong, then supplementation with 8 or more jays added per year to the metapopulation results in the SC Mainland metapopulation growing and then remaining above 50% occupancy, there is no likelihood of extinction, and inbreeding stays below 0.05.

What if Jordan and Valkaria populations could be connected, and acquisitions added to BABC (+12 potential territories), CORA (+9), CORR (+5), CP (+12), JORD+VALK (+10), and FELS (new population, +5)?

If these acquisitions, which increase potential territories by 24%, are made, the metapopulation still declines but would typically have about 10 more breeding groups at any time during the decline. The accumulation of inbreeding is slowed but still results in levels ($F > 0.10$ within 50 years) that accelerate the decline and cause extinction typically sometime between about 40 years and 80 years. Thus, the acquisitions help, but do not achieve metapopulation viability because the continued isolation of the small local populations results in damaging inbreeding.

The damaging levels of inbreeding can be reduced or avoided by increased connectivity among all local populations. If increased dispersal and acquisitions are combined with improving habitat to 70% Strong, then for 60 or more years the metapopulation remains at more than 50% occupancy, inbreeding stays at low levels, and extinction is avoided.

North Mainland metapopulation management scenarios

Improvements in the existing potential habitat would not be sufficient to prevent the rapid decline of the N Mainland populations. Increasing connectivity among N Mainland populations also would not be sufficient to stabilize the populations. Habitat improvement combined with connectivity could result in the metapopulation persisting for decades. However, the metapopulation would eventually go into decline because the metapopulation is too small to avoid damage from accumulating inbreeding, and extinction is likely after about 50 years.

Regular additions of jays could prevent genetic problems, reinforce the populations after any declines, and allow for population growth to fill available habitat. For example, releasing about 8 jays each decade to each local population could sustain a viable N Mainland metapopulation if habitat is improved to be 70% Strong. Increasing connectivity between local populations would further enhance the effectiveness of supplementation, because local populations that otherwise go extinct between releases would be reinforced by dispersal from nearby populations. If there is high dispersal between populations, then releasing 4 jays per decade to each local population could sustain a viable metapopulation and avoid extinctions.

Ongoing use of the PVA model to assist FSJ population and habitat management

The PVA model can now be a platform for ongoing evaluation of the likely complex and often indirect effects of options for management of both habitat and the FSJ directly, in ways that could not be assessed intuitively and would require years of field research to test experimentally. Recognizing the imprecision of estimates of population characteristics and the uncertainty of population trajectories, it will be important to maintain monitoring of the populations and their responses to habitat change and management actions. The model provides the structure for periodically updating analyses with new data or assumptions. One potentially valuable direction for extending the PVA is to link the population model with models of habitat change, so that impacts on the FSJ populations of management regimes can be assessed.

The FSJ model developed for the Brevard populations can also be a template for building models specific to other regional populations, such as the Ocala and Lake Wales metapopulations. Values of input parameters – both local demographic rates and the habitat and population structure – would need to be customized for any regional differences, but the structure for representing the habitat complexity, life history, and social dynamics of FSJs is now in place, and the model was configured so as to facilitate revising input values.

To enable and support ongoing use of the PVA for evaluating future scenarios and other populations, a core team of scrub-jay biologists or managers will need to develop a detailed understanding of both the mechanics of the Vortex software and the specific ways in which the FSJ model was constructed. Training in such advanced uses of Vortex can be provided to scientists working with the FSJ populations.

Introduction

Background on the Florida scrub-jay

The Florida Scrub-Jay (FSJ) is the only species of bird unique to Florida. This endemic non-migratory species occupies year-round, multi-purpose territories. It is well-known worldwide for a cooperative breeding system in which young can remain with their parents for several years, enhancing their reproductive success as non-breeding helpers (Woolfenden and Fitzpatrick 1984, Woolfenden and Fitzpatrick 1991, Breininger et al. 2014b, Mumme et al. 2015, Fitzpatrick and Bowman 2016). Most natal dispersals involve helpers transitioning to breeders in adjacent territories or the next closest ring of territories (Fitzpatrick et al. 1999, Breininger et al. 2006, Coulon et al. 2010, Coulon et al. 2012). Fragmented systems have longer mean dispersal than do intact systems where occupied territories are contiguous.

The FSJ continues to decline because of habitat loss, habitat degradation, and extinction debt associated with habitat fragmentation (Woolfenden and Fitzpatrick 1991, Stith et al. 1996, Breininger 1999, Breininger et al. 1999, Breininger et al. 2006, Chen et al. 2016). Many FSJ population sizes have declined to levels where their long-term viability is becoming doubtful because of the reduction in local population resiliency in isolated habitat patches. Local populations are often compromised from the limitations of accessible habitat or the reduction of fire regimes that has caused the habitat to become unsuitable or of such poor quality (demographic sinks) that mortality exceeds recruitment (Breininger and Carter 2003, Breininger and Oddy 2004). Restoring scrub habitat quality to conditions where recruitment exceeds mortality (sources) can be expensive, take long periods, and involve cutting trees that produces shade that many recreationalists desire (Duncan et al. 1999, Johnson et al. 2011, Eaton et al. 2021). Potential habitat (i.e., scrub) occurs on ancient beach ridges associated with changes in sea level and that vary in many characteristics. Inland scrub habitat are often large, well-drained, nutrient poor ridges (e.g., Lake Wales, Ocala) that contrast with small coastal ridges that have higher water tables and nutrients available to plants resulting in differences in habitat management regimes (Breininger et al. 2002, Breininger et al. 2010, Breininger et al. 2018). Local populations in coastal ecosystems can be described as a dynamic checkerboard of sources and sinks (Breininger and Carter 2003, Breininger and Oddy 2004).

Brevard County contains two metapopulations that occur in distinct genetic units (Breininger et al. 1996, Breininger et al. 2003, Coulon et al. 2008). The largest metapopulation occurs largely on federal lands (Kennedy Space Center [KSC], Merritt Island National Wildlife Refuge [MINWR], and Cape Canaveral Space Force Station [CCSFS]) providing large conservation landscapes. The total population size in this metapopulation is between 400-500 breeding pairs in 8 local core populations. The KSC/MINWR and CCSFS clusters of populations might be considered to be separate demographic metapopulations, as the amount of exchange between them is unknown and perhaps limited. The second metapopulation, on the mainland, is highly fragmented and comprised of local populations that are further apart than normal dispersal distances. The mainland populations can be considered to consist of two metapopulations – a cluster of 14 populations in south and central Brevard, with about 110 breeding pairs, likely is no longer exchanging jays with the cluster of 5 breeding populations in north Brevard, with another 10 breeding pairs. Not all the "populations" would be considered functional biological populations, as some have as few as a single breeding pair. In both the south-central and north mainland metapopulations, there are a few additional sites that could potentially hold small breeding populations. Both the island/cape and the mainland genetic units have declined by greater than 50% in the past 30 years because of reductions in the natural fire regime and extensive habitat loss on the mainland. There is a need to establish management priorities in both genetic units.

Meeting recovery goals for the federal properties requires large habitat restoration expenditures and changes in federal fire management strategies. Given projected sea level rise scenarios, the goals for population size might be unattainable. However, there is opportunity to maintain large populations with low extinction risk by prioritizing habitat management scenarios. For example, it might be better to more carefully manage existing local populations than to expend resources to recover the entire population with insufficient resources. Maintaining the genetic integrity of FJS along the central Florida Atlantic Coast should benefit by cooperation in conservation efforts and the development of a long-term strategy.

The mainland unit requires the most complex management decisions soon. None of the reserve designs recommended through a habitat conservation planning process were implemented in their entirety, resulting in an incomplete and highly fragmented conservation system with expenditures exceeding 100 million dollars. Most conservation areas were purchased after habitat degradation occurred, requiring population reestablishment or supplementation because the reserves are too isolated to allow for natural immigration. Future conservation alternatives include further conservation acquisition, prioritizing habitat restoration efforts, and translocation.

Using Population Viability Analysis models for exploring management options

Population Viability Analysis (PVA) simulations are powerful tools that are increasingly used by governmental agencies, conservation organizations, and researchers to project the viability of wildlife populations, assess threats to populations, and evaluate management options (Beissinger and McCullough 2002; Morris and Doak 2002; Lacy 2019). Management of wildlife populations is challenged by the multiple threats to populations, trade-offs resulting from competing goals and interacting biological processes, the randomness of many biological and environmental (and sometimes people) processes, and lack of complete information about the species, the habitat, and the future. PVA simulation models address these challenges by allowing consideration of the data that are available on a species, the local habitat, and specific threats. The effect of uncertainty in the situation can be explored, and the use of the models can highlight what key data are missing that might influence decisions. Management options can be evaluated across the range of uncertainties to determine which options will be most robust to uncertainties and therefore most assured of reaching conservation goals. Importantly, simulation models allow projecting future consequences of processes already underway, or even past events, for which there might be time lags between causal events and impacts apparent in population size or structure.

Understanding and projecting accurately the dynamics of the FSJ is even more challenging than is the case for most species. First, the spatial distribution of the species is a complex hierarchy – with breeding pairs within local populations, interconnected to varying degrees within metapopulations, together comprising the species distribution in several types of habitats in Florida. Those habitats are dynamic, with changing total area, quality, and connectivity – all determined by fire regimes, development, habitat restoration, and sea level rise. The dynamic mosaic of habitats likely creates a source-sink pattern of population dynamics, so that the metapopulation must be studied to understand long-term trends. Because of the fragmentation of the habitat, with some populations being very small and isolated, local inbreeding can impact population growth both directly (e.g., through reduced fecundity) or indirectly (e.g., through unavailability of acceptable mates if the birds avoid inbreeding).

The social structure – with progeny often remaining on natal territories as helpers – might help either stabilize or destabilize the populations, depending on the interactions with demographic growth (e.g., recruitment rates), opportunities for dispersal, and habitat quality. PVA models almost always assume that species are asocial – that is, the demographic performance of individuals is unaffected by their social environment, and all individuals have equal probability of reproducing and surviving. Thus, most PVA models would not provide a good representation of FSJ populations for assessing population status and threats and evaluating management options. A highly flexible, individual-based PVA is required to be able to model the social behavior of FSJ, with helpers not breeding but being important to the reproductive success of the breeding pair of their family group.

The above issues create dynamics that cannot be represented well using the traditional demographic models of population ecology and wildlife biology (Caswell 2001), nor even by the population-based simulations used in many PVAs. However, the multiple factors above can be modeled using highly flexible individual-based models that can be linked to dynamic models of landscape configuration and habitat quality (Lacy 2000a; Walters et al. 2002; Keith et al. 2008; Lacy et al. 2013; Carroll et al. 2014; Williams et al. 2017).

The population dynamics of the FSJ were modeled using the Vortex (version 10.5.3) population viability analysis software (Lacy 2000b; Lacy and Pollak 2020; Lacy et al. 2020; software and manual available as freeware at www.scti.tools/vortex/). Vortex is an individual-based model that simulates the fate of each individual through an annual cycle of breeding, mortality, increment of age, dispersal among subpopulations, removals (or emigration from the population), supplements (managed or natural immigration), and truncation if the population exceeds the carrying capacity (ceiling density dependence). Stochasticity in demographic processes is modeled as annual variation in each demographic rate at the population level (environmental variation) and random, binomial sampling variation in the fates of individuals (demographic stochasticity) (Lacy 2000a, 2000b). Individual fates are summed to provide outputs of projected population sizes (mean, SD, and distribution across independent iterations), population growth rates, population age and sex structure, and probabilities and times to local extinction or quasi-extinction (N falling below a threshold size). Projecting the effects of population structure on loss of genetic diversity, and in turn the impacts of loss of diversity on fecundity and survival (and, hence, population growth), is an intrinsic component of the Vortex model. Vortex provides the flexibility to specify demographic parameters as functions of environmental (e.g., climate, prey base), population (e.g., density, social structure), or individual (e.g., age, social status, inbreeding, genotype) properties through the use of state variables to track properties of the system (Global State Variables), each local population (Population State Variables), and each individual bird (Individual State Variables).

There are a handful of PVAs on cooperative breeding vertebrates (e.g., red-cockaded woodpecker, Walters et al. 2002), and some of these focus on helper and breeder stage abundances and transitions between stages as functions of other population variables. However, few other PVA models include the enhancement of recruitment by non-breeding helpers and the effects of management actions and disturbances being dependent on the abundance of helpers. For example, in a PVA for the Mexican wolf (Carroll et al. 2014) that was used by U.S. Fish and Wildlife Service to set recovery criteria (USFWS 2017), the modeling included complex functions to define the probability that a wolf would disperse from its natal pack and become a breeder. However, the analyses did not include consideration of the influence of pack size on success in rearing pups.

A major advantage that makes possible the modeling FSJ populations accurately enough to provide a platform for testing management options is that a lot of data about the species and its habitats have been gathered over decades of intensive research. Much more is known about the local population locations and sizes, habitat use, demography, social structure, and genetics than is known for most other species. The complexity of demographic rates being dependent on the habitat quality of each breeding territory can be modeled in Vortex by specifying the habitat of each breeding group as an individual state variable, and then specifying breeding and mortality rates to be distinct for each type of habitat. The social system, with helpers often remaining with the natal breeding group for up to several years before becoming breeders, can be modeled by specifying helper or breeder status as an individual state variable, and using functions to define the probability of helper to breeder transitions as influenced by breeding opportunities and available habitat. Thus, transitions among social status (e.g., dispersing from a natal group, acquiring breeding status) can be modeled within Vortex by specifying rules that govern those transitions. Moreover, the breeding rates can be specified to be influenced by the size of the breeding group, and mortality rates can be specified to be different for helpers vs breeders.

The abundance of data on FSJ does not mean that there are not gaps in our knowledge and a level of uncertainty about almost every parameter. An important feature of PVA is that allows examination of the effects of uncertainty on our understanding, and therefore enables consideration of the uncertainties in management decision-making (Mills and Lindberg 2002; Saether and Engen, 2002; McGowan et al., 2011). First, the uncertainties about the precise values of demographic rates and other species properties, habitat characteristics, and the relationships of demography to habitat can be included in the PVA simulation. In this way, the distribution of population projections under each scenario will reflect these uncertainties, rather than giving us false confidence in our ability to predict a precise future for the species. Similarly, our uncertainty about future environments can be explored through examining a range of environmental outcomes or testing specific scenarios. Most importantly, the likely results of various proposed management actions can be explored. A highly specific model such as Vortex is well-suited for testing very specific management actions. For example, the effects of translocating a given number of birds of designated age, sex, and social status between pairs of populations can be projected.

Once a model is in place that adequately captures the complex dynamics of the FSJ populations, it can be a platform for ongoing testing of management options, even while it continues to be refined as the population changes, new data become available, and new options proposed. Further modification of the model to represent the dynamics in different areas of habitat, such as the inland ridges, might require replacement of the model component for describing habitat structure and dynamics, and revision of species demographic rates, but the basic structure of the overall model of habitat-populations-social structure will already be available.

Using PVA models to guide conservation and management decisions

The FSJ is a species in decline because of extinction debt caused by habitat fragmentation and degradation. There is very limited opportunity left for habitat acquisition in most Brevard County metapopulations and limited funding for restoration in any given year, but there is a wealth of long-term data on habitat, population, and management history. Populations range from a comparably large metapopulation presumably having low extinction risk following habitat restoration effort to populations that are relatively small and isolated that may remain viable only under the most extreme conservation efforts. Successful and efficient management will require understanding the prospects for each population and projecting the consequences of proposed management actions. The detailed PVA model that can be built with Vortex and accessory tools can provide that understanding and forecasting.

Species recovery planning seeks to set targets and timelines for population recovery. For the FSJ, setting realistic metrics for success will require taking source-sink dynamics and helper effects into account. For example, habitat restoration near a population with an abundance of helpers is likely initially to make great progress as potential breeders are available nearby, but restoration actions might have very slow effect if few helpers are nearby to take advantage of breeding opportunities. An important advantage of PVA simulation models is that they provide quantified projections of the time course for expected recovery under the proposed management scenarios. These targets are based on the current information, in a documented and repeatable analysis that can be refined and updated as new information or options become available.

We followed a phased approach to constructing population modeling tools that incorporated the best available science to address a variety of conservation actions. The first phase focused on constructing a population model that incorporates sociobiology and source-sink habitat dynamics. This model allowed us to address some of the most important questions about population size and habitat quality. Once the model framework was in place, we considered the real landscapes and actual local populations, rather than just generic representations of typical FSJ dynamics. In this way, these analyses can be used to guide and support specific recovery actions.

Further development that builds on the work done within this project could involve expanding across the species range to examine management actions for other populations. Assessment of other metapopulations will likely involve connecting population models to models of those habitat dynamics. The integrated use of coupled habitat and population models might be valuable because temporal variation in management efforts (e.g., fire, population harvest) is likely to effect the sociobiological attributes of populations in a manner that effects how to prioritize management and set reasonable targets and timelines for recovery. As a final phase of this project, we developed the structure of population models that can make use of projections of habitat at the level of FSJ territories and on an annual basis. These extended models can now be a platform for ongoing evaluation of the likely complex and often indirect effects of options for management of both habitat and the FSJ directly, in ways that could not be assessed intuitively and would require years of field research to test experimentally.

PVA models, and Vortex in particular, are often used as a core tool within broader conservation strategic planning processes, such as the Endangered Species Act Recovery Teams and similar conservation planning in many other countries and at various levels of government. PVA provides to those planning processes a transparent methodology to assemble data, categorize levels of endangerment, assess threats, identify data gaps, evaluate options, and set management targets. The PVA for the FSJ should similarly be used as a basis for broader planning efforts in the future.

Modeling the complexity of the FSJ populations and social system, in the dynamically changing mosaic of habitats, requires development of an integrated set of population and habitat models that go beyond what has generally been used before in wildlife management. Therefore, the analyses performed in this PVA can be an example of how to include highly complex individual, social, population, and landscape processes in other species where such specificity is necessary to represent the population dynamics adequately to guide local conservation decisions.

Florida Scrub-Jay PVA model

Summary of demographic data

Demographic rates (% pairs successfully producing juveniles, number of juveniles produced per pair, and annual survival rates for juveniles and adults) were tallied from the long-term field surveys of the populations on Merritt Island and mainland areas of Brevard County that included about 30 sites and up to 30 years of long-term studies. These tallies were produced by D Breininger, with assistance from colleagues (G. Carter, S. Legare, J. Lyon, E. Stolen, D. Breininger, B. Payne) at KSC. Demographic performance was tallied separately for each year from 1988 through 2015, separately for breeding territories in Strong, Weak, and Sink habitats (see papers by Breininger and colleagues for definitions of habitat quality classifications: Breininger et al. 2002, Breininger et al. 2009, Breininger et al. 2010, Breininger et al. 2014a, Breininger et al. 2014b, Eaton et al. 2021), and separately for breeding pairs with no helpers vs with helpers. The category strong refers to open medium and weak refers to closed medium in previous studies; sink refers to all other habitats. Most of the vital rates used herein are the most recent updates from long term studies previous published or new manuscripts under development.   Detection probabilities for the field surveys that contributed to the estimation of demographic rates are very high (Breininger et al. 2009), so we used direct calculations of breeding and survival rates of monitored breeding groups rather than estimating rates from mark-recapture methodologies that fit models to account for unobserved birds.

These estimates were reviewed with FSJ experts who met at Archbold Biological Station in August 2019 (with subsequent discussion), in order to confirm consistency with the extensive data on the Archbold population. Differences in estimates of reproductive success and survival were few and were explainable by differences in the habitats. Similarly, data from KSC and Archbold on the impact of the number of helpers on breeding success were reviewed. Although breeding success of pairs is correlated with number of helpers, the trend is weak after pairs have at least one helper. In addition, it is not possible to assign causality with certainty. The mean number of helpers might be higher in groups with better breeding success because there are more surviving previous progeny, or better breeding success might be a consequence of having more helpers, or both. Validation tests that compare the observed mean number of helpers per breeding group to projections in the models were used to help confirm that the PVA represents well the relationship between presence of helpers and breeding success.

From the observed annual variation in breeding success and survival rates for each habitat, we estimated of the annual variation at the population level due to fluctuations in the environmental conditions (the "environmental variation", EV). EV is calculated by removing the expected binomial sampling variation (the random fluctuation in each demographic rate expected due to the independent fates of individuals exposed to the same probabilities of each demographic event) from the total inter-annual variation in the data (Akçakaya 2002; Lacy et al. 2020). These estimates of EV are then used in the Vortex PVA model to specify the distribution of each demographic rate that represents the fluctuations in environmental conditions over time.

Mortality

Annual mortality rates for breeders, juveniles (from independence up to 1 year of age), and helpers (age 1 and beyond) for FSJs in territories classified as Strong, Weak, or Sink habitats are shown in the Table 1. The mean rates are the means of 28 annual rates, not weighted by annual sample sizes, to represent the distributions of rates that will be sampled each year in the simulations. EV for each mortality rate is given as a SD representing the annual variation around the mean value, after removing the binomial sampling (demographic stochasticity). As expected, mortality rates are generally lower for FSJ in Strong habitat territories than in Weak, and lower in Weak than in Sink. Breeders had lower mortality than helpers, and all adults had lower mortality than juveniles.

The estimates of annual variation in rates (EV) are generally less reliable than are estimates of mean rates, because of the extra calculation steps that are required for removing estimated random sampling variation (which is itself dependent on the estimates of mean rates each year). Usually, however, the magnitude of EV in population models for long-lived species has much lesser impact on results than do the mean demographic rates, so it is usually not important to obtain highly accurate estimates of EV. Differences among Strong, Weak, and Sink habitats in EV for each demographic rate were not consistent in direction, were mostly non-significant, and were most likely due to the low accuracy of estimates of EV. Therefore, for the modeling, EV was calculated from the annual variation in demographic rates pooled across all three habitats (shown in the last row of Table 1), and these values were used in the modeling. Sensitivity analyses (see below) indicate that projections were not highly sensitive to the precise values of EV used in the models. Moreover, results were nearly indistinguishable when habitat-specific EVs were tested. EV in mortality rates was lowest for breeders, next lowest for helpers, and highest for juveniles – suggesting that juveniles are most susceptible to annual variation in the environment, and breeders least susceptible to environmental fluctuations.

The estimates of demographic rates are subject to error, both because the observations are on a finite (although large by the standards of most monitoring data for endangered species) number of years (28y), because the population is relatively small and subject to random fluctuation in rates, and because classification of breeding territory habitat quality is imprecise. A necessary part of any PVA modeling is to examine a range of plausible values via sensitivity analyses (McCarthy et al. 1995; Mills and Lindberg 2002). As a starting point, we conducted sensitivity analyses that allow the mean rates to vary across a distribution with the variation as estimated from the standard errors (SE) around each mean rate across years. Other plausible ranges that can be tested include the variation observed across years or across sites (Manlik et al. 2018). These sensitivity analyses allow us to determine (a) the confidence that can be placed on population projections; (b) the demographic rates for which refinements in estimates will be most valuable; (c) the rates that have greatest influence on the stability and growth of the populations, and (d) the aspects of demography for which enhancement via management would have the greatest positive impact on the population viability.

Table 1. Estimated mean annual mortality rates and annual variation in rates (EV) for FSJ in breeding territories classified by habitat quality. SE for each value is given in parentheses. Values in bold were used in the Vortex PVA model.

	Breeder Mortality	Breeder Mort. EV	Juvenile Mortality	Juvenile Mort. EV	Helper Mortality	Helper Mort. EV
Strong	**0.185 (0.017)**	0.060 (0.011)	**0.306 (0.025)**	0.197 (0.037)	**0.287 (0.029)**	0.085 (0.016)
Weak	**0.206 (0.022)**	0.054 (0.010)	**0.306 (0.040)**	0.207 (0.039)	**0.322 (0.032)**	0.034 (0.006)
Sink	**0.253 (0.008)**	0.079 (0.015)	**0.456 (0.022)**	0.148 (0.028)	**0.313 (0.015)**	0.120 (0.023)
Combined	0.242 (0.007)	**0.068 (0.013)**	0.379 (0.019)	**0.189 (0.036)**	0.306 (0.011)	**0.089 (0.017)**

Reproductive rates

Breeding success was calculated as the proportion of breeding pairs that produce juveniles each year, in each of the three levels of habitat quality, and separated by those pairs that have at least one helper vs those without helpers. The mean rates are the means of 28 annual rates, not weighted by annual sample sizes, to represent the distributions of rates that will be sampled each year in the simulations. As expected, breeding success was greater in Strong than Weak, and greater in Weak than in Sink habitats, and greater when breeding pairs had helpers than when they did not.

Data were insufficient to estimate EV separately for breeders with helpers and those without helpers, so EV was calculated for the data pooled across both categories of breeders. In addition, the differences in EV among habitats was most likely due simply to the difficulty in estimating EV accurately, so the value calculated across all three habitat types (EV = 0.209 SD) was used in the modeling.

Table 2. Mean annual breeding success for FSJ pairs that do not have helpers, those pairs with helpers, and combined. SE for each value is given in parentheses. EV is calculated for the data combined across breeders with and without helpers, and for data combined also across habitats. Values in bold were used in the modeling.

	No Helpers	with Helpers	Combined	EV
Strong	**0.482 (0.033)**	**0.544 (0.034)**	0.511 (0.028)	0.206 (0.039)
Weak	**0.268 (0.022)**	**0.343 (0.026)**	0.389 (0.044)	0.211 (0.040)
Sink	**0.226 (0.011)**	**0.282 (0.015)**	0.236 (0.010)	0.100 (0.019)
Combined	0.261 (0.010)	0.337 (0.013)	0.289 (0.009)	**0.209 (0.040)**

The mean number of juveniles produced annually per breeding pair and per successful pair (with success defined as producing at least one juvenile), calculated separately for the three levels of habitat quality and for pairs with and without helpers, are given in Table 3. As expected, number of juveniles produced was greater for pairs in Strong habitat and for pairs with helpers. The distributions of numbers of juveniles produced per pair closely fit zero-inflated Poisson distributions (distributions expected if production of successive offspring is independent, but the zero class has extra values). For modeling purposes, this is convenient, because the number of juveniles produced per brood can be sampled from such a distribution, rather than requiring exact counts for each possible brood size to be entered into the PVA model.

Table 3. Distribution of brood sizes (number of juveniles produced per pair and per successful pair), calculated separately for breeding pairs with helpers vs without helpers, and for pairs in territories classified as Strong, Weak, or Sink habitats. The Poisson mean columns give the means for Poisson distributions that would produce the observed mean numbers of juveniles per successful pair. The values in columns labeled "All" combine data for pairs with and without helpers, and values in the last row combine data across habitat quality.

	Juveniles/Pair			Juveniles/Successful Pair			Poisson mean		
	No Help	w Helpers	All	No Help	w Helpers	All	No Help	w Helpers	All
Strong	1.049	1.256	1.150	2.176	2.308	2.244	**1.825**	**1.994**	1.915
Weak	0.508	0.715	0.601	1.894	2.085	1.991	**1.450**	**1.707**	1.553
Sink	0.411	0.539	0.457	1.820	1.913	1.856	**1.346**	**1.476**	1.400
All	0.497	0.691	0.574	1.904	2.053	1.972	1.463	1.664	1.556

With the availability of tools developed by Billy Payne and Dan Breininger to extract demographic rates from census data, we can now more quickly update the PVA models as new data become available. To facilitate this, the demographic rates, as described above, were accessed by the Vortex model from file Rates.txt and RatesSE.txt (both available in the zenodo.org repository at http://doi.org/10.5281/zenodo.4469885). Placing the demographic rates in an external file, rather than entering the rates individually in each of the many scenarios, will allow rapid updating of all model scenarios as new data or otherwise refined estimates become available.

Additional demographic parameters and settings

- Maximum lifespan is set at 17 y; the oldest age observed (n= 3) and oldest known breeder (n = 1).
- FSJ can start breeding as early as age 1 year, with probability 0.12; otherwise they remain as a helper in the natal territory.
- Initial population size will be varied across scenarios to be tested. In the initial baseline models used to explore factors that enhance or degrade population viability, potential territories were assigned arbitrarily (and rather optimistically) as 40% Strong, 30% Weak, and 30% Sink, with territory occupancy set to 70% , 50%, and 30% of Strong, Weak, and Sink, respectively, being occupied at the outset, for a total initial population size of 52% of the potential. The proportion of potential

territories assigned to each habitat in this phase of modeling do not correspond to any particular population, but rather are just a possible distribution that will be used as a starting point for exploring the impacts of various amounts and quality of habitat. The proportion of each that is initially occupied was chosen to represent that breeders preferentially select better habitat. Within a few years of the simulation the relative occupancies will shift toward the equilibrium that arises from the other input values specified in the scenario.

- Carrying capacity (an upper limit on the number of FSJ that can be in a population) was set to be 4 times the number of potential territories. This carrying capacity was imposed in the model by causing some helpers to be removed from the population when the carrying capacity was exceeded. (I.e., we assume that under crowded conditions, some helpers could be driven out of the population.) However, in the model with a mix of Strong, Weak, and Sink territories, this upper limit is rarely reached, because as more FSJ are pushed into Sink habitat, breeding rates and survival rates go down and the population experiences demographic decline (or at least stops growing).
- Inbreeding depression was modeled as a decrease in juvenile survival for inbred offspring, with the severity of inbreeding depression as estimated by Chen et al. (2016) (7.478 Lethal Equivalents for impacts on survival from 11-day nestling to yearling, with SE of approximately 3, based on reported 95% CI). (Lethal equivalents, LE, measures the severity of inbreeding depression by representing the impact in terms of the number of recessive lethal alleles per individual that would result in the observed damage from inbreeding. Thus, with 1 LE, the inbreeding depression might be due to a mean of one lethal allele per individual, or two alleles each causing 50% mortality when homozygous, or other combinations of deleterious alleles with comparable effect.) Impacts of inbreeding on later stages (e.g., yearling to breeder) were not significant in Chen et al. analysis, but estimates could be added to the PVA model later if desired. It is recognized that the smaller populations of FSJ may already have reduced genetic diversity and greater average kinship among individuals. This can lead to more rapid inbreeding than is being projected currently in the PVA. This effect can be incorporated in future refinements of the Vortex FSJ model if we obtain estimates from molecular genetic studies of the current kinships within and between local populations.
- FSJ are assumed to avoid mating with parents, offspring, siblings, maternal half-siblings, or paternal half-siblings. This is specified in the model via a function used in the Criteria for Acceptable Mates.
- In the baseline model, no catastrophes were included, and it is assumed that any bad years for fecundity or survival are encompassed within the annual variation in demographic rates that are entered into the model. Although there are – almost by definition – few data on low frequency, but high impact catastrophes (such as severe disease epidemics), it was noted that in 1979 there was a severe mortality event – likely due to an outbreak of encephalitis. This was before the systematic data collection of the KSC/Brevard population, so the impact would not have been captured in the time series of survival rates that have informed the demographic rates in the PVA. In that event, it is estimated that almost no juveniles survived and adult mortality (for both breeders and helpers) was about 50% in the Archbold population. There was also observed a decline in breeding the following year. A few scenarios with catastrophes were used for testing the resilience to any such sudden and severe declines in population size. Other outbreaks in east coast populations were likely in subsequent years but annual variation in survival varies greatly and suggests these events might not add additional information (Breininger et al. 2009).

- Harvest and Supplementation options in Vortex were also not used in the baseline model, although they were used later to examine options for translocations among populations and to model the impact of occasional immigrants from external populations.
- The initial Vortex FSJ model included only a single population and assumes that the population is isolated demographically and genetically. After exploring the viability of such isolated populations of varying size and habitat quality, we extended the model to include multiple populations within a metapopulation, with the possibility of dispersal between some of the populations.

Modeling the social and habitat determinants of population dynamics

Habitat selection by breeders

To model the selection of new breeding territories from among the available (unoccupied) territories of Strong, Weak, and Sink habitat, we used an exponential function, such that:

- A new breeding female would choose a territory with Strong habitat with probability = (proportion of available territories that were Strong)^(1/Pref), in which Pref is a parameter that can be varied from 1 (habitat preference matches proportional availability) to higher values (Fig. 1). For example, if Pref = 2, and 33% of available territories are Strong, then the probability that a new breeder will select a Strong territory is (0.33)^0.5 = 0.574.
- If a new breeder does not select a Strong territory, then she will select a Weak territory (rather than Sink) with probability equal to (proportion of Weak available territories among those that are not Strong)^(1/Pref).
- If neither Strong nor Weak are selected, then the new breeder is placed into a Sink territory. For example, if Strong, Weak, and Sink habitats are equally common among the unoccupied territories, and if Pref=2, then a new breeder has a 57.4% probability of selecting a Strong territory, a 30.1% probability of selecting Weak habitat, and a 12.5% probability of going into Sink habitat. If Pref=6, then a new breeder has 83% probability of selecting a Strong territory, 15% probability of selecting Weak habitat, and 2% probability of going into Sink habitat.
- We examined data on the pattern of territory selection by new breeders to determine what value for the Pref variable provides the best representation of the territory choices made by the FSJs. We validated the habitat selection model by examining whether the distribution of territory occupancy by habitat type generated by the model mirrors what is seen in the Brevard populations.
- When a new breeding female selects a territory and then is assigned a mate, that mate is automatically assigned to the same territory quality as his new mate.
- We assumed that after a breeding pair becomes established in a territory, they do not move to a new territory in subsequent years, even if better habitat becomes available.

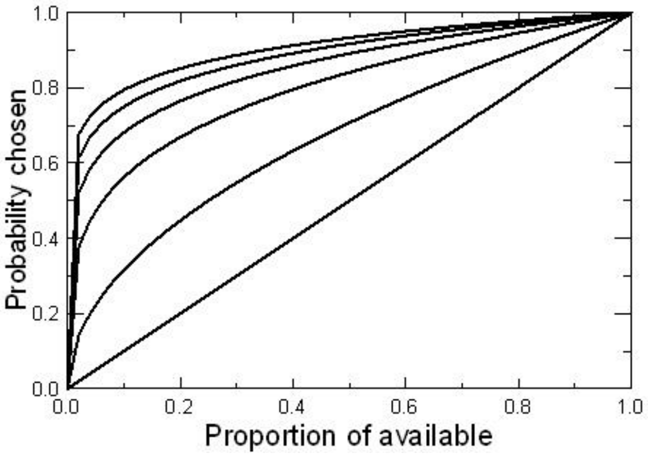

Figure 1. Functional relationship used to model the probability that a new female breeder will establish a territory in Strong habitat, based on the proportion of available (unoccupied) habitat that is Strong. The exponent parameter was set to Pref = 1, 2, 4, 6, 8 (lines from bottom to top).

Although we term the habitat selection parameter "Pref" in the Vortex model, it is more appropriate to think of the parameter as defining the probability of optimal habitat selection, rather than necessarily a strength of preference. Higher probability of occupying the most optimal available habitat might occur because of the preference, or it could result from the accessibility due perhaps to distance from natal territory or vigorousness of defense by adjacent breeding groups. Jays search for new territories and breeding opportunities only short distances from their natal territory. Therefore, even within local populations they might establish breeding territories in less optimal habitat than what is otherwise available, because of what is nearby (i.e., accessible). The performance of a population in areas with a mixture of habitat quality of potential territories is strongly dependent on the accessibility of the better habitat.

Helper to breeder transitions

We used State Variables in Vortex to model the transitions of jays between helper and breeder status. This overlay of social state transition modeling on top of the demographic modeling, and specification of the interactions between social status and demography, is necessary for representing the dynamics of Florida scrub-jay populations.

Helpers will often transition to breeders in response to breeding opportunities when good territories become available due to the death of breeders. This response to opportunities might have a stabilizing effect on the populations, because the pool of helpers becomes a source for rapid replacement of breeders after a decline in the population. For example, it was noted that after a (presumed) disease epidemic decimated the Archbold population, with the deaths of many breeders, the breeding population recovered within a few years as prior helpers filled the breeding opportunities. We have built this process into the Vortex model for the scrub-jays, using a logistic function to define the probability that a female helper will transition to become a breeder: Pr[HtoBr] = exp(-1+B*pAvail)/[1 + exp(-1+B*pAvail)], with pAvail being the proportion of Strong potential territories unoccupied, and the slope parameter B defining the strength of the relationship (Fig. 2). We do not (yet) have good data with which to estimate the slope of this relationship, and we tested scenarios with varying degrees of response to breeding opportunities.

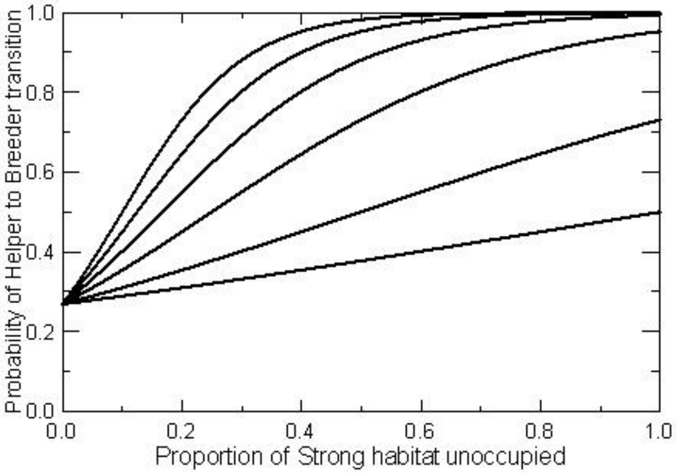

Figure 2. Functional relationship used to model the rate of female FSJs transitioning from helpers to breeders in response to available Strong habitat. The slope parameter for the logistic function was set to B = 1, 2, 4, 6, 8, and 10 (lines from bottom to top).

The above relationship was constrained with the additional assumption that helpers would not transition to become breeders if there were no unoccupied potential habitats in their local population.

In our scenarios, typically most of the Strong habitat is occupied (due to the Habitat selection model, above), and the mean annual probability that a female helper leaves the natal territory to become a breeder is very close to the rate of 0.46 that has been observed in the KSC populations (see *Validatio*n section, below).

We specify in the model that when a breeder dies, the helpers remain with the surviving breeder in that territory, and a replacement for the dead breeder is recruited. This can stimulate the transition of additional helpers to breeders, beyond that predicted from the above functional relationship, if there are otherwise not enough new breeders of one sex or the other to fill vacancies created by the deaths of breeders. Modeling this process in Vortex requires that the female and male breeders of the breeding group are tracked for each helper, and the helpers become re-assigned to the new parent when a replacement occurs. Although other outcomes after the loss of a breeder are possible – such as helpers dispersing to other breeding groups or becoming breeders themselves in the natal group – the overall population dynamics would not likely be affected significantly by exactly which jays move into the social status roles. Some of the specifications in the PVA to model the helper to breeder transitions include:

- The probability that a male helper leaves the natal territory to become a breeder is set each year in the model so that the number of new male breeders will equal the number of new female breeders that will be searching for mates.
- The mean number of helpers per breeding group at the start of the simulation was set at 0.7, in accord with the reported 2.7 mean size of breeding groups at KSC. The probability that a jay was a helper at the start of the simulation was therefore set to 0.259 (=0.7/2.7). However, sensitivity testing of the effect of the starting proportion of helpers indicates that it has little impact on long-term projections, because within a few years the simulated population approaches an equilibrium.

- If the female or male of a breeding pair dies, then the single breeder is paired with a new mate the next breeding season.
- Probability that a breeder leaves its family group and becomes a helper elsewhere was set to 0 (as it is a rare event).

Additional assumptions in the models

The FSJ populations are assumed to be non-inbred at the start of the simulations, and all jays are assumed to be unrelated to each other. This results in inbreeding not occurring in the model until two or more generations later. Thus, the onset of damaging levels of inbreeding in the model might be delayed relative to when it could occur in the actual populations (which might already have some inbred jays).

Variance among breeders in lifetime reproductive success is assumed to be a consequence of variable durations of breeding lifetimes and random variation in breeding success. We assumed no intrinsic (e.g., phenotypic) individual variation in annual breeding success. If there is such individual variation, the demographic performance of the overall population might be affected little if at all (as the demographic rates average across breeders), but genetic diversity would decline more rapidly across the generations, due to a smaller genetically effective population size.

Demographic rates (breeding success and mortality) were assumed not to be dependent on the age of the birds (except in that older breeders are more likely to have accumulated helpers, and that allows better breeding success). The available data on the populations show only a weak and non-significant relationship between breeder age and breeding success, after the effect of helpers is removed.

Several variations on the typical breeding structure have been observed, but they are relatively uncommon and to have little impact on overall population trends, so that they can be safely ignored in the PVA modeling. These include:

Breeders leaving their breeding group and becoming helpers in another group;

Widowed breeders (upon the death of the male breeder) losing breeding status while an older son acquires a mate from elsewhere and inherits the breeding territory;

Helpers dispersing from their natal group and becoming helpers in an unrelated breeding group.

Often, demographic models of wildlife populations include density dependent effects, such that fecundity or survival decline at high densities. A difficulty of including density-dependence in demographic rates is that very rarely are data adequate to allow any more than very crude estimates (mostly wild guesses) of the shape of density-dependent effects. However, in our Vortex model of the FSJ populations, density dependence in both breeding success and mortality emerges from the model structure, in that as local density increases, more of the breeding groups will occupy suboptimal habitat where they have lower breeding success and higher mortality. (Poor quality habitat is unable to support positive population growth.) Moreover, the number of potential territories is limited, and that puts an upper limit on the number of breeding pairs in each population. No additional density dependence was imposed in the model via statistical relationships of survival or breeding success with population density. Density dependence in dispersal occurs only in that jays are assumed not to disperse into local populations that have little (< 10%) or no unoccupied Strong or Weak habitat.

State Variables used in Florida Scrub-Jay PVA models

The modeling of the complexities of state transitions and impacts on demography required the use of many "state variables" in Vortex to describe characteristics of the population (such as number of available potential territories of each level of habitat quality) and the individuals (such as number of years as a helper, the identity of the breeding pair with which each helper is associated, and the quality of the breeding territory). In addition, we are using a number of other state variables to track statistics (such as the mean number of helpers per breeding group) that can be used to describe the population dynamics and to validate the model projections against field observations. A listing of the state variables in our model, with short descriptions of how they are being used, is provided here. Note that the variables listed below match those used in the metapopulation scenarios (such as KSC-Dx, SCMainland-Dx, and NMainland-Dx). Some other scenarios did not use all of these variables or added others for tracking additional results. See the Vortex input files for complete listing of the model structure input values used for each scenario.

Global state variables

Global state variables were used to specify high-level parameters that might be changed in different scenarios. Putting these parameter values into the model as state variables, rather than specifying them within the various input pages of Vortex, makes it easier to test different values, because key model parameters are all listed on the one State Variable tab of Vortex.

GS1: Y1BREED Initialization: 0.12 Transition: 0.12

Probability that a yearling will become a breeder, rather than a helper.

GS2: PREF Initialization: 6 Transition: =6

Measure of the strength of preference for Strong vs Weak vs Sink habitat among jays seeking breeding territories. See PS27, PS28, and PS29 below.

GS3: InbrDepr1 Initialization: 7.478 Transition: 7.478

InbrDepr1 is the lethal equivalents for Day11 to yearling; from Chen et al. 2016
InbrDepr1 is used in the model to capture overall impacts on reproduction. Impacts on later stages are not significant in Chen et al. (2016) analysis but could be added to the model later if desired.

GS4: PrBtoH Initialization: 0 Transition: 0

Probability that a breeder reverts to being a helper to another pair. Set to 0 for now (because it is rare) but left in the model so that it can be modified later if desired.

GS5: KN0 Initialization: 4 Transition: 4

The maximum population size allowed, as a multiple of the number of potential territories. If this size is exceeded, then some helpers are removed from the population. Note, however, that in scenarios with some suboptimal (Weak and Sink) habitat. This maximum would be unlikely ever to be reached, because population growth will slow and then stop as jays are forced to use suboptimal habitat.

GS6: LOGA Initialization: -1 Transition: -1
GS7: LOGB Initialization: 6 Transition: 6

Parameters for the logistic function that is used to model helpers transitioning to breeders in response to vacant Strong habitat (see PS44).

GS8: PrDtoB Initialization: 0.7 Transition: 1

Probability that a helper dispersing to a new population will transition to breeder status.

GS9: NBrMeta Initialization:
=LOOKUP(6;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";4))+LOOKUP(6;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";5))+LOOKUP(6;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";6))
Transition: =ITOT4

Number of female breeders, tallied across all populations. Files read for the initialization will be specific to the scenario run.

Population state variables

– used for variables that might be set differently for different subpopulations in metapopulation scenarios. Used also for output metrics that we might want to examine, but not used in the simulation model itself (indicated in italics). Files read for initialization will be specific to the scenario and population. Shown below are examples from KSC-Dx, Happy Creek.

PS1: POTSTRONG =LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";1))
Transition: =POTSTRONG

Number of potential territories that are in “Strong” (best) habitat.

PS2: POTWEAK Initialization: =LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";2))
Transition: =POTWEAK

Number of potential territories that are in “Weak” (marginal) habitat.

PS3: POTSINK Initialization: =LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";3))
Transition: =POTSINK

Number of potential territories that are in “Sink” (poor) habitat.

PS4: POTTERR Initialization: =POTSTRONG+POTWEAK+POTSINK
Transition: =POTSTRONG+POTWEAK+POTSINK

Total number of potential territories

PS5: NDISPERSE Initialization: 0 Transition: =ITOT14

Tally of number dispersing from a different population

PS6: NSTRONG Initialization: =LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";4))
Transition: =ITOT11

Number of breeding pairs occupying Strong habitat

PS7: NWEAK Initialization: =LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";5))
Transition: =ITOT12
Number of breeding pairs occupying Weak habitat

PS8: NSINK Initialization: =LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC4Terr.txt";6))
Transition: =ITOT13
Number of breeding pairs occupying Sink habitat

PS9: NBREEDERS Initialization: =NSTRONG+NWEAK+NSINK Transition: =ITOT4
Number of breeding pairs; tallied by counting the number of female breeders

PS10: POCCSTRONG Initialization: =IF(POTSTRONG>0;NSTRONG/POTSTRONG;0)
Transition: =IF(POTSTRONG>0;NSTRONG/POTSTRONG;0)
Proportion of Strong habitat occupied by breeding pairs

PS11: POCCWEAK Initialization: =IF(POTWEAK>0;NWEAK/POTWEAK;0)
Transition: =IF(POTWEAK>0;NWEAK/POTWEAK;0)
Proportion of Weak habitat occupied by breeding pairs

PS12: POCCSINK Initialization: =IF(POTSINK>0;NSINK/POTSINK;0)
Transition: =IF(POTSINK>0;NSINK/POTSINK;0)
Proportion of Sink habitat occupied by breeding pairs

PS13: MEANHELPERS Initialization: 0.7 Transition: =IF(NBREEDERS>0;ITOT1/NBREEDERS;0)
Mean number of helpers per breeding pair

PS14: PSUCCSTRONGH
Initialization: =BETAM(LOOKUP(1;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1));
LOOKUP(2;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1)))
Transition: =BETAM(LOOKUP(1;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1));
LOOKUP(2;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1)))
Breeding success, as a proportion of pairs producing juveniles, in Strong habitat when helpers are present. Sampled from a beta distribution each year to simulate annual variation in the environment.

PS15: PSUCCWEAKH
Initialization: =BETAM(LOOKUP(1;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2));
LOOKUP(2;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2)))
Transition: =BETAM(LOOKUP(1;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2));
LOOKUP(2;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2)))
Breeding success, as a proportion of pairs producing juveniles, in Weak habitat when helpers are present.

PS16: PSUCCSINKH

Initialization: =BETAM(LOOKUP(1;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)); LOOKUP(2;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)))

Transition: =BETAM(LOOKUP(1;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)); LOOKUP(2;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)))

Breeding success, as a proportion of pairs producing juveniles, in Sink habitat when helpers are present.

PS17: PSUCCSTRONGNoH

Initialization: =BETAM(LOOKUP(3;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1)); LOOKUP(4;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1)))

Transition: =BETAM(LOOKUP(3;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1)); LOOKUP(4;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";1)))

Breeding success, as a proportion of pairs producing juveniles, in Strong habitat when there are no helpers.

PS18: PSUCCWEAKNoH

Initialization: =BETAM(LOOKUP(3;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2)); LOOKUP(4;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2)))

Transition: =BETAM(LOOKUP(3;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2)); LOOKUP(4;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";2)))

Breeding success, as a proportion of pairs producing juveniles, in Weak habitat when there are no helpers.

PS19: PSUCCSINKNoH

Initialization: =BETAM(LOOKUP(3;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)); LOOKUP(4;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)))

Transition: =BETAM(LOOKUP(3;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)); LOOKUP(4;FILECOL("C:\Vortex10Projects\FSJ\Rates.txt";3)))

Breeding success, as a proportion of pairs producing juveniles, in Sink habitat when there are no helpers.

PS20: AVAILSTRONG Initialization: = POTSTRONG-NSTRONG Transition: =POTSTRONG-NSTRONG

Number of available (unoccupied) Strong territories

PS21: AVAILWEAK Initialization: = POTWEAK-NWEAK Transition: =POTWEAK-NWEAK

Number of available (unoccupied) Weak territories

PS22: AVAILSINK Initialization: = POTSINK-NSINK Transition: =POTSINK-NSINK

Number of available (unoccupied) Sink territories

PS23: TOTAVAIL Initialization: =AVAILSTRONG+AVAILWEAK+AVAILSINK

Transition: =AVAILSTRONG+AVAILWEAK+AVAILSINK

Total number of available (unoccupied) territories

PS24: PROPSTRONG Initialization: =IF(TOTAVAIL>0;AVAILSTRONG/TOTAVAIL;0)

Transition: =IF(TOTAVAIL>0;AVAILSTRONG/TOTAVAIL;0)
Proportion of available territories in Strong habitat. Used to determine likelihood that a new breeding pairs will acquire a territory in Strong habitat

PS25: PROPWEAK Initialization: =IF(TOTAVAIL>0;AVAILWEAK/TOTAVAIL;0)
Transition: =IF(TOTAVAIL>0;AVAILWEAK/TOTAVAIL;0)
Proportion of available territories in Weak habitat

PS26: PROPSINK Initialization: =IF(TOTAVAIL>0;AVAILSINK/TOTAVAIL;0)
Transition: =IF(TOTAVAIL>0;AVAILSINK/TOTAVAIL;0)
Proportion of available territories in Sink habitat

PS27: PREFSTRONG Initialization: =NSTRONG/NBREEDERS
Transition: =IF(PROPSTRONG>0;PROPSTRONG^(1/PREF);0)
Probability that a new breeding pair will acquire a territory in Strong habitat

PS28: PREFWEAK Initialization: ==NWEAK/NBREEDERS
Transition: =IF(PROPWEAK>0;(1-PREFSTRONG)*[[PROPWEAK/(1-MIN(0.999;PROPSTRONG))]^(1/PREF)];0)
Probability that a new breeding pair will acquire a territory in Weak habitat

PS29: PREFSINK Initialization: =1-(PREFSTRONG+PREFWEAK) Transition: =1-(PREFSTRONG+PREFWEAK)
Probability that a new breeding pair will acquire a territory in Sink habitat

PS30: NMBREEDERS Initialization: =NBREEDERS Transition: =ITOT5
Number of male breeders

PS31: NMHELPERS Initialization: =0.5*NBREEDERS*MEANHELPERS Transition: =ITOT15
Number of male helpers

PS32: NFHELPERS Initialization: =0.5*NBREEDERS*MEANHELPERS Transition: =ITOT16
Number of female helpers

PS33: rTallyBr Initialization: 0 Transition: =(NBREEDERS>0)*(NBRPRIOR>0)
Count of number of years for which growth rate in breeding pairs can be calculated

PS34*: RBRY* Initialization: 0 Transition: =IF(RTALLYBR;LOG(NBREEDERS/NBRPRIOR);-100)
Transition: =IF(RTALLYBR;LOG(NBREEDERS/NBRPRIOR);-100)
Growth in number of breeding pairs from prior year

PS35: RBRCT Initialization: 0
Transition: =(RBRY>(-50))+(RBRY1>(-50))+(RBRY2>(-50))+(RBRY3>(-50))+(RBRY4>(-50))

Number of years for which the 5-year running average of growth in number of pairs can be calculated

PS36: RBRSUM   Initialization: 0   Transition: =RBRY*(RBRY>(-50))+RBRY1*(RBRY1>(-50))
+RBRY2*(RBRY2>(-50))+RBRY3*(RBRY3>(-50))+RBRY4*(RBRY4>(-50))
5-year sum of growth in number of breeding pairs

PS37*: RBRMEAN*   Initialization: 0   Transition: =IF(RBRCT>0;RBRSUM/RBRCT;0)
5-year running average of growth in number of breeding pairs

PS38: NBRPRIOR   Initialization: 0   Transition: =NBREEDERS
Tracks NBreeders in the prior year, for calculation of annual growth

The following 4 PSvars are used to track population growth and growth in number of breeders in the prior 4 years, for calculation of running averages
PS39: RBRY4   Initialization: -50   Transition: =RBRY3
PS40: RBRY3   Initialization: -50   Transition: =RBRY2
PS41: RBRY2   Initialization: -50   Transition: =RBRY1
PS42: RBRY1   Initialization: -50   Transition: =RBRY

PS43: PAVAIL
Initialization:=IF(POTSTRONG>0;AVAILSTRONG/POTSTRONG;(POTWEAK>0)*
(AVAILWEAK/POTWEAK)+ (POTWEAK=0)*(AVAILSINK/POTSINK))
Transition: =IF(POTSTRONG>0;AVAILSTRONG/POTSTRONG;(POTWEAK>0)*
(AVAILWEAK/POTWEAK)+ (POTWEAK=0)*(AVAILSINK/POTSINK))
Proportion of best habitat that is unoccupied

PS44: PrHtoB   Initialization: =EXP(LOGA+LOGB*PAVAIL)/[1+EXP(LOGA+LOGB*PAVAIL)]
Transition: =EXP(LOGA+LOGB*PAVAIL)/[1+EXP(LOGA+LOGB*PAVAIL)]
Probability that a female helper will transition to be a breeder, based on proportion of Strong habitat that is unoccupied

PS45: PrMHtoB
Initialization: =IF(NMHELPERS>0;(NBREEDERS+NFHELPERS*PRHTOB-NMBREEDERS)/NMHELPERS;0)
Transition: =IF(NMHELPERS>0;(NBREEDERS+NFHELPERS*PRHTOB-NMBREEDERS)/NMHELPERS;0)
Probability that a male helper transitions to become a breeder. Set so that the number of new male breeders will be equal to the number of female breeders that are seeking mates that year.

PS46: VACANCIES   Initialization: =(AVAILSTRONG+AVAILWEAK)/(POTSTRONG+POTWEAK)
Transition: =(AVAILSTRONG+AVAILWEAK)/(POTSTRONG+POTWEAK)
Proportion of Strong and Weak potential territories that are vacant; used for constraining dispersal.

Individual state variables – used to track individual states, or properties that influence demographic rates, or are used in tallies of output metrics (in italics)

IS1: NHELPERS Initialization: =POISSON(0.7) Birth function: 0 Transition: =IS1*(FBREEDER>0)
Number of helpers for each breeding female. Incremented automatically by the program when juveniles are produced, and decremented when helpers die or transition to become breeders.

IS2: UNHELPER Initialization: 0 Birth function: 0
Transition: IF[(CENSUS%2=1)*(A>0)*(TOTAVAIL>0)*(HELPER>0);
[(P!=PRIORPOP)*(RAND<PRDTOB)]OR[IF(S='F';(RAND<PRHTOB);(RAND<PRMHTOB))];0]
A code that indicates that a helper is transitioning to become a breeder that year. Will not transition to breeder if there are no available potential territories.

IS3: HELPER Initialization: =(RAND<0.3)*POISSON1(1.5) Birth function: 0
Transition: =IF(CENSUS%2=0;IS3;(A=1)*([TOTAVAIL=0]OR[RAND<
(1-Y1BREED)])+(A>1)*[IF(HELPER;(UNHELPER=0)*(HELPER+1);RAND<PRBTOH)])
Number of years that a helper has been helping. Set to 0 when no longer a Helper.

IS4: FBREEDER Initialization: =(HELPER=0)*(S='F') Birth function: 0
Transition: =(A>0)*(HELPER=0)*(S='F')
Code that the jay is a female breeder.

IS5: MBREEDER Initialization: =(HELPER=0)*(S='M') Birth function: 0
Transition: =(A>0)*(HELPER=0)*(S='M')
Code that the jay is a male breeder.

IS6: DAD Initialization: -1 Birth function: =SIREID
Transition: =IF[(HELPER>0)AND(OID>0)AND(OIS10=0);DAM7;DAD]
The breeding male of the family group. If a helper's former "Dad" is dead (detected because OIS10 will be 0), then the "Dad" is set to be the new mate of the widowed breeding female.

IS7: OID Initialization: -1 Birth function: -1 Transition: =IF[(MBREEDER)OR(FBREEDER);MATE;DAD]
Code for either: the mate of a breeder; or the breeding male for a helper.

IS8: DAM Initialization: 0 Birth function: =DAMID
Transition: =(IF[(DAM<1)OR(DAM10>0);IS8;(HELPER>0)*OIS7])*(UNHELPER=0)
The breeding female of a family group. Set to 0 when a helper transitions to become a breeder. If a helper's former "Dam" dies, then "Dam" is set to be the mate of the widower breeding male in the group. Assignment to a new "Dam" will cause that Dam to acquire the helpers of the breeding territory.

IS9: HABRAND Initialization: =RAND Birth function: =RAND Transition: =RAND
Number sampled from a (0,1) even distribution. Allows the next ISvar to use this random number twice.

IS10: HABITAT Initialization: =1+(HABRAND>PREFSTRONG)+(HABRAND>(PREFSTRONG+PREFWEAK))

Birth function: =DAM10

Transition:=IF[(HELPER>0)*(DAM10>0);DAM10;(IF[(MBREEDER)AND(OID>0);OIS10;[(UNHELPER=0)*IS10+(UNHELPER>0)*[1+(HABRAND>PREFSTRONG)+(HABRAND>(PREFSTRONG+PREFWEAK))]]]])

Habitat quality of the breeding territory, coded as Strong = 1, Weak = 2, Sink = 3.

IS11: STRONGBR Initialization: =(HABITAT=1)AND(FBREEDER) Birth function: 0

Transition: =(HABITAT=1)AND(FBREEDER)

A breeding female in Strong habitat

IS12: WEAKBR Initialization: =(HABITAT=2)AND(FBREEDER) Birth function: 0

Transition: =(HABITAT=2)AND(FBREEDER)

A breeding female in Weak habitat

IS13: SINKBR Initialization: =(HABITAT=3)AND(FBREEDER) Birth function: 0

Transition: =(HABITAT=3)AND(FBREEDER)

A breeding female in Sink habitat

IS15: MHelper Initialization: =(HELPER>0)*(S='M') Birth function: 0 Transition: =(HELPER>0)*(S='M')

A male helper.

IS16: FHelper Initialization: =(HELPER>0)*(S='F') Birth function: 0 Transition: =(HELPER>0)*(S='F')

A female helper

IS17: MYDAM Initialization: 0 Birth function: =DAMID Transition: =MYDAM

Biological dam. Used to model inbreeding avoidance.

IS18: MYSIRE Initialization: 0 Birth function: =SIREID Transition: =MYSIRE

Biological sire. Used to model inbreeding avoidance.

IS19: PRIORPOP Initialization: =P Birth function: =P Transition: =IF((CENSUS%2=1);P;PRIORPOP)

Prior population: used in IS2 to determine if jay just dispersed into the population.

Metrics of population performance

Commonly assessed outputs of PVA, measured at some discrete future time points of interest (e.g., at 25, 50, or 100 years), are:

- Mean population growth rate (expressed either as a mean annual rate of change, lambda = N[t]/N[t-1], or as an exponential rate, r = ln(lambda). The exponential rate, r, is generally more useful because the cumulative growth across years is the sum of the annual r values (whereas lambda compounds in a multiplicative fashion). r = 0 indicates a stable population; r < 0 indicates decline (at a proportional rate that is approximately r when r is small); r > 0 indicates population growth.

- Projected population size, N, averaged across the multiple iterations of the simulation. Population sizes were tallied as the number of breeding pairs, rather than the total number of jays, to be more easily compared to the census data from the field surveys.
- Variation or uncertainty in projected N, assessed as a SD of annual N.
- Proportion of initial gene diversity remaining and the mean level of accumulated inbreeding. Assessment of rates of loss of genetic diversity and concordant increase in inbreeding will allow us to determine how large the populations need to be in order to retain the high levels of genetic variation that are necessary for resilience and adaptation to changing environments.
- Probability of extinction, with the final biological extinction being defined as only one sex remaining.
- Quasi-extinction curves – the probabilities that the population size will be below any given threshold N. Quasi-extinction can be used to assess the probability of the population size declining below some threshold that is determined to fail to meet some other management or conservation targets, or perhaps indicate collapse of FSJs as a significant part of the ecological system.

The first 5 of the above measures of population performance can be misleading when population extinctions occur in the simulation. This is because mean values calculated across only those simulated trajectories in which the population did not go extinct. This will obviously be a subset of iterations that performed better than did those that went extinct. In Vortex, the mean population size, N, and any population or global state variables can be calculated over either only the extant simulated populations, or across all iterations (with N = 0 for extinct cases). For reporting projections of population size, we have used means across all iterations. To obtain estimates of mean population growth (r) that are not biased by exclusion of extinct cases, for the FSJ modeling it is useful to assess growth over a relatively small number of years, during early years of the projections. However, the first few years of a simulation can be influenced by initial conditions (such as the age structure and proportion of breeders vs helpers). Therefore, it is best to start the tally of population growth after about 5 years, so that the population will have shifted toward the structure generated by the demographic model. In most scenarios, we projected the population performance for 100 years, although metrics of success at intermediate intervals can be provided also. This will allow us to project the long-term genetic as well as demographic consequences of population reduction, fragmentation, and fluctuations.

Projections of single, isolated populations

Initial scenarios of hypothetical or exemplar populations of varying size, habitat quality, and accessibility of habitat were assessed:

- to confirm that the model structure and parameter values represented well the dynamics of FSJ populations in the region;
- to explore the importance of habitat, population size and structure, and population processes to population viability; and
- to serve as template scenarios for modeling specific, actual populations and metapopulations under scenarios of interest.

To illustrate the kinds of projections made by the Vortex simulation, Figure 3 shows the population trajectories from 25 iterations of the simulation for a sample scenario with 200 potential territories. (For more precise results, all data presented later in this report use an average of 250, 500, or more iterations.) The population is censused before and then after the breeding season, resulting in the jagged appearance of the census counts. The simulation shows the large uncertainty in trajectory that the population might follow, caused by the simulated fluctuations in the environment (resulting in annual variation in demographic rates) and stochasticity of the biological processes. Although it is difficult to extract patterns within the considerable variability, the population is, on average, about stable in size for the first 25 years, and then usually begins to decline as genetic diversity is lost and inbreeding begins to accumulate. Genetic diversity had declined to 0.88 of starting levels by year 100 (the average kinship between individuals then being about that expected for half-siblings), and 2 of the 25 iterations went extinct within 100 years.

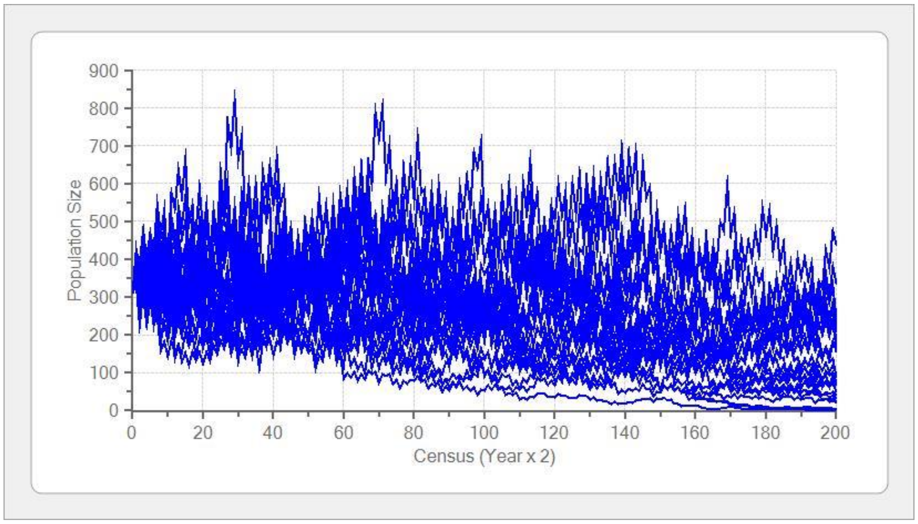

Figure 3. Sample of 25 iterations of a scenario with 200 potential territories; 0.4:0.3:0.3 proportions in Strong, Weak, and Sink habitat; initially 70%, 50%, and 30% of Strong, Weak, and Sink occupied; with accessibility parameter of Pref = 6, and helper to breeder transition parameter of B = 6.

Determinants of population trajectories, growth, and stability

PVA scenarios with many combinations of input parameters were examined to test the impacts of various input variables on population projections. Some of these scenarios help to identify which of the uncertain input values (e.g., strength of preference for or accessibility of Strong habitat, and probability that helpers will transition to breeders when breeding territories become vacant) can have large effects on population projections, and therefore should be the focus of additional efforts to determine more accurate values. Other scenarios are used to compare across values (e.g., number of potential territories, and proportion of territories in Strong habitat) that describe the range of populations that exist within the metapopulations. Except when noted otherwise, the comparisons presented below were from simulations over 100 years (200 census points on the graphs) of isolated populations with 100 potential territories; mid-level preference for (or accessibility of) Strong habitat (Pref = 6); helper to breeder transition parameter of B = 6; 40%, 30%, and 30% Strong, Weak, and Sink potential territories, respectively; and initially 70%, 50%, and 30% of Strong, Weak, and Sink territories occupied by breeding pairs.

Effect of accessibility of the best available habitat on population performance

One of the aspects of the FSJ biology that is difficult to measure is their ability to locate the best available habitat when establishing new breeding territories. New breeding pairs can end up in lower quality habitat because of limited search distance, reluctance to move far from a natal site, the imprecision with which current habitat characteristics predict future quality, or an inability to discern optimal habitat in the current landscape (which might differ from the landscape in which they evolved).

We tested scenarios that varied the Preference, or accessibility, parameter defining the likelihood that a new breeding pair will set up their territory in the best available habitat. Figure 4 shows the mean trajectory, with respect to number of breeding pairs, when the Pref parameter is varied from 1 (meaning new breeding pairs choose Strong, Weak, or Sink territories in the same proportion as they are available as unoccupied sites in the population) up to 10 (almost always choosing the best available territory).

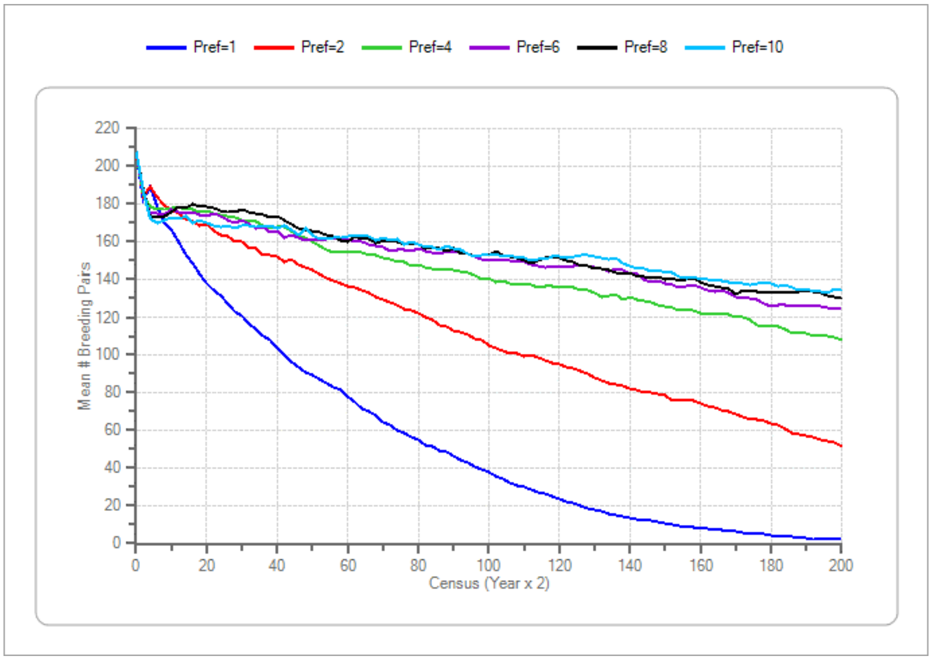

Figure 4. Projected population size with increasing accessibility of (or preference for) better quality habitat. Simulations had 400 potential territories (160 Strong, 120 Weak and 120 Sink), with initially 70%, 50%, and 30% occupied.

Table 4 shows the proportion of the habitat at each of the three levels of quality that were occupied at year 5 (after the initial shifts in habitat occupancy but before any collapses of overall population size). When accessibility was low to moderate, a substantial number of pairs were in Weak or Sink habitat, and consequently population growth was negative. As the accessibility was increased, most of the Strong habitat was occupied, some pairs spilled over into Weak habitat, and very few pairs had territories in Sink habitat. Consequently, populations with stronger preference for the best available habitat (Pref > 4) maintained nearly constant population size after the initial re-distribution of habitat occupancy largely filled Strong habitat, at least until accumulated inbreeding started to cause slow declines in later years (Fig. 4).

Although it will be difficult to observe directly the search process and the outcomes of new pairs seeking to establish territories, comparison of habitat occupancy between field surveys and model projections can give us an indication of the accessibility to the best habitat. However, simple comparison of numbers in Table 4 to field data might not be insufficient. The proportions of pairs in each type of habitat depends also on other factors such as the proportion of potential territories that are of each quality. Thus, we need to carefully match model scenarios to the characteristics of specific populations in order to test when the model predicts accurately the occupancy rates. (Further examination of the match between field data and model projections is provided in the *Validation* section, below.) Moreover, in assessing habitat use in the field, it will be necessary to analyze the data at an appropriate scale. For example, if one population has available almost all Strong habitat and another of equal size has available almost all Weak habitat – but the two populations are too far apart to allow dispersal – then an analysis that aggregated data across the two populations could incorrectly indicate that the jays are just as likely to seek out Weak as Strong habitat, when in fact they did not have a choice in this setting.

Table 4. Proportion of territories of each level of habitat quality occupied at year 5 of the simulation for increasing accessibility of (or preference for) better quality habitat. Simulations had 400 potential territories (160 Strong, 120 Weak and 120 Sink), with initially 70%, 50%, and 30% occupied.

Accessibility	Proportion of habitat occupied		
	Strong	Weak	Sink
1	0.43	0.41	0.37
2	0.64	0.45	0.20
4	0.78	0.38	0.08
6	0.84	0.32	0.04
8	0.86	0.29	0.03
10	0.87	0.26	0.02
12	0.88	0.25	0.01

Effect of helper to breeder transition in response to vacant breeding territories in Strong habitat

Figure 5 shows the mean projected number of breeding pairs when the slope (B) of the logistic regression describing the probability of helper to breeder transition was varied from 0 (no response to vacant Strong habitat) to 10 (virtually certain transition to breeder status when there are vacancies of Strong territories). For these comparisons, we simulated populations with 400 potential territories, with the accessibility parameter set at Pref = 6. Weak response (B = 2) had little effect on the population, larger responses (B = 4 to 8) resulted in populations that maintained size longer (before inbreeding became a factor), and parameter values greater than B = 8 had little further benefit.

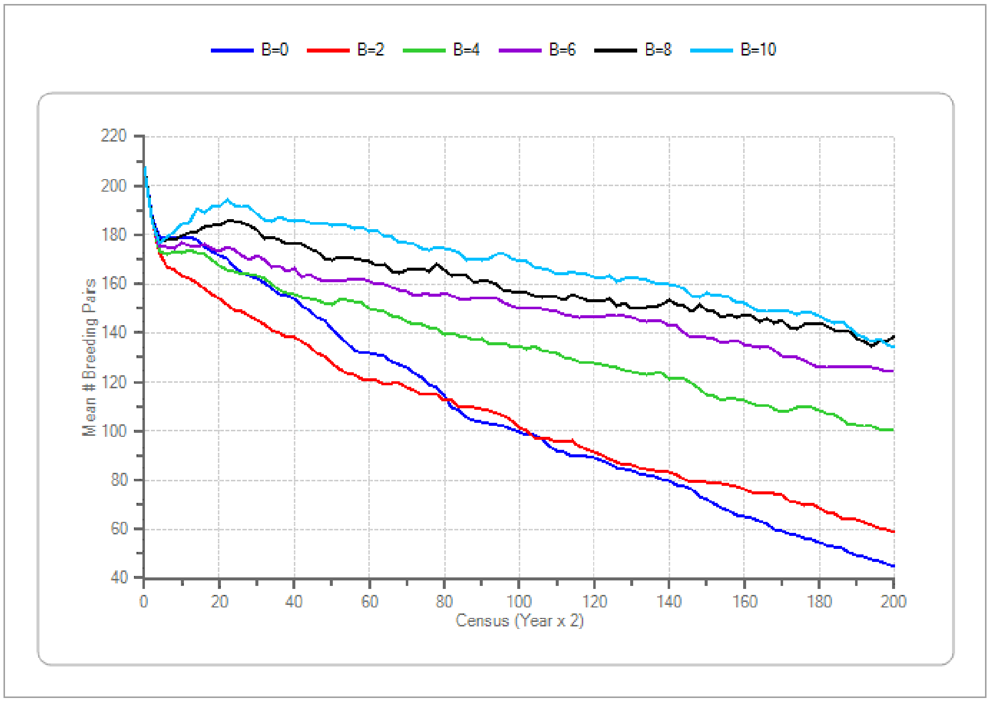

Figure 5 . Projected population size with increasing helper to breeder transition rate in response to availability of Strong habitat. Simulations had 400 potential territories (160 Strong, 120 Weak and 120 Sink), with initially 70%, 50%, and 30% occupied.

Another way to present a comparison across a range of values is with a “spider plot” that shows how an output metric changes with different levels of one or more input variables. The following two spider plots show the number of breeding pairs at 25 years and the probability of population persistence over 100 years, for scenarios with a range of values for the preference (accessibility) parameter (Pref = 2 to 10) and a range of values of the helper to breeder transition parameter (B = 2 to 10). All 100 combinations of the two parameters were tested, with the lines on the graph showing the mean outcome for a given value (e.g., B = 2) when averaged across scenarios using the range of the other parameter (e.g., Pref). The steeper slope of the green line (for the B parameter) in Figure 6 shows that across the ranges tested, it had somewhat greater effect on the breeding population size than did the Pref parameter. Conversely, the Pref parameter had a slightly greater effect on the probability of population persistence for 100 years (Figure 7). For both parameters, however, there was not a large change within the middle portion of the ranges that were tested – from about 4 to 8 – and the effect neared a plateau at about 6. Until these parameters can be estimated from field data, most further models will be run with intermediate values of B = 6 and Pref = 6.

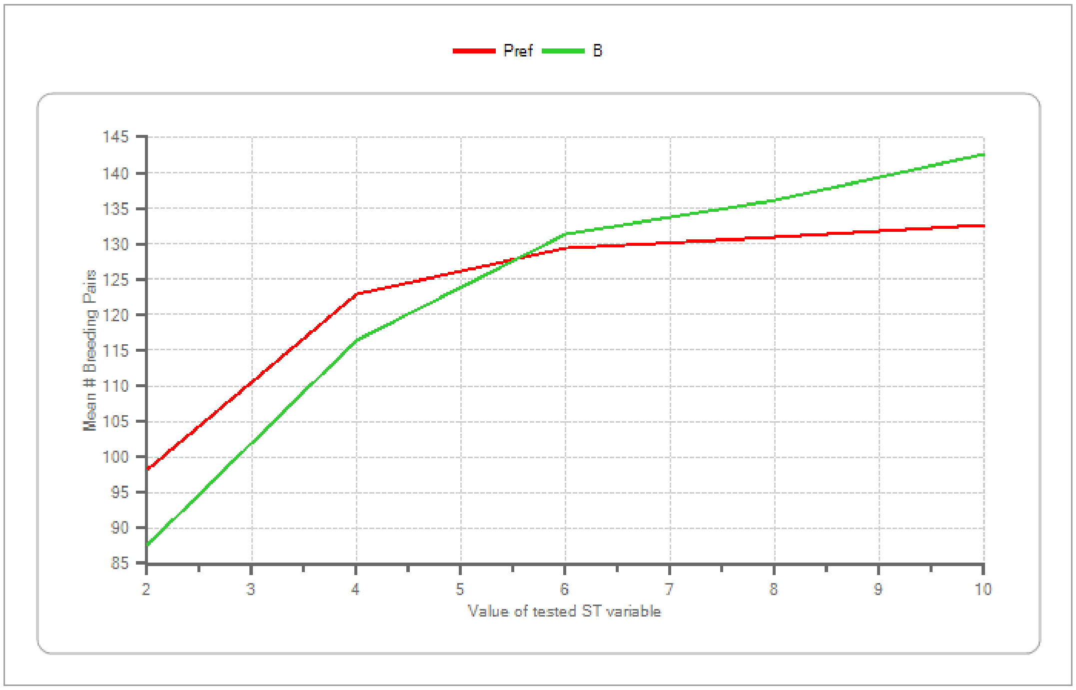

Figure 6. Effects of the accessibility of optimal habitat (model parameter Pref, in red) and the helper to breeder transition parameter (B, in green) on the projected population size at year 25.

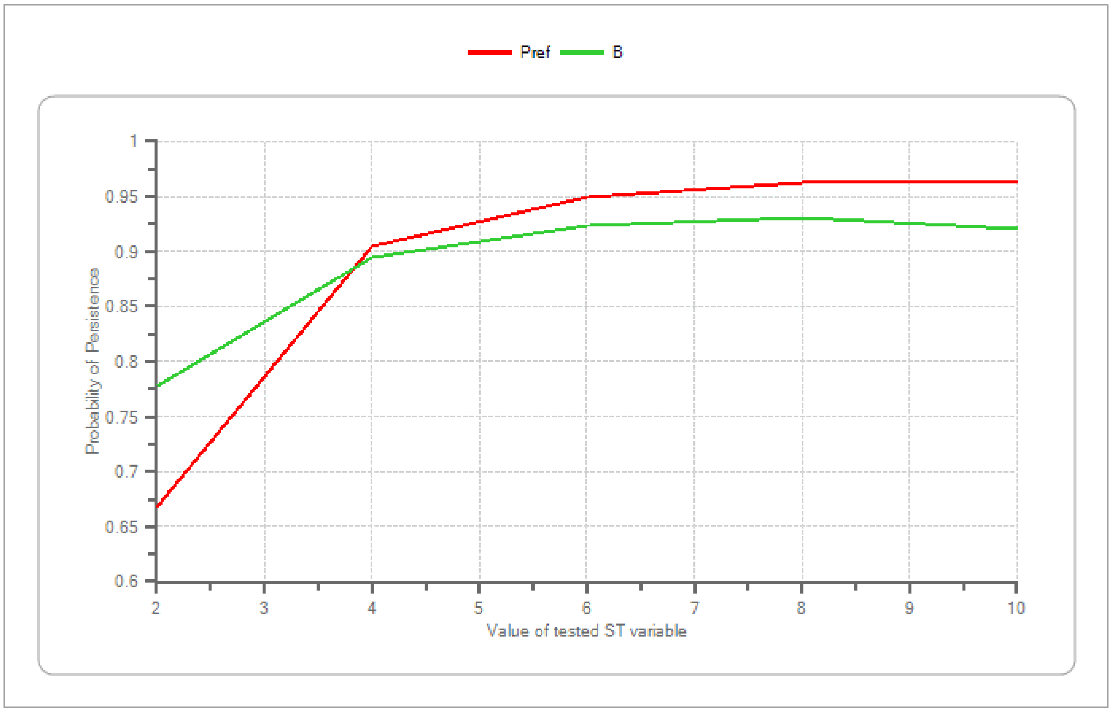

Figure 7. Effects of the accessibility of optimal habitat (model parameter Pref) and the helper to breeder transition parameter (B) on the probability of population persistence through 100 years.

Demographic projections in Strong, Weak, and Sink habitats

Scenarios were created to explore what combinations of factors might allow growth of an isolated population of Florida scrub-jays. These scenarios do not represent any specific local population, but rather use average demographic rates that were observed across the Brevard populations during the last three decades. Unless indicated otherwise, Pref=6 and B=6 in the scenarios below.

Figure 8 shows the projected growth (or decline) in the number of breeding pairs for a large population (400 potential territories) with all Strong, Weak, Sink, or a mix of 0.4:0.3:0.3 habitat quality. Populations were started with 50% occupancy. The habitat classified as Strong can support population growth (exponential growth rate about r = 0.06 over the early years). Habitat classified as Weak or Sink is not adequate to sustain the population: the demographic rates that have been estimated in those habitats result in declines of r = -0.14 and r = -0.22, respectively, over early years of the simulations. In the scenario with a mix of habitat quality, the population is initially stable for about 10 years and then declines slowly at a rate of r = -0.01.

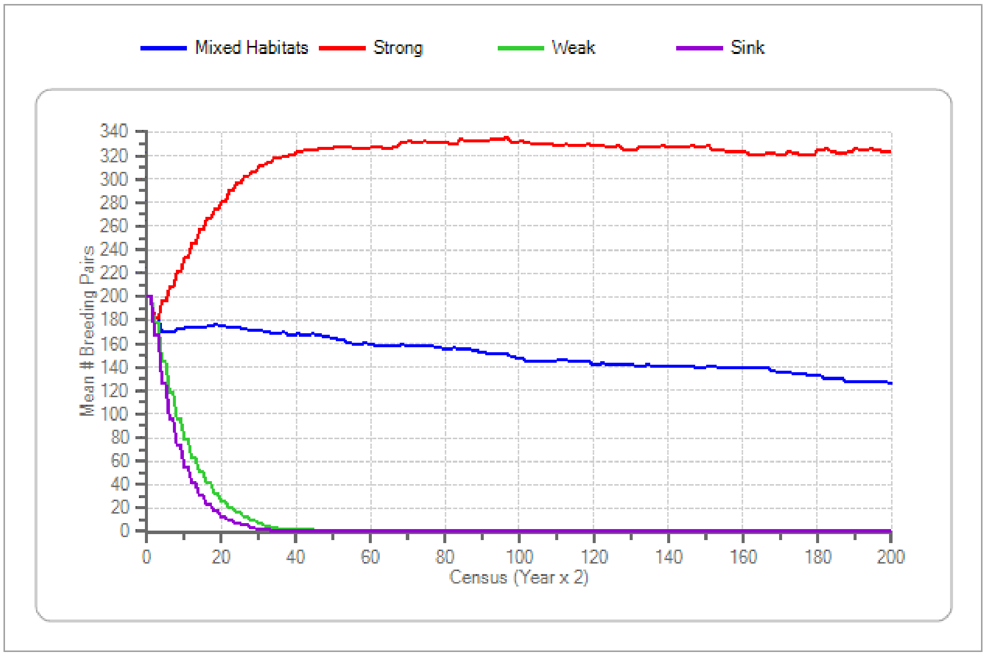

Figure 8. Projected numbers of breeding pairs over 100 years for initially large populations (400 potential territories) with Strong, Weak, Sink, or a mix of 0.4:0.3:0.3 habitat quality.

Thus, the models for the “Weak” quality habitats – given the estimated reproduction and survival rates of those breeding groups – projects that the population would have a negative growth rate. (This was even more so in the “Sink” habitats.) Moreover, tallies of habitat quality in potential breeding territories in the populations indicate that “Sink” habitat is currently more abundant than “Strong” or “Weak” habitat. Consequently, the PVA models predict that the overall FSJ population would be in continuing decline. This may represent accurately the expected fate of the population, or it might suggest that the population will be expected to contract until it occupies primarily the better-quality habitat. Further scenarios are examined, below, to explore if populations with observed configurations and extents of habitat will be expected to persist and perhaps stabilize at smaller numbers, or instead continue to decline toward extinction.

Effect of extent of habitat (# potential territories) if all habitat is Strong

The next three graphs display the projected number of breeding pairs, the probability of population persistence, and the retention of gene diversity across a range of population sizes (potential habitat), when all habitat is Strong. Isolated populations with 100 or more potential Strong breeding territories mostly maintain their population size (Fig. 9), have low probability of extinction (Fig. 10), and retain more than 90% of initial gene diversity (Fig. 11). With less than 100 potential territories in Strong habitat, the populations are vulnerable to decline, loss of gene diversity, and possible extinction due to inbreeding depression and random demographic fluctuations in small populations.

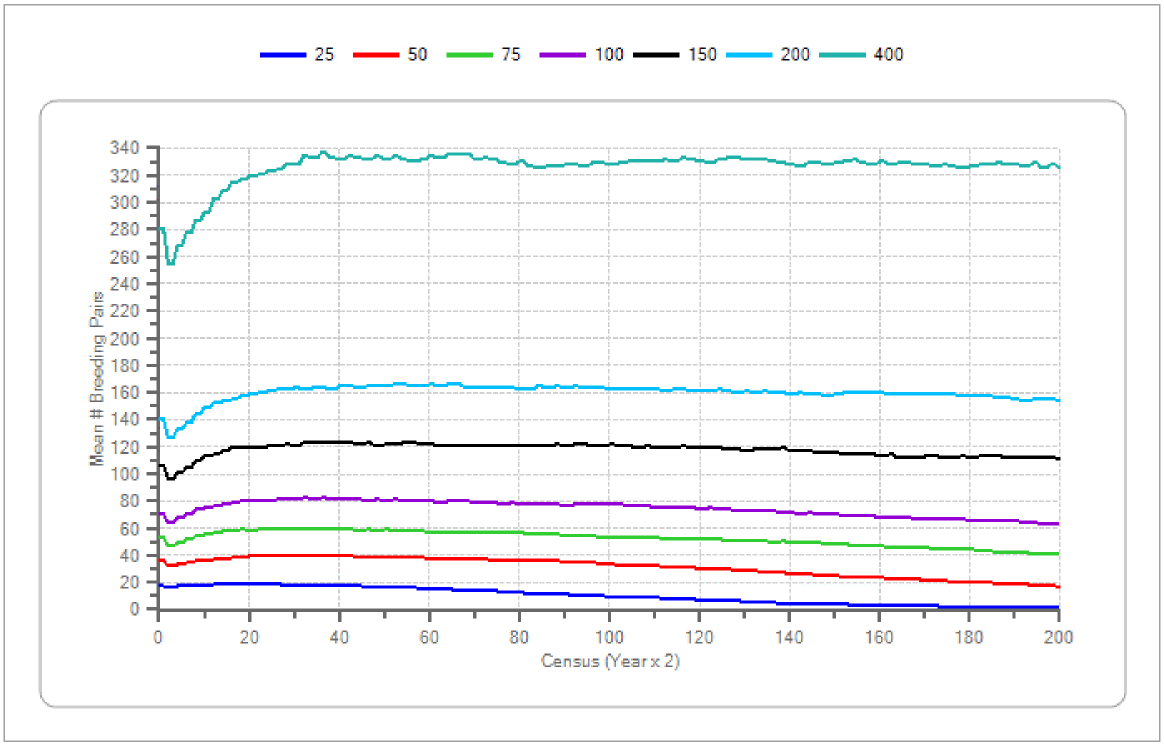

Figure 9. Projected numbers of breeding pairs in populations with 25, 50, 75, 100, 150, 200, or 400 potential territories, initially 70% occupancy, and all habitat classified as Strong.

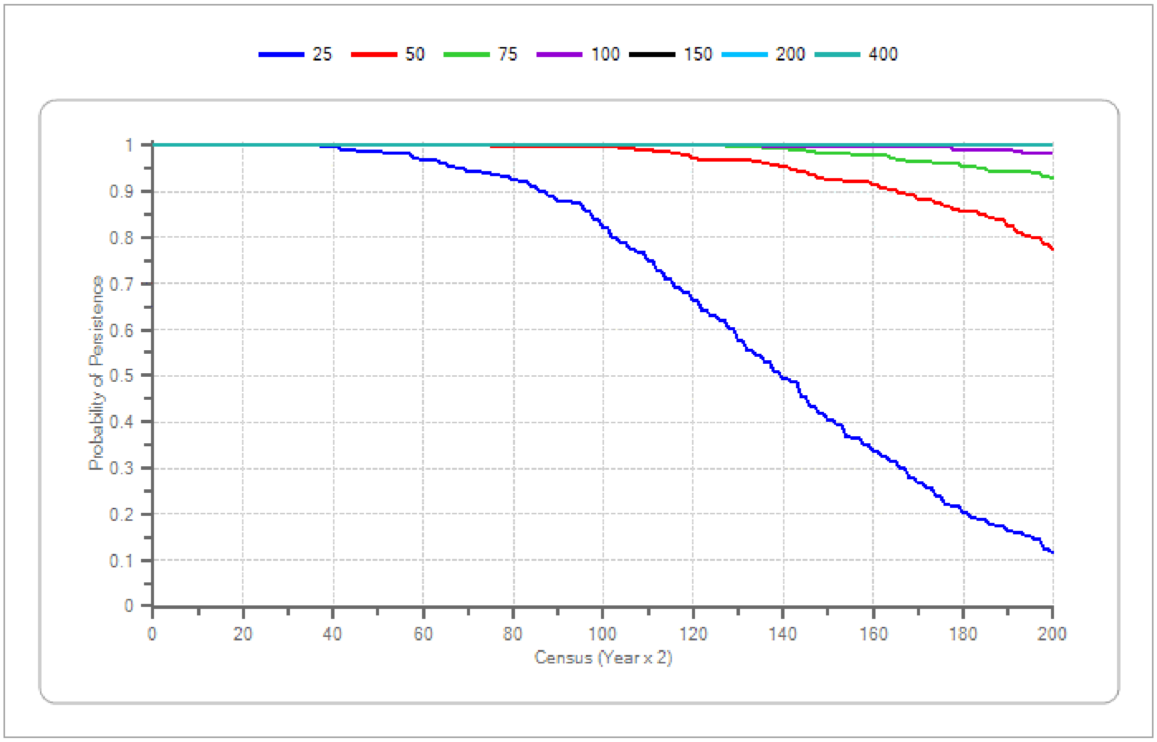

Figure 10. Probability of persistence of populations with 25, 50, 75, 100, 150, 200, or 400 potential territories, initially 70% occupancy, and all habitat classified as Strong.

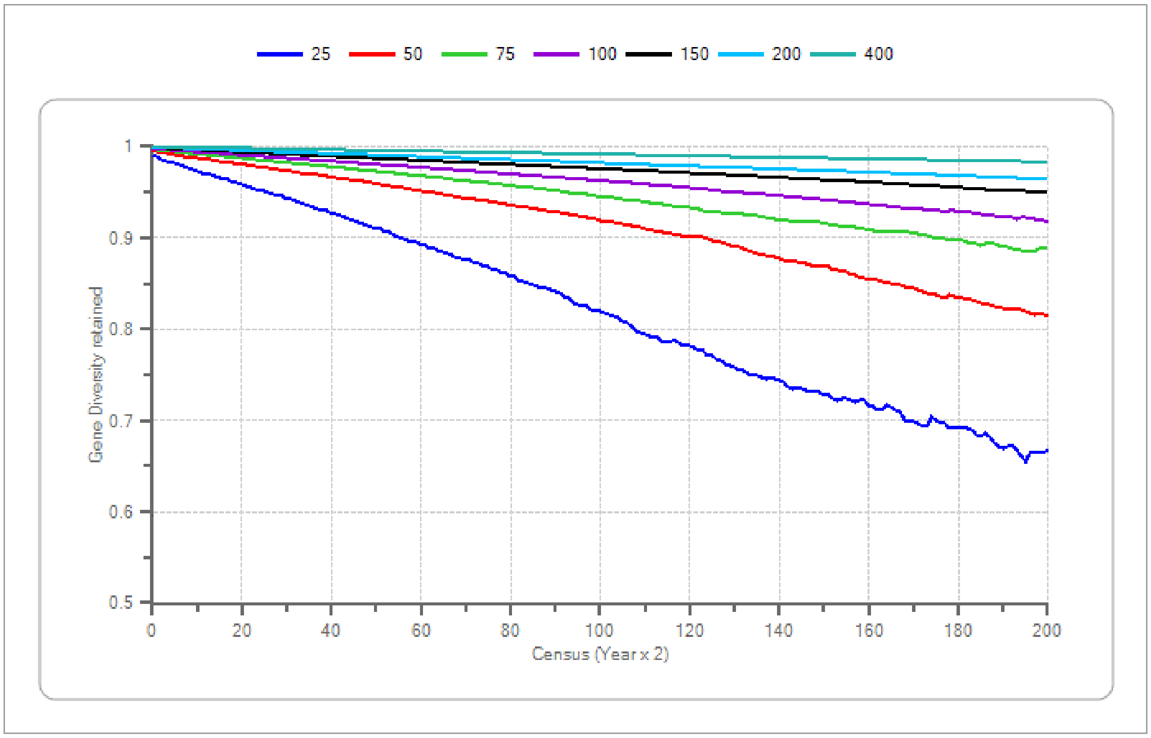

Figure 11. Proportion of gene diversity retained in populations with 25, 50, 75, 100, 150, 200, or 400 potential territories, initially 70% occupancy, and all habitat classified as Strong.

The quasi-extinction graph (Fig. 12) shows the probability that the total population size (breeders + helpers) will be below any given N at 100 years. Thus, it can be used to read the median population size (the N at 0.50 frequency on the graph) or the probability of the population falling below any specific size. For example, with 100 Strong potential territories, although the median N is about 240, there is a 10% probability that the population would be as low as about 80 jays.

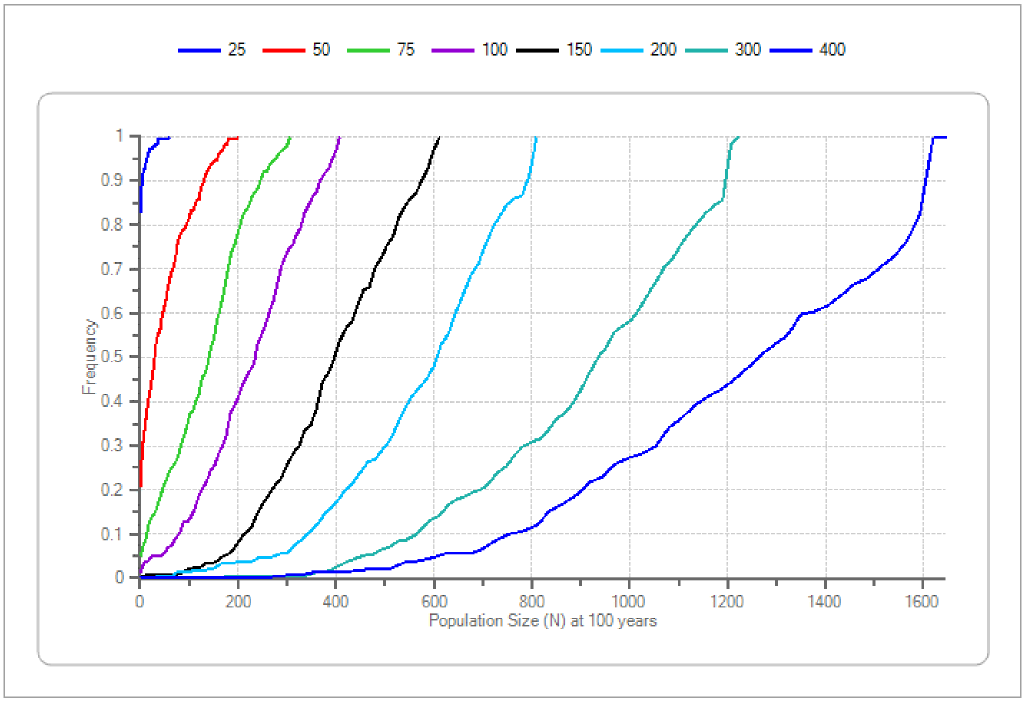

Figure 12. Quasi-extinction curves for populations with 25, 50, 75, 100, 200, 300, and 400 potential territories, 70% occupied at the outset, and all habitat classified as Strong.

Effect of extent of habitat (# potential territories) if not all habitat is Strong

The next four graphs display the results when 40%, 30%, and 30% of habitat is Strong, Weak, and Sink, respectively, with initial occupancies of 70%, 50%, and 30%. Isolated populations with 250 or more potential territories (100 of which would be Strong) have 10% probability of extinction (Fig. 14) and maintain more than 90% of gene diversity (Fig. 15) over 100 years, while they decline to population sizes (Fig. 13) that would occupy only most, but not all, of the Strong habitat. With less habitat (200 or fewer potential territories, with 80 or fewer in Strong habitat), the populations are vulnerable to decline and extinction, due to inbreeding depression and random demographic fluctuations in small populations.

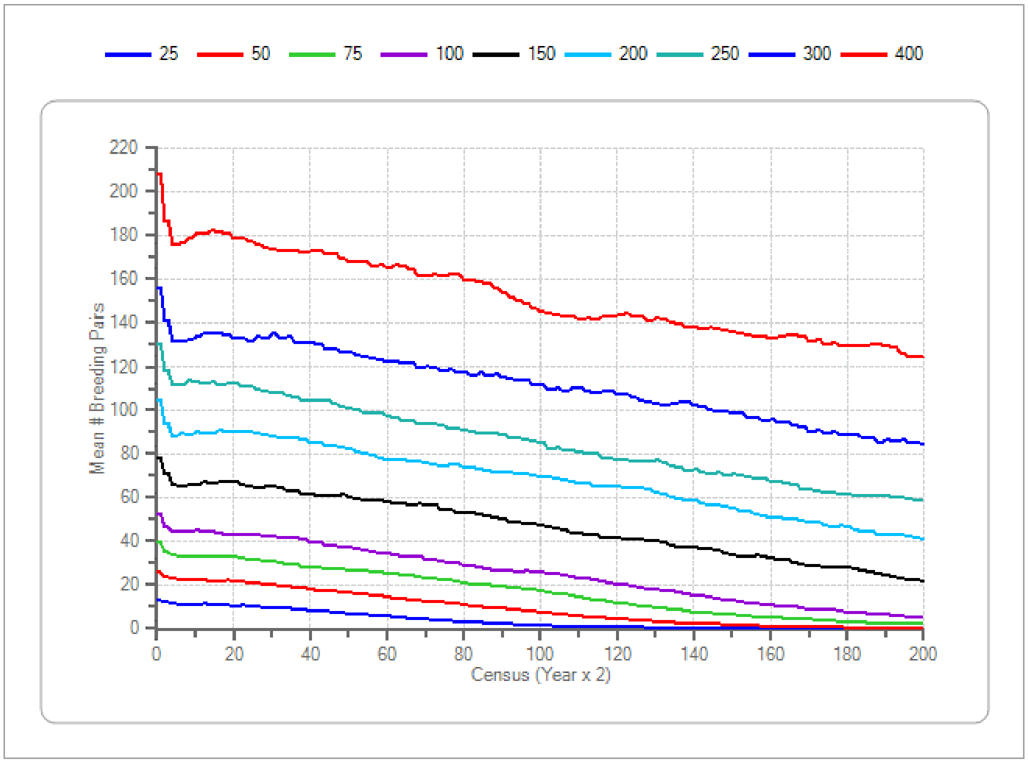

Figure 13. Projected numbers of breeding pairs in populations with 25, 50, 75, 100, 150, 200, 250, 300, or 400 potential territories, with 40%, 30%, and 30% being in Strong, Weak, and Sink habitat.

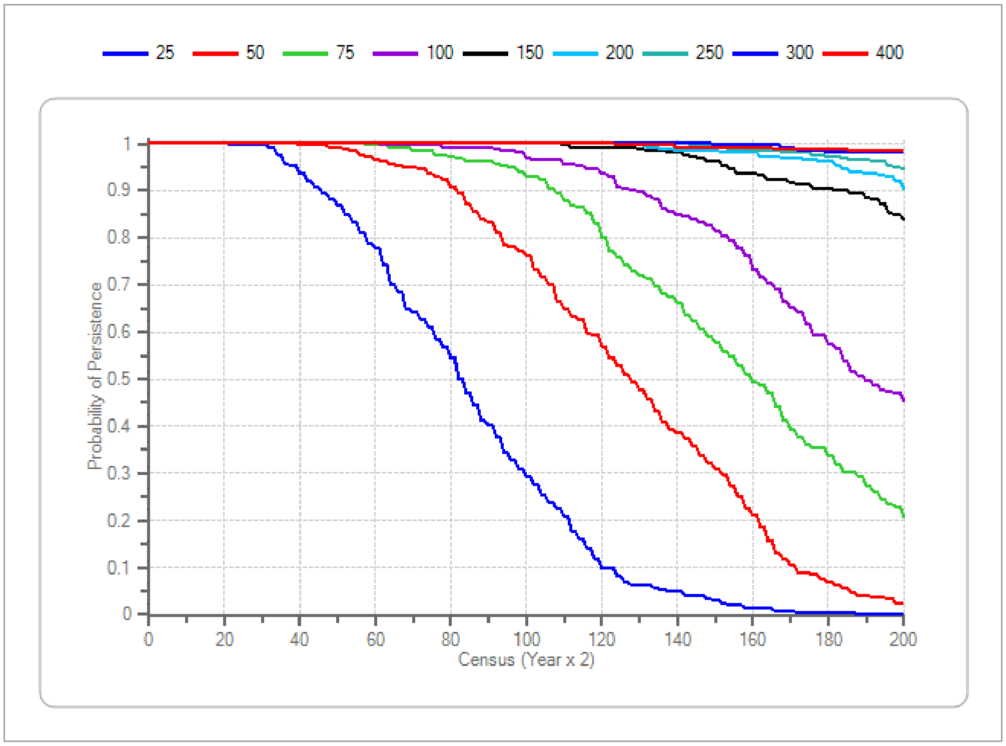

Figure 14. Probability of persistence of populations with 25, 50, 75, 100, 150, 200, 250, 300, or 400 potential territories, with 40%, 30%, and 30% being in Strong, Weak, and Sink habitat.

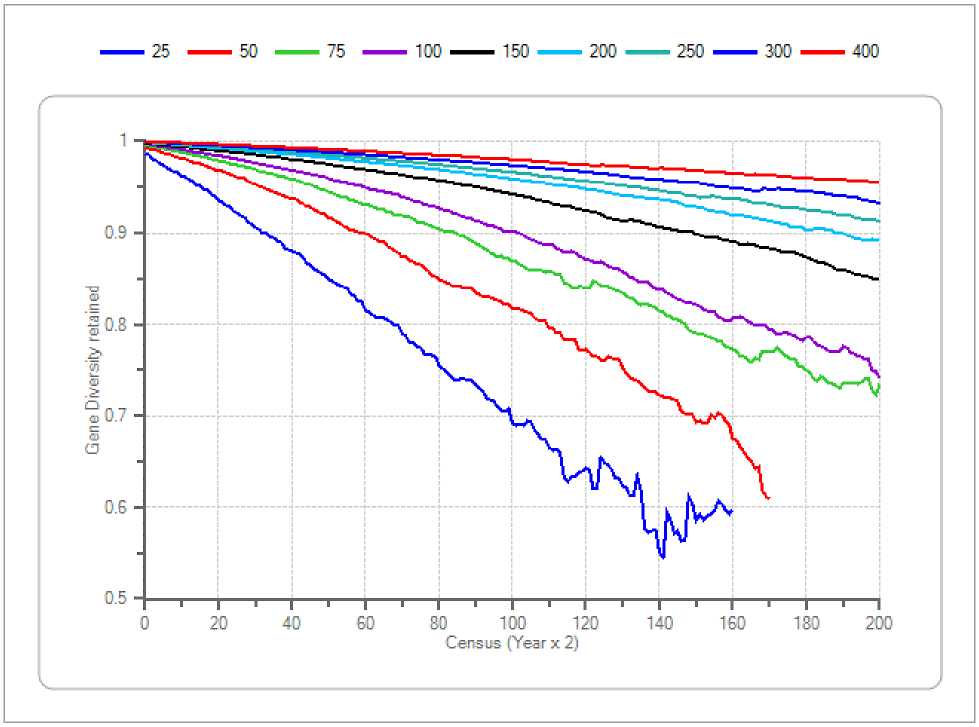

Figure 15. Proportion of gene diversity retained in populations with 25, 50, 75, 100, 150, 200, 250, 300, or 400 potential territories, with 40%, 30%, and 30% being in Strong, Weak, and Sink habitat**.** (Two lowest lines are truncated when most iterations have become extinct.)

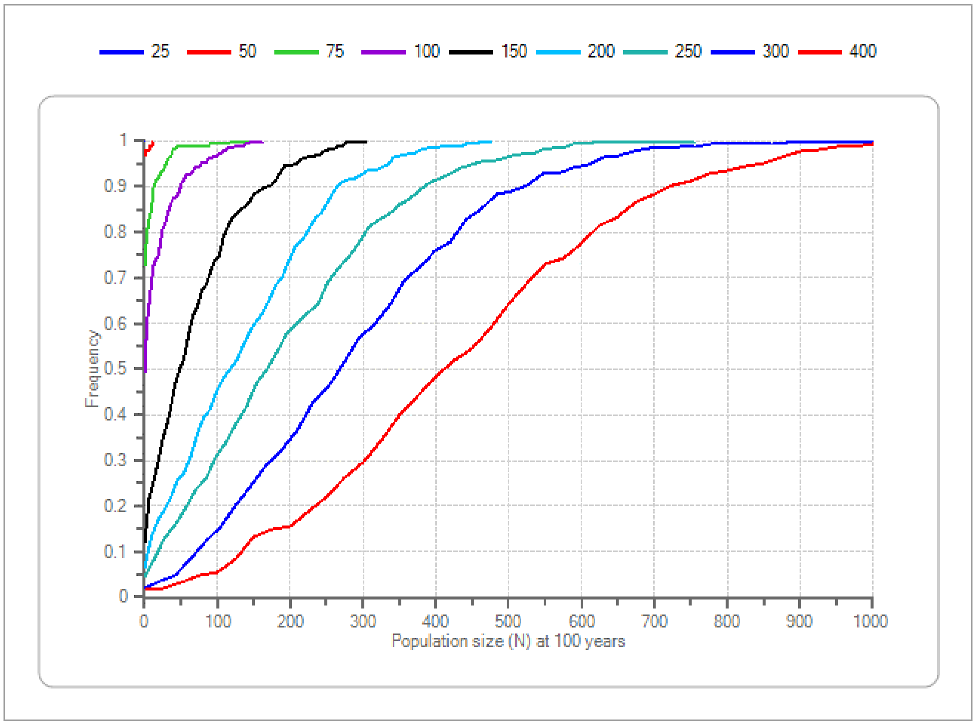

Figure 16. Quasi-extinction curves for populations with 25, 50, 75, 100, 150, 200, 250, 300, or 400 potential territories, with 40%, 30%, and 30% being in Strong, Weak, and Sink habitat.

What is the Minimum Viable Population size (MVP)?

Strong habitat allows for positive population growth. (See Figure 8.) However, even when mean demographic rates would result in a positive maximum biological growth rate, in small populations the stochastic effects of limited mating opportunities, inbreeding and loss of diversity, variation in demographic rates across years, and random fluctuations in births and deaths (each effect compounding others) can result in depressed mean population growth or even population extinction (Shaffer 1981; Gilpin and Soulé 1986). All it takes is a few unlucky years to put a small, isolated population into an unstable state or even a negative spiral (termed the "extinction vortex").

The above results can be used to define an approximate MVP for the FSJ populations. If we use common definitions of MVP and Endangered, less than 5% probability of extinction and retention of more than 90% of gene diversity over 100 years, then results (Figs. 9, 10 and 11) for populations in all Strong habitat suggest that a Minimum Viable Population might require about 100 potential territories of high quality (Strong) habitat. That size of habitat would be projected to support, on average, about 60-80 breeding pairs (Figure 9), and a median total population size of about 250 (Figure 12). If there is a mix of habitat quality (Figs. 13-15), then large populations are projected to decline to occupy about 75% of the available Strong habitat (largely vacating the Weak and Sink habitat), and smaller populations decline to occupy smaller proportions of the potential Strong territories. The scenarios with 250 potential territories (100 Strong) just meet the MVP criteria, again suggesting that at least 100 Strong territories are required for long-term viability of an isolated population.

Addition of Weak and Sink habitat to a population with a fixed amount of Strong habitat

The above findings suggest that an isolated population with at least 100 potential territories in Strong habitat would be relatively robust and safe from imminent collapse. We obtained a similar result, with about 100 Strong potential territories needed for stability when we modeled populations with a specific mix of Strong, Weak, and Sink habitats. We explored further if the addition of Weak and Sink habitat to a population (without changing the amount of Strong habitat) would be beneficial or harmful. The addition of lower quality habitat could be beneficial if it provides a buffer for excess jays unable to find territories in Strong habitat, but able to move back into the Strong habitat if some of those territories become vacant. Also, even with reproduction insufficient to completely offset mortality in Weak and Sink habitat, some breeding pairs would still be successful. On the other hand, if the array Weak and Sink habitat mixed in with the Strong habitat tends to draw jays away from the Strong habitat (or makes the best habitat harder to access), then the addition of lower quality habitat could accelerate population decline.

Costs or benefits of Weak habitat

The next three graphs show the effect on the number of breeding pairs, probability of population persistence, and gene diversity when no, 25, 50, 75, or 100 Weak potential territories are added to a population with 100 Strong territories. The addition of Weak habitat (and additional initial breeding pairs) allowed for the population to maintain larger size, but the benefit diminished over time as the populations contracted to occupy mostly only much of the Strong habitat (Fig. 17). Moreover, after about 50 years, there was little further benefit of adding more than 25 Weak territories. Even the temporary benefit, however, indicates that retaining existing Weak habitat would allow the population to remain at somewhat larger size. Thus, there is no cost to retaining or adding Weak habitat, even though reproduction does not offset mortality in those territories. Adding Weak habitat might have caused marginally more extinctions (Fig. 18), but none of these scenarios suffered from more than a few percent extinctions, and the differences between the scenarios are within the sampling error of the simulations. Adding Weak habitat had no noticeable effect – neither benefit nor cost – on gene diversity (Fig. 19).

It should be noted, however, that habitat is dynamic, and the areas that are currently Weak or Sink habitat might become – perhaps after management actions – the Strong habitat of the future. Thus, the benefit of Weak or Sink habitat could be its potential to become more optimal habitat, rather than its current benefit as breeding habitat for the scrub-jays.

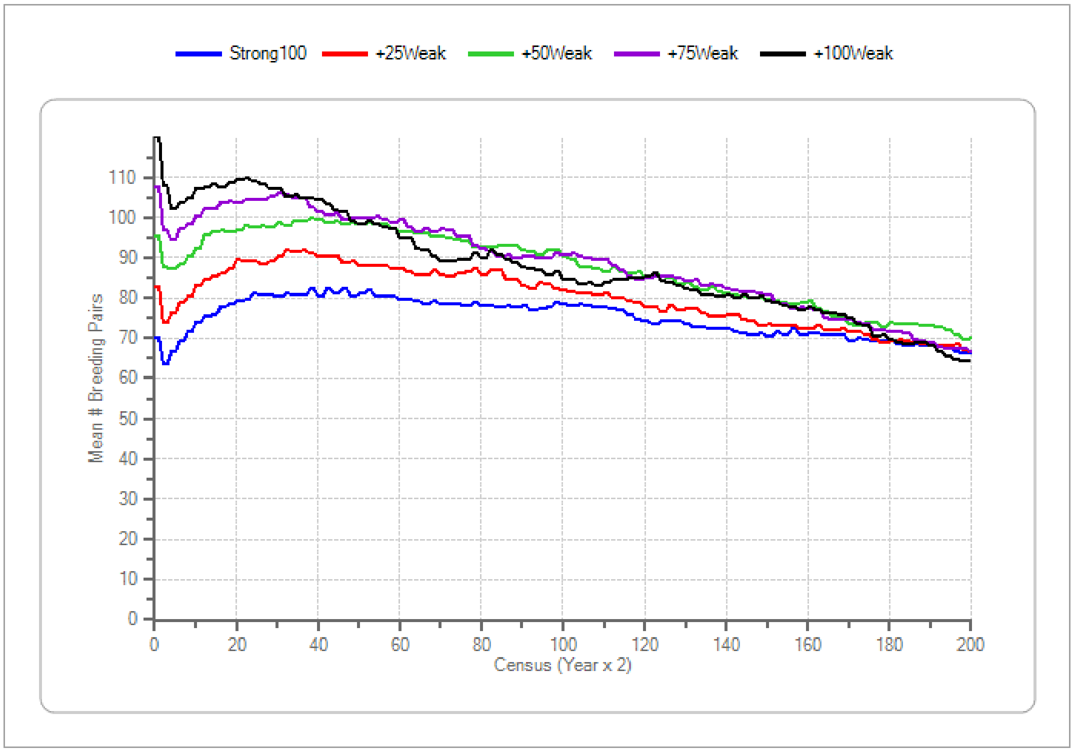

Figure 17. Projected numbers of breeding pairs in populations of 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Weak habitat added.

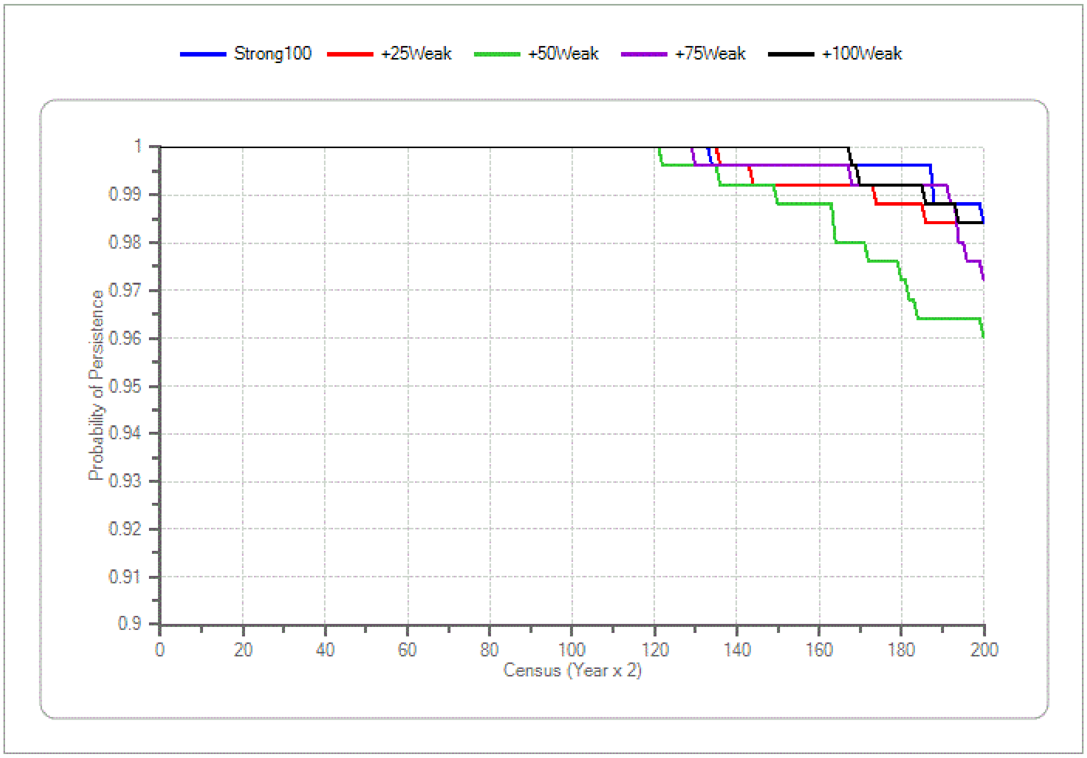

Figure 18. Probability of persistence of populations with 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 territories of Weak habitat added. Note y-axis scale starts at 0.90.

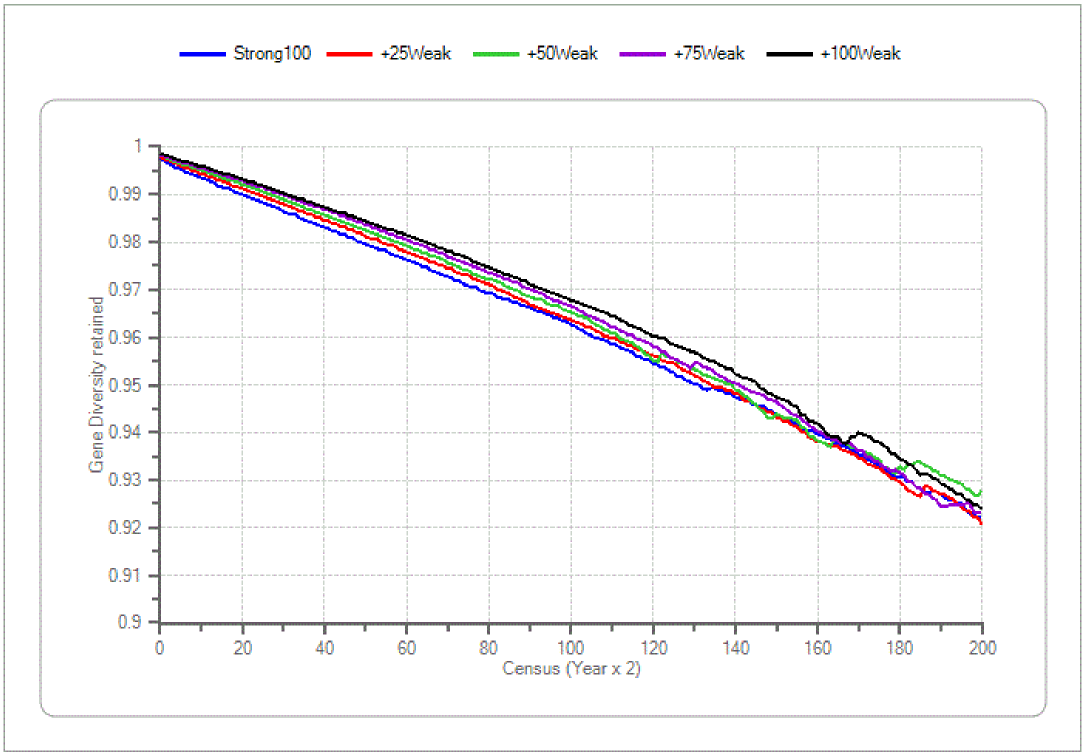

Figure 19. Proportion of gene diversity retained in populations with 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Weak habitat added.

The benefit of adding suboptimal habitat might be highly dependent on the ways in which jays respond to the lower quality habitat with respect to whether they fill all available Strong habitat first (a large Pref parameter in the model). The next two graphs show the projected number of breeding pairs and probability of population persistence when 0, 25, 50, 75, or 100 potential territories of Weak habitat are added to 100 territories of Strong habitat, when the jays display little preference for (or ability to access) the Strong habitat. In such cases, the initially larger size of the population when there is more (Strong + Weak) habitat is lost over time, such that between years 30 and 40 the additional Weak habitat becomes a drain on the population rather than a benefit (Fig. 20). Moreover, the addition of Weak habitat increases the rate of extinction, starting at about year 50 (Fig. 21). Thus, Weak habitat is a long-term detriment to population viability if the jays do not show preference for and the ability to find the better habitat.

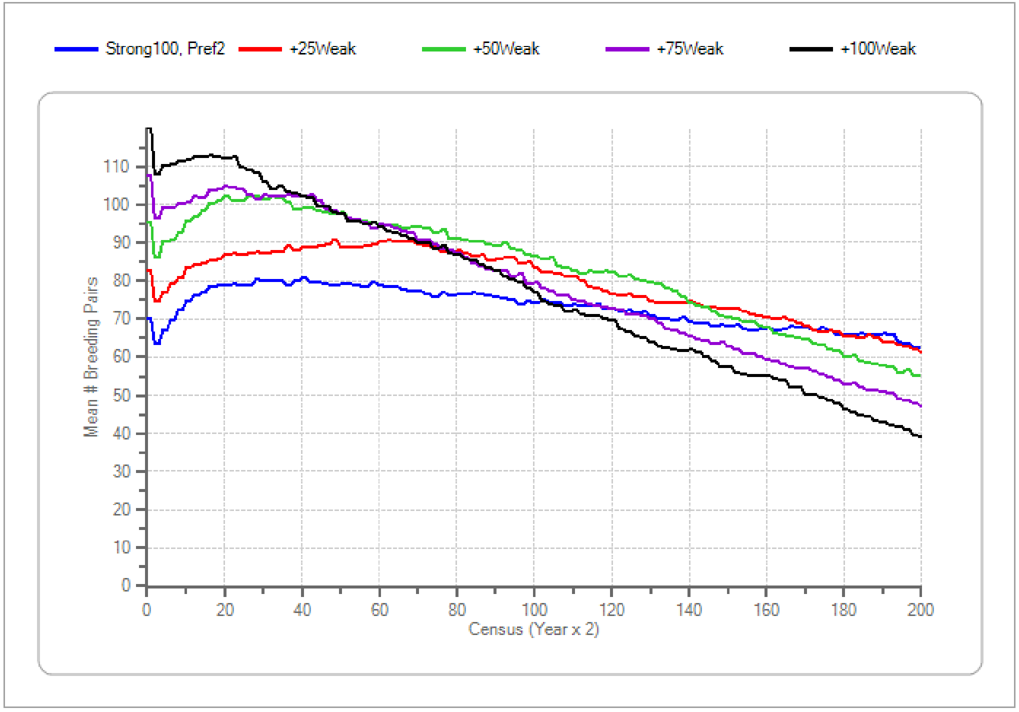

Figure 20. Projected numbers of breeding pairs in populations of 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Weak habitat added, when there is little preference for Strong habitat (Pref = 2).

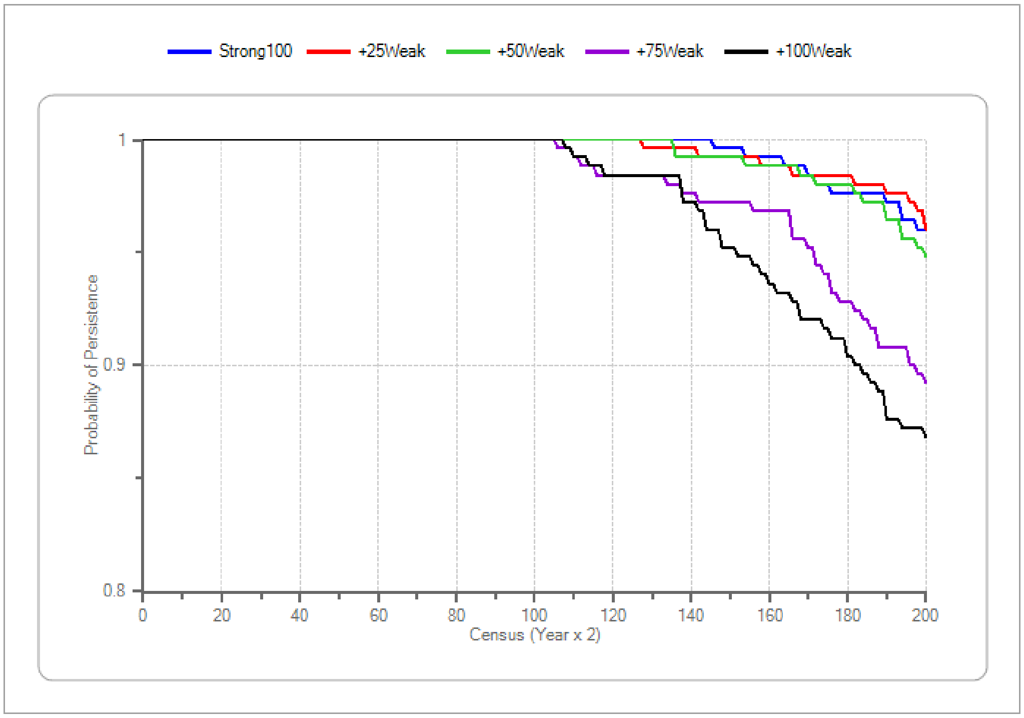

Figure 21. Probability of population persistence of populations with 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Weak habitat added, when there is little preference for Strong habitat (Pref = 2). Note y-axis scale starts at 0.80.

The above findings support the need for field data on the responses of the jays to vacant Strong habitat. However, it should be noted that the observed high proportion of Strong territories that are occupied and much lower proportion of Weak and Sink occupied, suggests that the jays do prefer and are able to access better habitat when it is available. The negative ("drain") impact of adding suboptimal habitat will lessen and perhaps be reversed if jays seeking new breeding territories can exploit all or most of the available Strong habitat before using the Weak habitat. Figure 22 repeats the above analysis, but with the accessibility parameter set to 10 – specifying that Strong habitat will almost always be used first, much of Weak habitat would be vacant, and few breeding pairs would end up in Sink habitat. (See Table 4.)

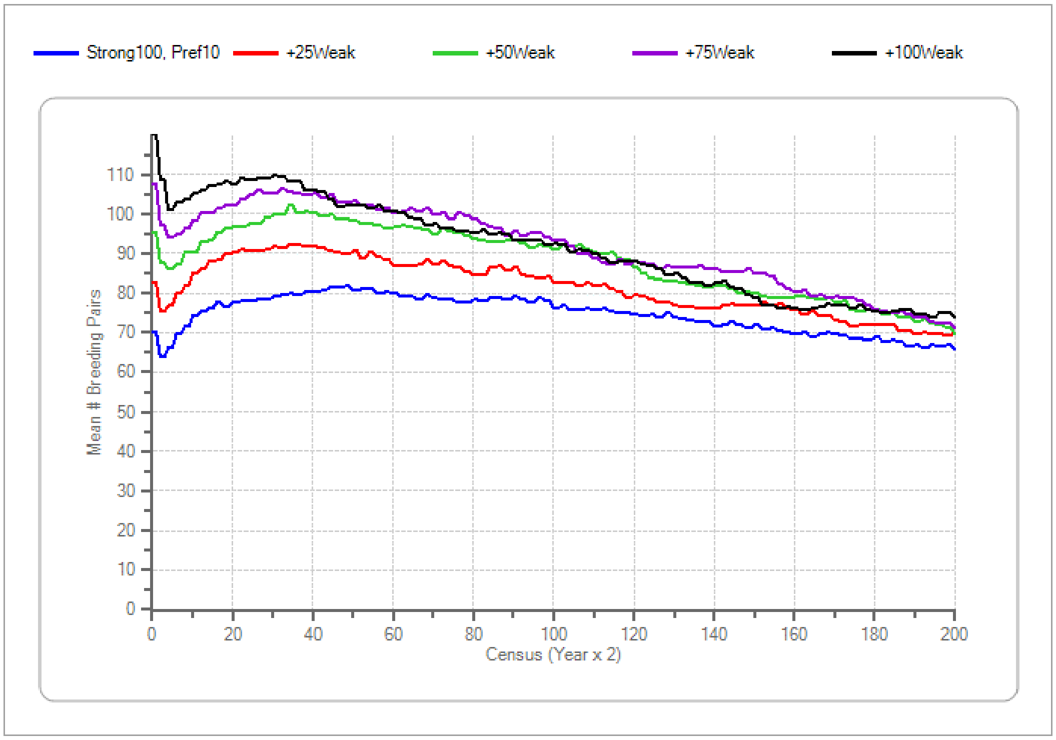

Figure 22. Projected numbers of breeding pairs in populations of 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Weak habitat added, when there is large preference for Strong habitat (Pref = 10).

In these cases, with jays showing a large preference for establishing new territories in the optimal available habitat, adding some Weak habitat improves maintenance of the population. The Weak habitat would serve as a buffer when there are more breeding pairs than can use the available Strong habitat. However, over the long-term (50 to 100 years), it appears that it might be optimal to keep the amount of Weak habitat below the amount of Strong habitat.

Costs or benefits of Sink habitat

Figures 23 and 24 show similar but more dramatic results when Sink habitat (starting at 30% occupancy) is added to Strong habitat. Compared to scenarios that added Weak habitat, which showed little cost or benefit, the addition (or retention) of Sink habitat results eventually (after about 40 years) in lower population sizes (Fig. 23), and (after about 60 years) higher probability of population extinction (Fig. 24).

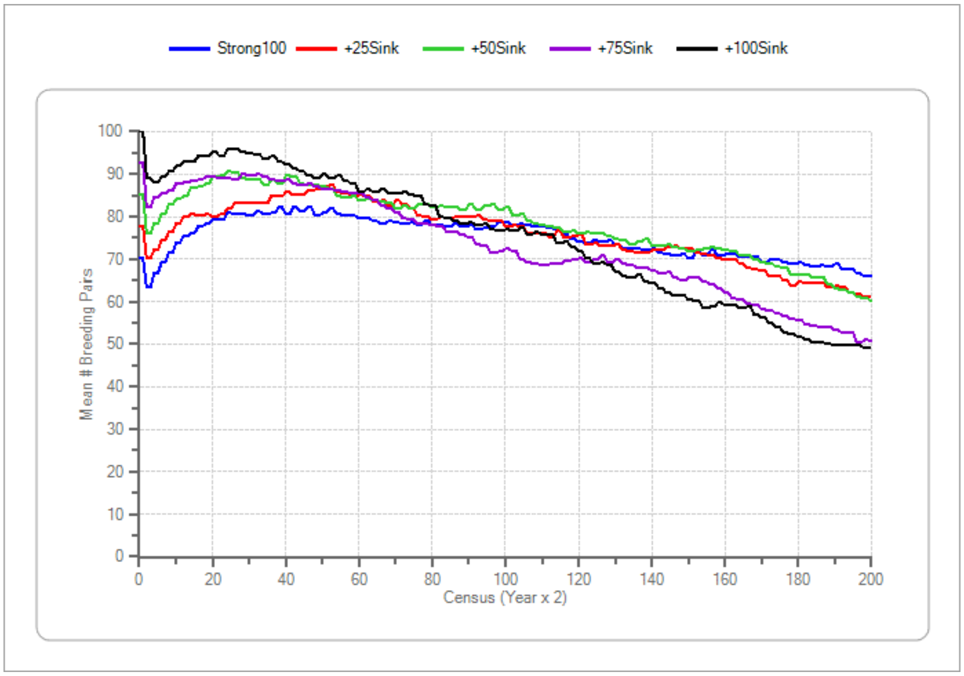

Figure 23. Projected numbers of breeding pairs in populations of 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Sink habitat added.

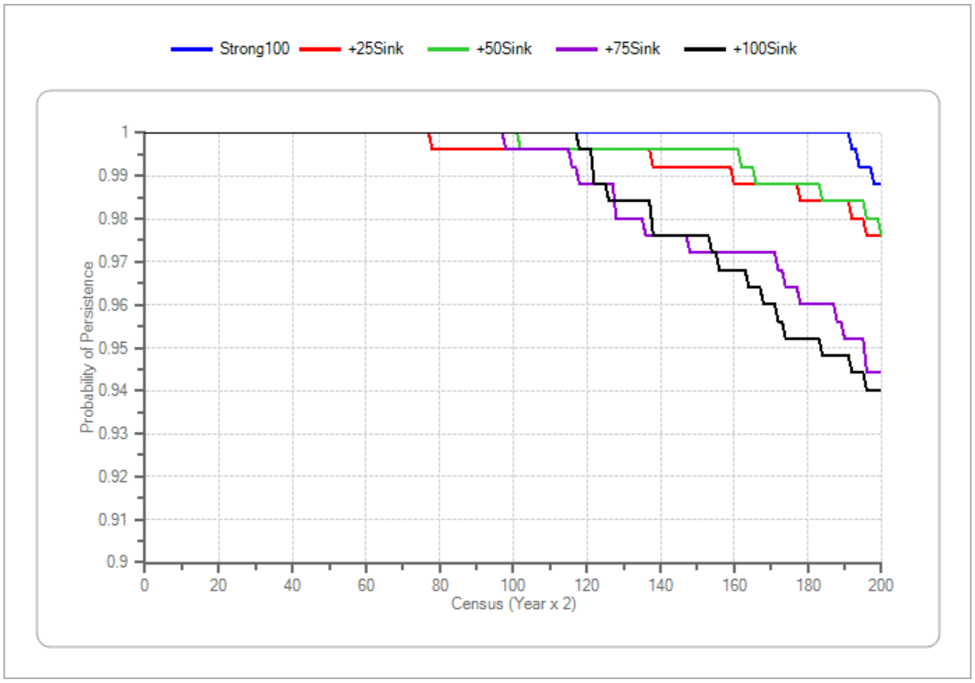

Figure 24. Probability of population persistence of populations with 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Sink habitat added. Note y-axis starts at 0.90.

The cost of added Sink habitat is much greater and occurs more quickly if the jays do not show much preference for or ability to access the Strong habitat (Figs. 25 & 26).

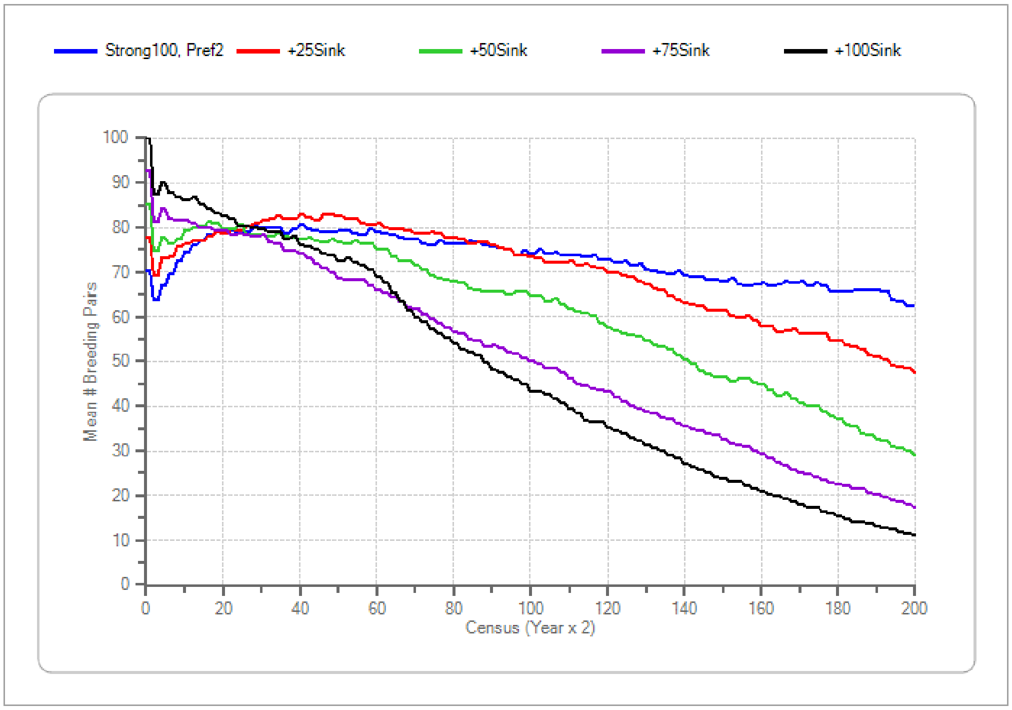

Figure 25. Projected numbers of breeding pairs in populations of 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Sink habitat added, when there is little preference for Strong habitat (Pref = 2).

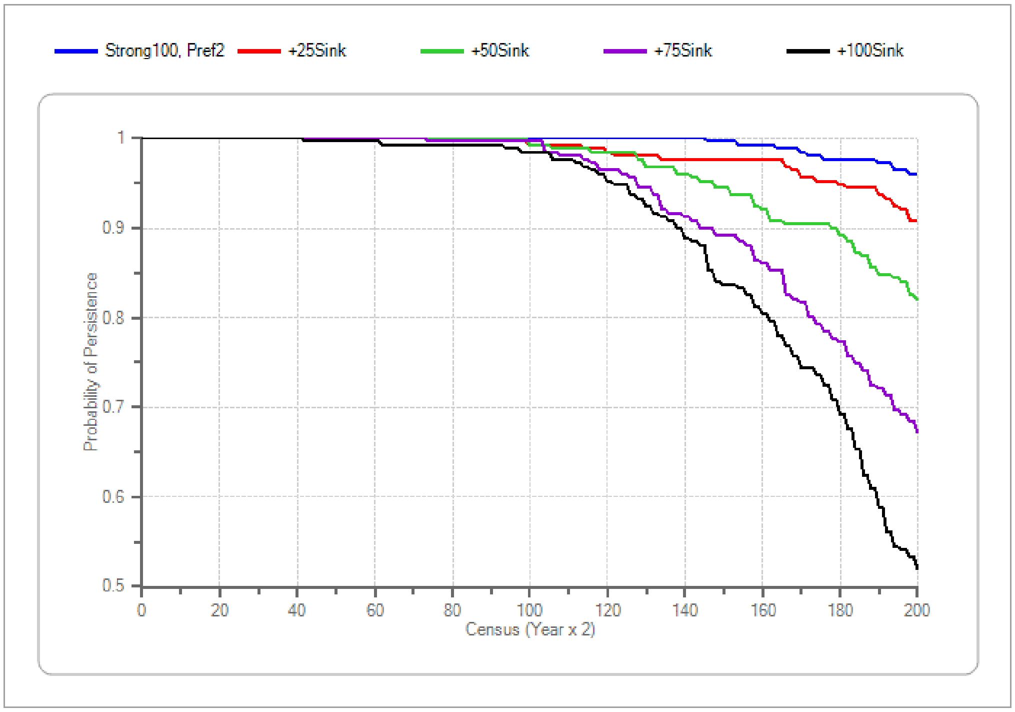

Figure 26. Probability of population persistence of populations with 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Sink habitat added, when there is little preference for Strong habitat (Pref = 2). Note y-axis starts at 0.50.

Conversely, the negative impacts of adding Sink habitat are largely removed if the scrub-jays show a large preference for the best available habitat (Figs. 27 & 28).

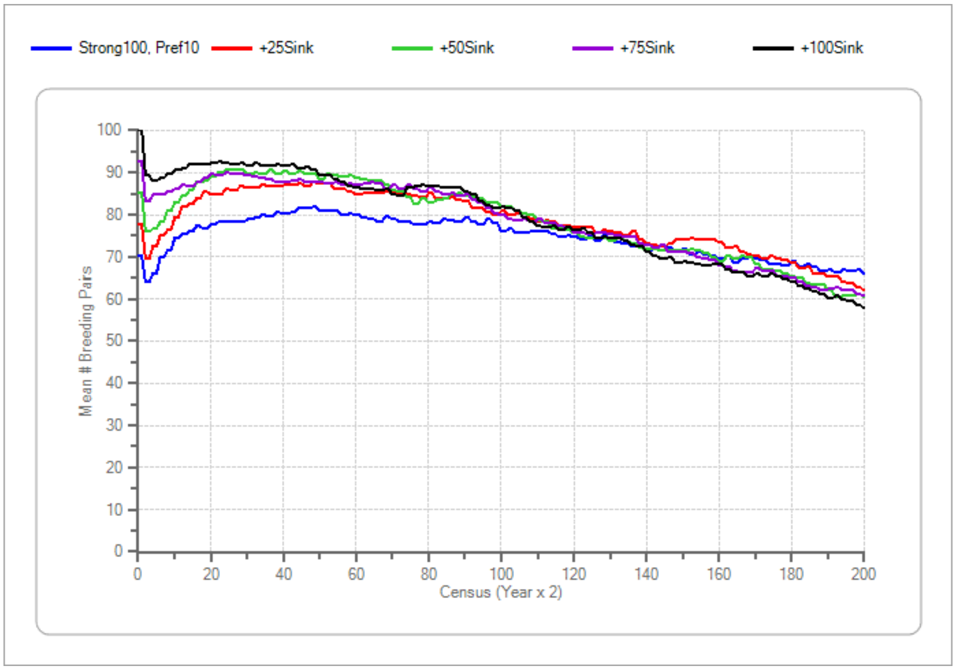

Figure 27. Projected numbers of breeding pairs in populations of 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Sink habitat added, when there is large preference for Strong habitat (Pref = 10).

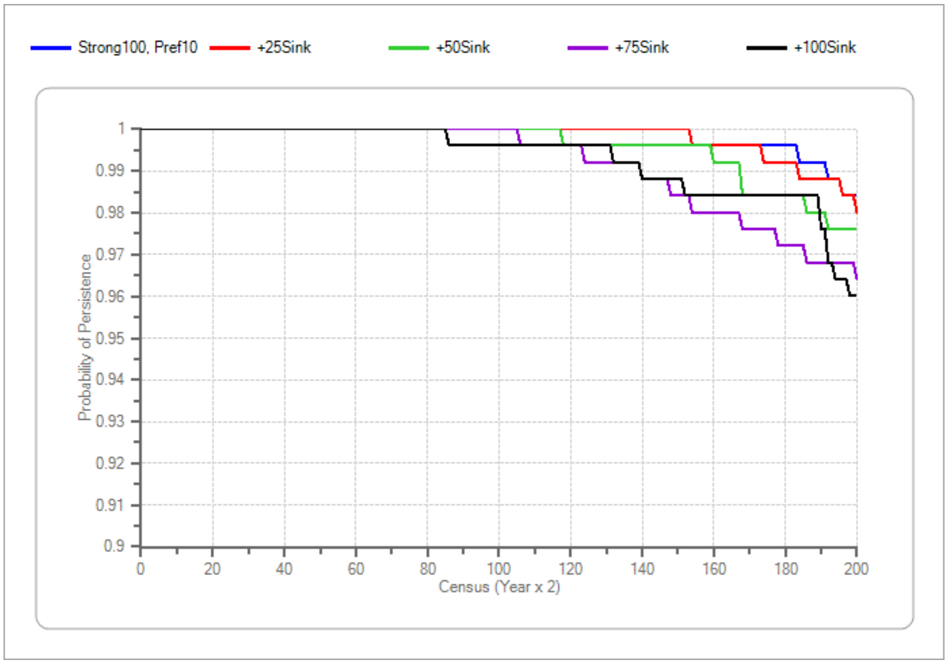

Figure 28. Probability of population persistence of populations with 100 potential territories of Strong habitat, and with 25, 50, 75, or 100 potential territories of Sink habitat added, when there is large preference for Strong habitat (Pref = 10). Note y-axis starts at 0.90.

The above results suggest that habitat quality and spatial and temporal continuity (i.e., accessibility) might be more important than the overall quantity of FSJ habitat. However, in the more complex dynamics of metapopulation configurations of partly isolated populations, suboptimal habitat might improve metapopulation dynamics by providing stepping stones or corridors for dispersal. This possible effect was explored with scenarios that modeled the actual distributions of habitat quality in each metapopulation (see *Metapopulations* section below). In addition, habitat that is currently Weak or even Sink might be the habitat that becomes Strong in the future after management and succession from short vegetation.

Population connectivity

Benefits of occasional immigration into small populations

The above simulations examined the viability of populations that were completely isolated and received no immigrants from other populations. However, occasional exchange between local populations within the metapopulations has been documented, and such dispersal could be augmented either by habitat restoration that creates more connectivity or by translocations of jays between sites. Scenarios were tested with varying rates of immigration into small populations. The next four figures show the number of breeding pairs and the probability of persistence for populations with 25 (Figs. 29 & 30) or 50 (Figs. 31 & 32) potential territories when there are no, 1, or 2 immigrants per year.

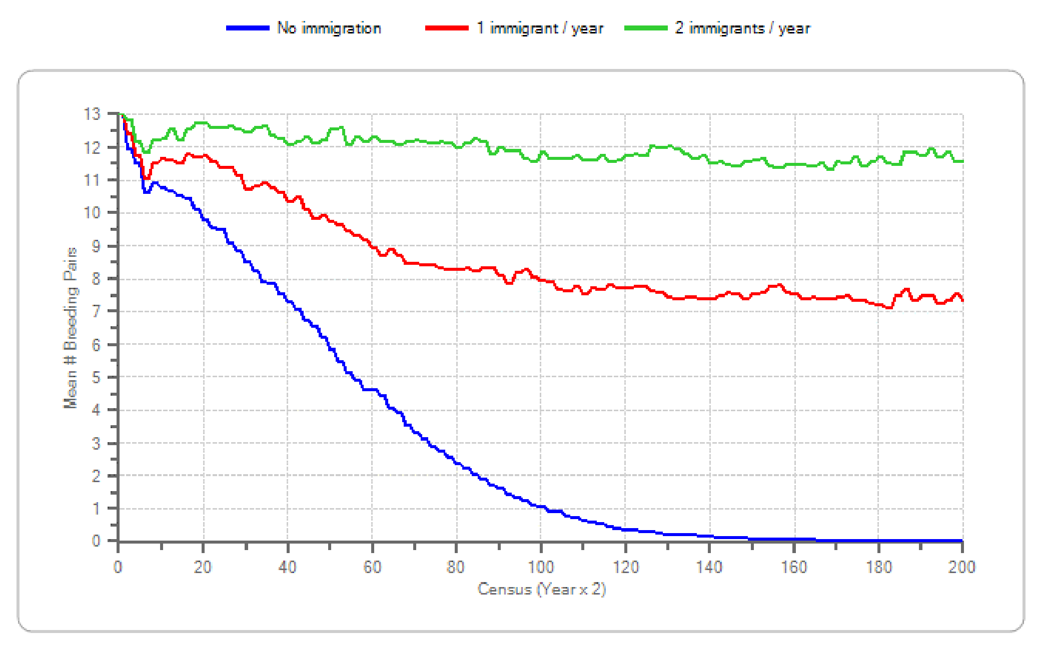

Figure 29. Projected numbers of breeding pairs in populations of 25 potential territories (10 in Strong habitat), and with 0, 1, or 2 immigrants added each year.

Even in populations as small as 25 potential territories, 2 immigrants per year appears sufficient to avoid local extinction and stabilize the populations at a number of breeding pairs that approximates the number of Strong habitat territories in the model (10 and 20, respectively in the two cases examined).

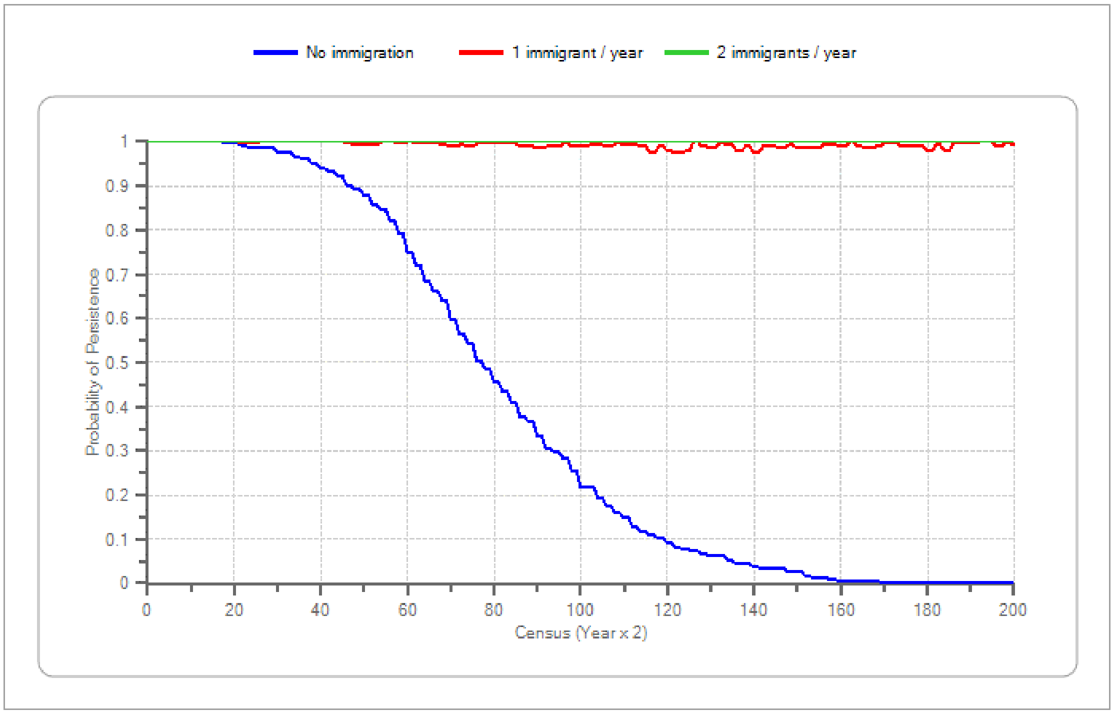

Figure 30. Probability of persistence of populations with 25 potential territories (10 in Strong habitat), and with 0, 1, or 2 immigrants added each year.

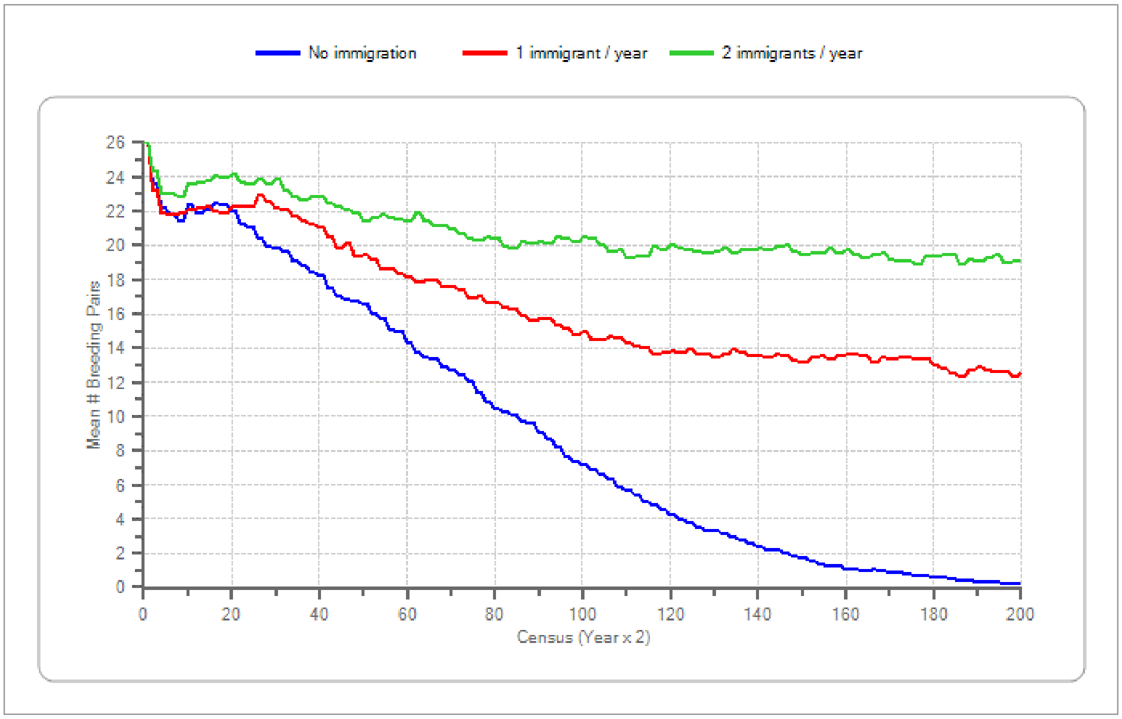

Figure 31. Projected numbers of breeding pairs in populations of 50 potential territories (20 in Strong habitat), and with 0, 1, or 2 immigrants added each year.

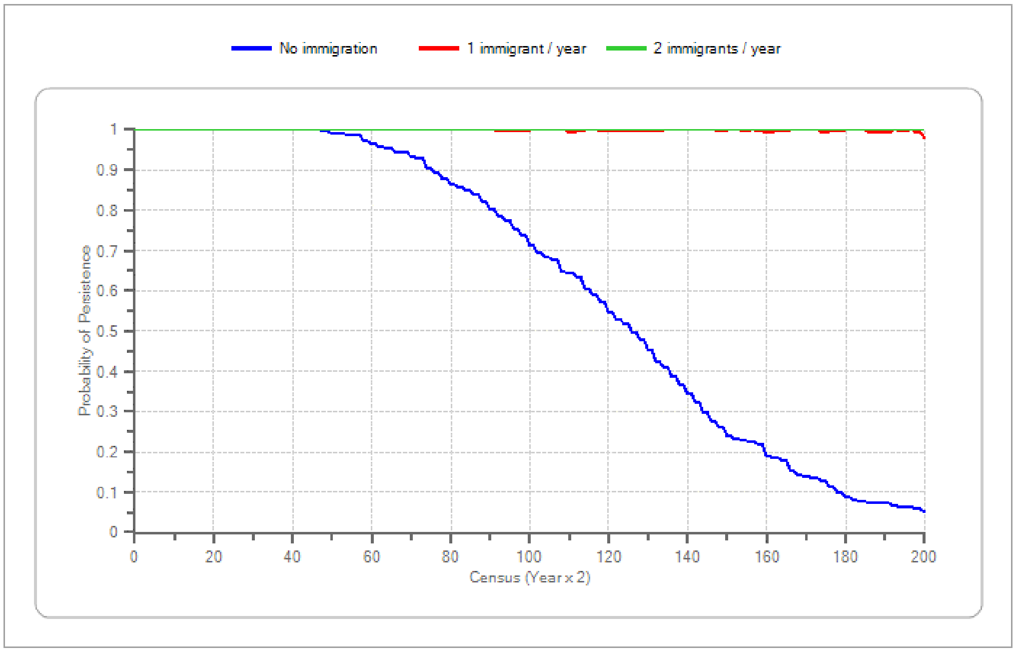

Figure 32. Probability of persistence of populations with 50 potential territories (20 in Strong habitat), and with 0, 1, or 2 immigrants added each year.

To test even lower levels of immigration, scenarios were run with 1 female and 1 male added to the populations at 1, 2, 4, or 8-year intervals. Figures 33 and 34 show the benefits of periodic immigration to populations with 25 and 50 potential territories.

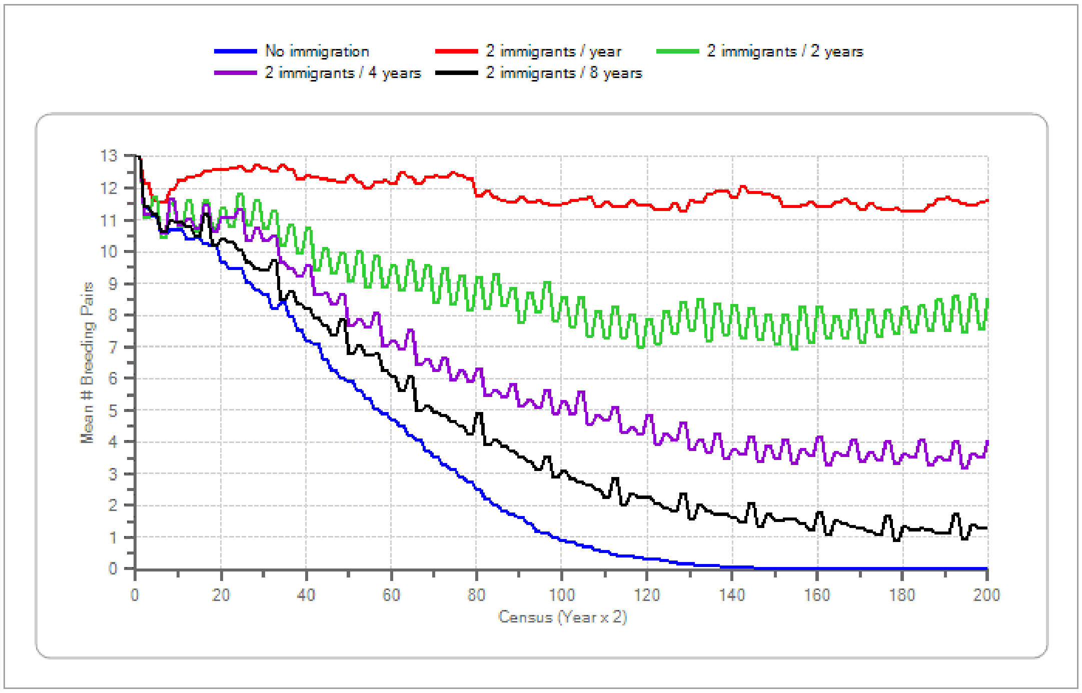

Figure 33. Projected numbers of breeding pairs in populations of 25 potential territories (10 in Strong habitat), and with one male and one female immigrant added every 1, 2, 4, or 8 years.

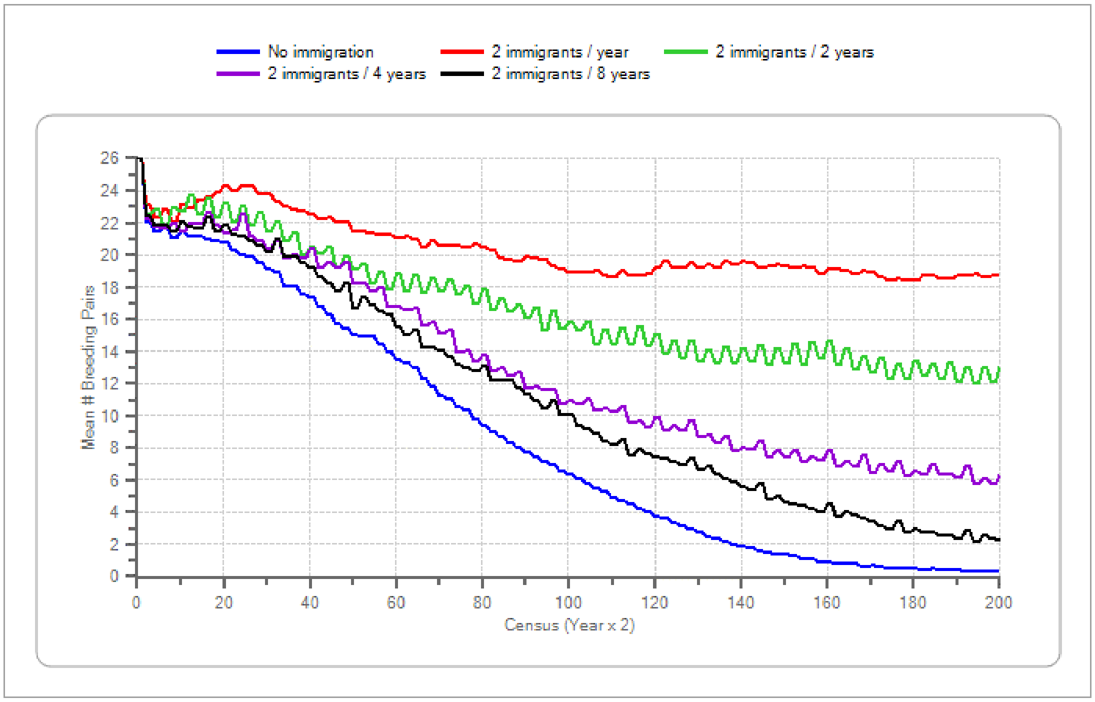

Figure 34. Projected numbers of breeding pairs in populations of 50 potential territories (20 in Strong habitat), and with one male and one female immigrant added every 1, 2, 4, or 8 years.

The above graphs indicate that with less frequent immigration (e.g., every 4th or 8th year), there is still some benefit, but the populations sizes decline to much lower numbers and the populations often suffer extinction in the years in between the supplementation via immigration. The next two graphs show the probabilities of population persistence for populations of 25 and 50 potential territories, receiving 2 immigrants at intervals of 1, 2, 4, or 8 years (top to bottom; blue line is with no immigration).

Overall, these results indicate that immigration rates of 1 or 2 jays per year is necessary to protect small populations from demographic instability and long-term damaging effects of inbreeding.

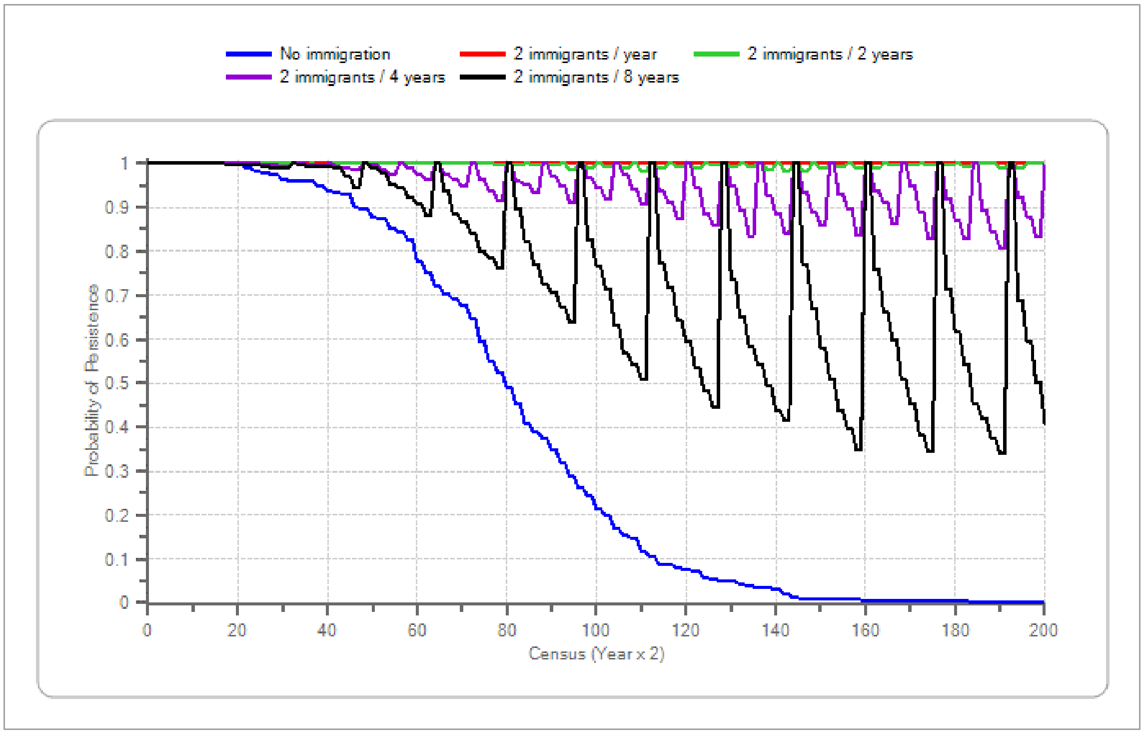

Figure 35. Probability of persistence of populations with 25 potential territories (10 in Strong habitat), and with one male and one female immigrant added every 1, 2, 4, or 8 years.

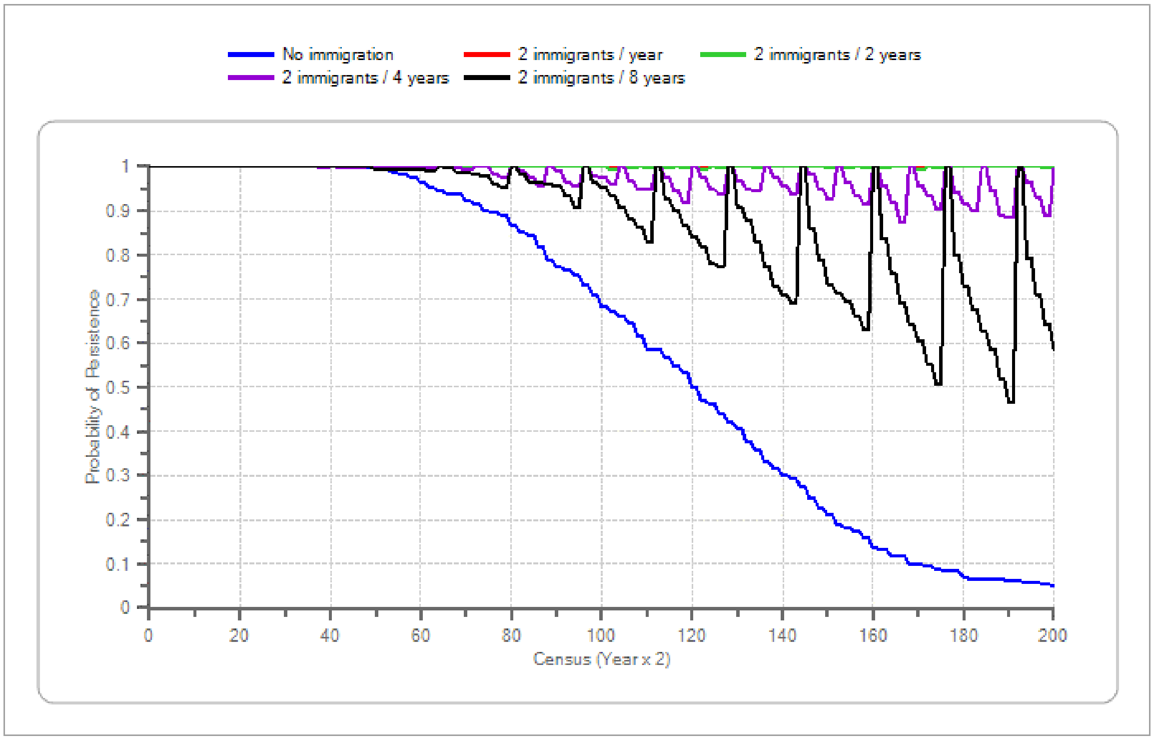

Figure 36. Probability of persistence of populations with 50 potential territories (20 in Strong habitat), and with one male and one female immigrant added every 1, 2, 4, or 8 years.

Benefits of population connectivity, when there is no net immigration into small populations

The benefits of immigration illustrated above could result from either the demographic benefit of adding occasional jays to the small population or the genetic benefit of adding unrelated jays that reduce inbreeding. To distinguish between these effects, some scenarios were examined in which immigration was balanced by equal numbers of emigrants. The next two graphs compare the effects of 0, 1, or 2 immigrants and emigrants per year for populations with 25 and 50 potential territories. The top lines are the projections when there is no exchange but also no inbreeding depression.

These results show that if emigration balances immigration, so that the demographic benefit of added jays is removed, there is only a small improvement in the number of breeders. This benefit does not become apparent until after about 35 years (census 70 in the model), because it arises from a reduction in the accumulation of inbreeding. However, even with 2 immigrants and 2 emigrants per year, inbreeding still rises to damaging levels, as can be seen in the much better performance of the populations when inbreeding depression is removed from the simulation model.

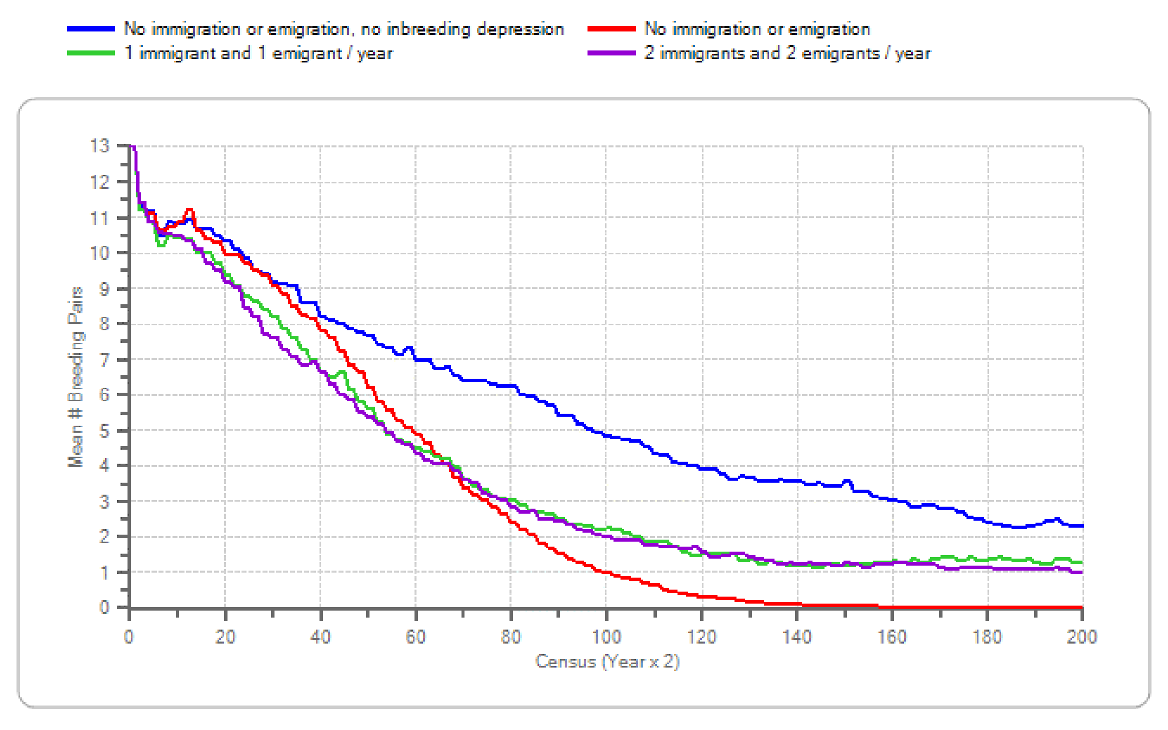

Figure 37. Projected numbers of breeding pairs in populations of 25 potential territories (10 in Strong habitat), and with 0, 1, or 2 immigrants and emigrants each year. Top line has no immigration, but also no effect of inbreeding.

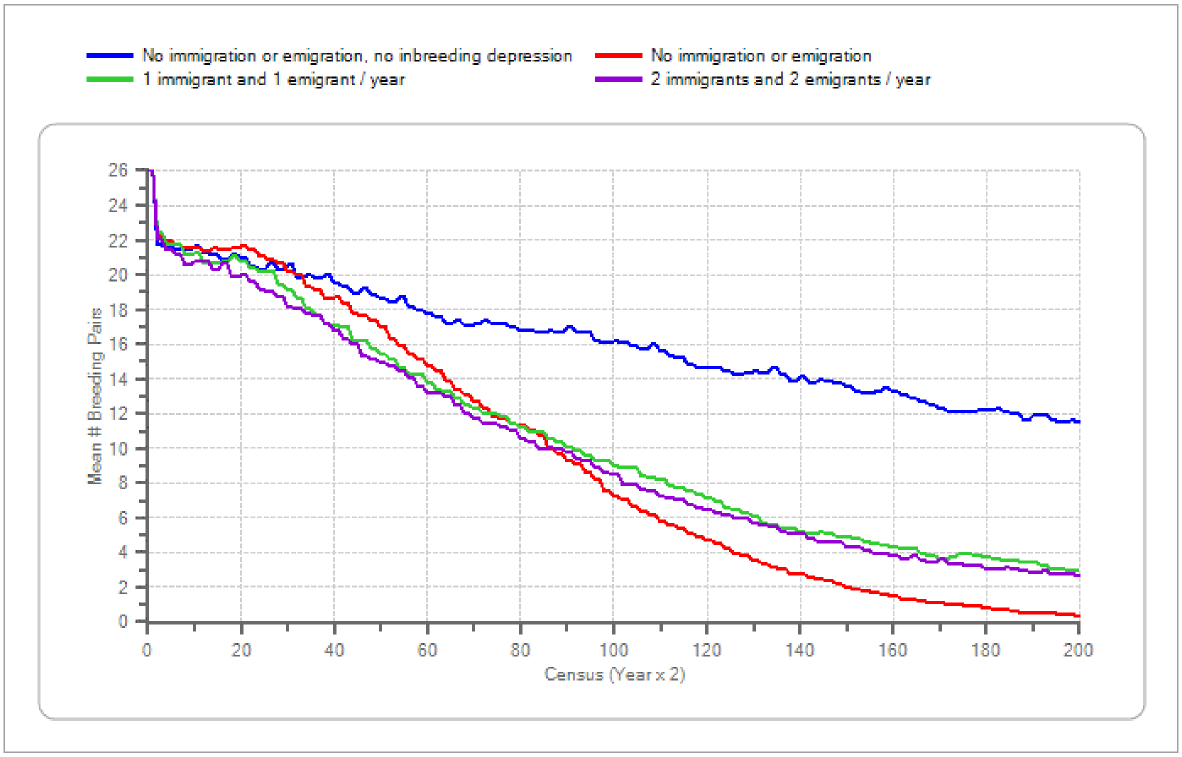

Figure 38. Projected numbers of breeding pairs in populations of 50 potential territories (20 in Strong habitat), and with 0, 1, or 2 immigrants and emigrants each year. Top line has no immigration, but also no effect of inbreeding.

Resilience to periodic catastrophes

A population can appear to be viable and relatively stable across a number of years of typical environmental conditions, but then be unable to recover after an unusual catastrophic event drives it down to a small and unstable population size and structure. Such catastrophes can occur due to disease epidemics, severe weather events (e.g., storms, floods, droughts), large scale environmental contamination events, arrival of an invasive predatory or competitor species, or other events that cause large mortality or reductions in reproduction. The frequencies and severity of such catastrophes are difficult to predict, because – by their very nature – they are unusual and severe events. However, they can and do occur and they can cause population decimation or even extinction. Reed et al. (2003) reported that vertebrate populations typically experience a catastrophic die-off of 50% or more with an average frequency of about 14% per generation.

In 1979 there was a severe mortality event – likely due to an outbreak of encephalitis – in Florida scrub-jays. In that event, it is estimated that almost no juveniles survived and adult mortality (for both breeders and helpers) was about 50% in the Archbold population. There was also observed a decline in breeding the following year. Although we cannot predict accurately the likelihood of future such events, we can use the PVA model to examine how likely it is that FSJ populations will recover from such catastrophes. We tested scenarios that imposed a 2% probability of catastrophe each year that caused 50% mortality and a failure of reproduction for the year – as might happen with a severe outbreak of encephalitis. Figure 39 shows one sample run of this catastrophe scenario for an isolated population with 100 territories of Strong habitat with initially 70% occupied. In this run, the simulated population grew to fill the available habitat, then in about year 45 was hit by a catastrophe. It dropped to about half its former size and did not recover because of the demographic and genetic instability of the small surviving population. Some repeats of the simulation sometimes were able to recover following a catastrophe, while others went extinct.

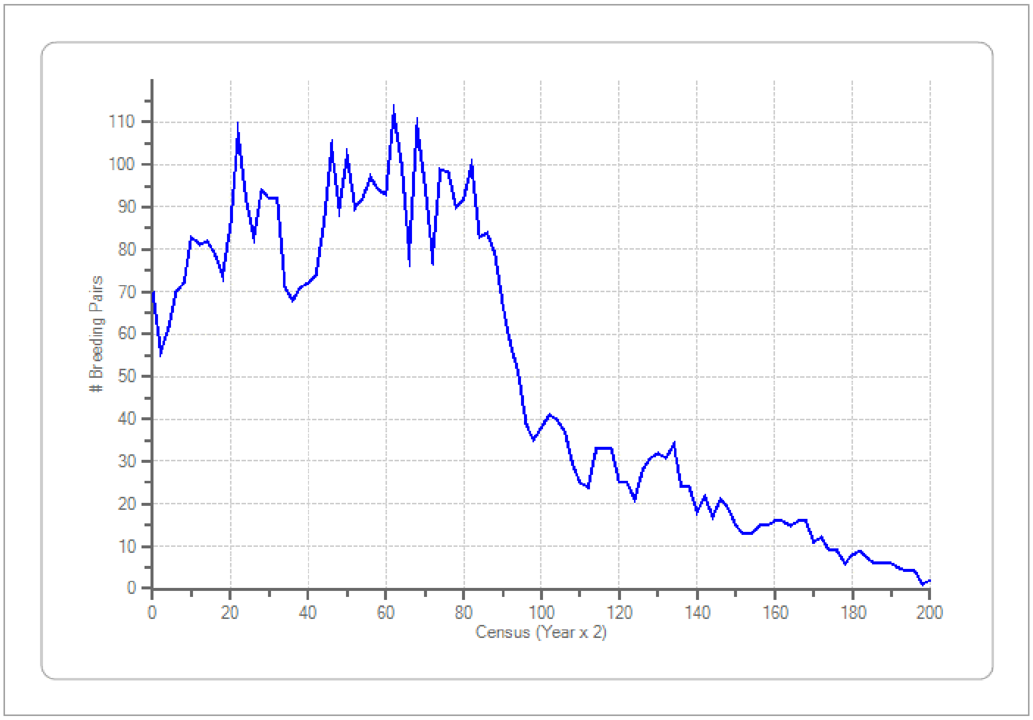

Figure 39. A sample run of a population with 100 Strong potential territories, subjected to catastrophes at a frequency of 2% per year, causing 50% mortality and failure of reproduction.

Figure 40 compares the mean trajectories for populations with 100, 200, 400, or 1000 Strong territories (70% initially occupied) – either without catastrophes or subjected to catastrophes with a frequency of 2%, causing 50% mortality and failure of reproduction for that year. The individual catastrophes are not apparent in the graph, because the lines average across 250 iterations and the catastrophes occur randomly at any time. The pairs of lines (e.g., purple and blue for the 1000 Strong territories) show that, on average, the FSJ populations do not fully recover from catastrophes, but instead decline, even though populations with more than 100 Strong territories are stable and viable in the absence of such occasional catastrophic events. As shown in Figure 41, the occurrence of such catastrophes causes significant probabilities of local extinction, while extinctions are rare in comparable scenarios without the catastrophic events.

Wild populations of all species are vulnerable to severe catastrophic events, but catastrophes are usually local or regionally confined. Thus, recolonization from unaffected populations can reverse the occasional local extirpation due to decimation by a catastrophic event. Catastrophes become a threat to species persistence when local populations become too isolated to allow for such reinforcement or reestablishment of local populations that have been reduced in size.

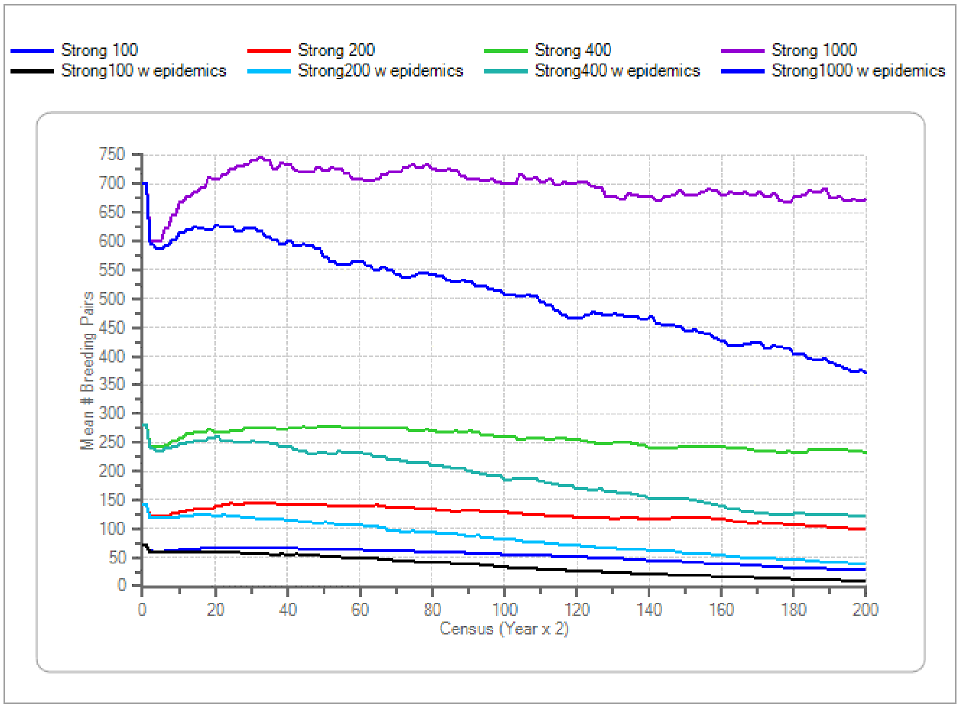

Figure 40. Projected mean number of breeding pairs in populations with 100, 200, 400, or 1000 Strong territories, either subjected or not to catastrophes with a frequency of 2%, causing 50% mortality and complete reproductive failure.

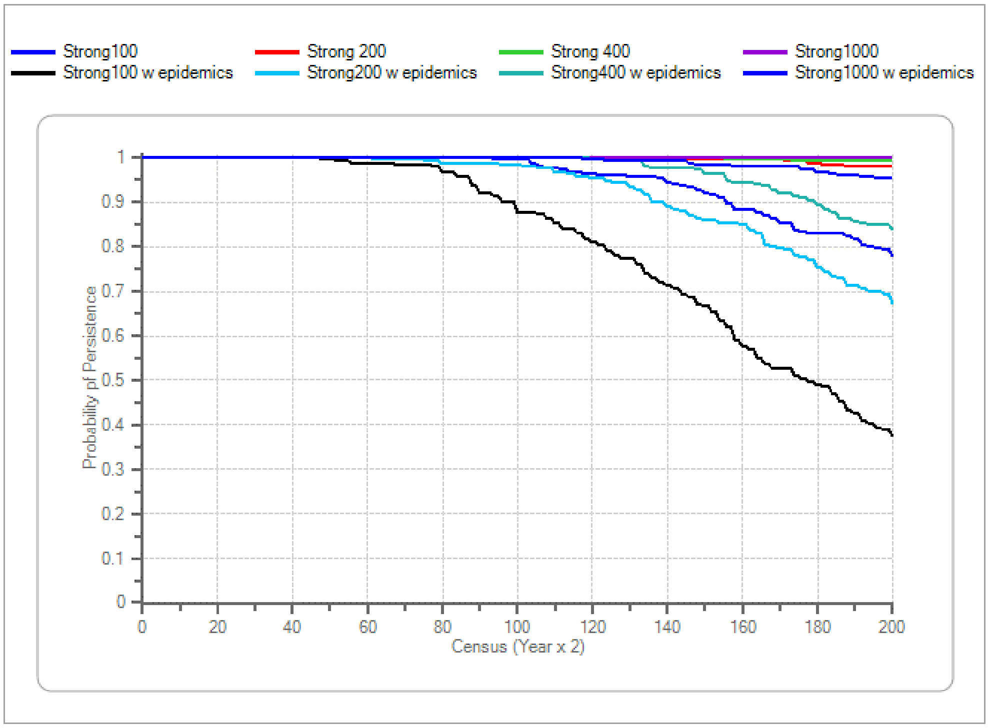

Figure 41. Probability of persistence of populations with 100, 200, 400, or 1000 Strong territories, either subjected or not to catastrophes with a frequency of 2%, causing 50% mortality and complete reproductive failure.

Global Sensitivity Analyses

Sensitivity analyses assess which of the uncertain parameters in the PVA model have the largest impact on the population projections. The most influential factors are those for which:

- it would be most useful (in terms of providing confidence in predictions about the population trajectories) to obtain more precise estimates from field data;
- the population might be most vulnerable if the rates declined over time;
- the population would be expected to respond most positively if the rates improved;
- could be targets for future management actions.

In sensitivity analyses, the parameters of concern are varied, singly or in many or all combinations, over a range of plausible values. “Global sensitivity analysis” refers to examination of the sensitivity of model outcomes to many or all the uncertain parameters simultaneously, rather than testing only a small subset of factors, often one at a time (Prowse et al. 2016).

There are several different approaches to determining what ranges of value to test, and they are suitable for different purposes (Manlik et al. 2018):

- If the purpose is to determine for which factors our present ability to obtain accurate estimates causes the largest uncertainty in the population trajectories, then parameter values should be varied across the distribution of present uncertainty (e.g., as expressed by standard errors in the estimates of parameter values).
- If the purpose is to determine what factors threaten the population viability, then the parameters would be varied across the range of possible values experienced by the population. This would often be determined by looking at the variation observed over a number of years, but with the caveat that consideration must also be given to the likelihood that rates will change as the environment changes, perhaps outside of the range previously observed.
- If the purpose is to determine for which factors management actions designed to improve the rates would have greatest positive effect, then parameters would be varied across ranges that represent best estimates of the extent to which management could lead to improvement.
- If the purpose is to explore which factors have the largest leverage on population performance of species with similar life history (separate from any consideration of the actual variation in rates observed or possible in the focal population), then all model parameters would usually be varied by a fixed percent (as in “elasticity analysis”).

A useful approach is often to start by examining the uncertainty in rates (the first point above), then further explore possible ranges observed in the past (second point above) and possible under future management (third point above). The fourth approach above is more applicable to work in theoretical ecology than to risk assessment and management of specific wildlife populations (Mills et al. 1999).

The first approach – examining the impact of our uncertainties on model projections – was carried out with a global sensitivity analysis on a representative (hypothetical) population. Testing focused on responses to environmental change (2nd approach) might be pursued in conjunction with modeling of habitat transitions (underway by the research team at KSC). Testing of impacts of management (3rd approach) has been explored within the detailed models of the metapopulations (see below). Table 5 presents the model input parameters that were tested in the global sensitivity analysis, the range across which each was varied, and the consequent percent of total variation in model outcomes caused by the variation in each parameter. (These proportions of the variation explained by each parameter were determined from generalized linear models.) When an SE is displayed, the uncertain parameter was varied by sampling from a normal distribution with that error variance. When a series of values is given, the parameter was varied by sampling one of those values at random for each iteration. The notation "f(Hab; Help)" indicates that the mean value varied depending on the habitat quality (Strong, Weak, or Sink) and the presence or absence of helpers in the breeding group. The model projection was repeated for 100,000 iterations that sampled across the parameter space, in accord with the recommendations of Prowse et al. (2016). The percent of variance gives the variation in the population size projected at year 25 and in the probability of extinction by year 100 that is accounted for by the uncertainty in the model parameter. The percent of variance is given both as a percent of the total variation among simulation iterations and as the percent of the variation accounted for uncertainty in this set of model parameters (not including the Residual variance). The Residual variation is the percent of variation in model results that is due to the sources of stochasticity intrinsic to the model: random individual variation in breeding and survival (demographic stochasticity); annual variation in demographic rates (environmental variation); and unpredictability of Mendelian genetics.

These tests were conducted for an isolated population with 100 potential territories, distributed as 40 Strong, 30 Weak, and 30 Sink habitat, with initially half of territories occupied. It should be noted that the relative importance of factors would change with smaller or larger populations. For example, in smaller populations the impact of inbreeding depression would likely be greater. Population size was assessed at year 25, rather than after 100 years, because for many combinations of input parameters the population would be extinct before year 100.

Model parameters varied in the Global Sensitivity Analysis, and shown in the following table, were:

Inbreeding impact = Lethal Equivalents

Habitat preference = parameter defining likelihood of a jay dispersing from the natal territory locating available Strong habitat. 1 would mean random habitat selection, 4 is moderate preference for better habitat, 8 is large preference for better habitat. (See section *Habitat selection by breeders*, above, for more details on the function used.)

Opportunity response = parameter defining the rate at which helpers transition to breeder status in response to available Strong habitat. (See section *Helper to breeder transitions*, above, for more details on the function used.)

Breeding success = Proportion of pairs that produce juveniles each year

EV = environmental (annual) variation in the demographic rate

Table 5. Results from Global Sensitivity Analysis. Each model parameter tested was varied by sampling from the designated range. Generalized Linear Models were used to assess relative proportion of variation caused to the # Breeders and Probability of complete extinction.

Model parameter	Estimated mean	Range tested	# Breeders @ 25 y		Prob Extinct by 100 y	
			% of total variance	% of V due to uncertain parameters	% of total variance	% of V due to uncertain parameters
Inbreeding impact	7.478	SE = 3	0.20	0.53	6.56	15.17
Habitat preference	6	(4;5;6;7;8)	0.12	0.32	0.91	2.10
Opportunity response	6	(4;5;6;7;8)	0.88	2.31	0.23	0.54
Breeding success	f(Hab; Help)	SE	7.19	18.83	7.32	16.92
Juvenile mortality	f(Hab)	SE	2.41	6.31	2.21	5.12
Adult mortality	f(Hab; Help)	SE	27.08	70.98	25.34	58.59
EV(breeding succ)	20.9%	SE = 4.0%	0.04	0.11	0.09	0.21
EV(juv mortality)	18.9%	SE = 3.6%	0.09	0.23	0.17	0.38
EV(adult mortality)	f(Help)	SE	0.14	0.37	0.42	0.98
sum			38.15	100	43.16	100
Residual			61.85		56.84	

The sensitivity testing shows that intrinsic biological and environmental stochasticity causes more than half of the uncertainty in long-term projections, as indicated by the % of variation in outcomes that is in the residual variance after all uncertainties in input parameters are accounted for statistically. Greater predictability would be expected with populations that have more than 100 potential territories, but even less predictability in smaller populations. Thus, even if we had perfect knowledge of mean demographic rates, there would be a lot of unpredictability in the fates of scrub-jay populations in highly fragmented habitats.

Among the uncertain variables that were tested, adult mortality is the dominant parameter determining population growth (as assessed here by the number of breeding pairs at year 25) and population persistence (as measured by probability of extinction within 100 years). The uncertainty in adult mortality accounts for more than 25% of the total variation in projected N and in extinction, and 71% and 59%, respectively, of the variation caused by uncertainty in the set of 9 variables. Breeding success is the next most influential variable with respect to both output measures. Uncertainty in the juvenile mortality rate also has a considerable effect on population size and probability of extinction. The impact of inbreeding on juvenile survival, quantified by the "lethal equivalents", has a large effect on probability of extinction within 100 years, but very little impact on the population size at year 25. This indicates that inbreeding does not rise to high enough levels to be a threat within 25 years, but it is an important threat to the long-term persistence of isolated populations.

The two measures of response to the availability of quality habitat – the preference for or accessibility of optimal habitat by new breeding pairs, and the response of helpers transitioning to breeders when breeding vacancies open up in good habitat – have smaller but not unimportant effects on the population performance, within the ranges that were tested. This is encouraging from the standpoint of trusting the PVA to provide useful projections, because these two model parameters are difficult to estimate from field data.

Uncertainty in the several aspects of annual variation – EV in breeding success and mortality rates – had very little effect on population projections. This does not mean that environmental variation has little effect on population stability and predictability (some other analyses suggest otherwise), but rather that our estimates of annual variation based on many years of data are sufficiently precise (with CV = SD/mean ~ 0.19 for each EV) to give us confidence in their impacts on model projections.

Criteria for metapopulation viability

Assessing the status of populations and efficacy of management scenarios necessarily depends on how we define population "viability". What do we define as a "safe" and "healthy" population? What would we accept as successful management? Viability is as much a specification of our values as it is a biological term, as it depends on our goals for the populations, the time frame over which we want to ensure viability, and our risk tolerance. Different agencies, organizations, and people might prescribe different criteria for viability against which management options are to be evaluated, and we can re-assess conclusions drawn from the PVA modeling with alternative definitions of viability. As a start, we can use criteria that align with those used in many endangered species recovery programs and used by many wildlife management agencies in the US and around the world. Common, although not universal, criteria for population viability are that a population has less than a 5% probability of local extirpation over the long-term (often 100 years); the population remains demographically stable, growing or at least not projected to decline; and that the population retains more than 90% of the initial genetic diversity (equivalent to inbreeding being kept below F = 0.10). Other criteria that are more difficult to generalize across species include maintaining population size above some percent (often 50%) of carrying capacity; sustaining mean population growth at a level deemed typical for that species or for other species with similar life history; resilience to short-term unusual events (i.e., ability to rebound after a catastrophe); and occupancy of some defined amount and representative types of habitat.

Several of the criteria for viability refer to the carrying capacity of the habitat (K), and K is almost as hard to define and measure as is viability. Loosely, K can be defined as the population size that can be sustained in the available habitat over the long-term -- without over-exploiting the resources or triggering density dependence effects (such as increased disease or predation) that would drive the population back down to lower levels. This concept of K, however, depends on the quality and extent of habitat, so it is not necessarily well-defined nor what we want to use in criteria for viability. For example, it might be easy to maintain N > K/2 if K itself is very low and declining due to inadequate protection of habitat, but that does not align well with concepts of population health and recovery. Thus, a species conservation or recovery plan needs to define what K is the goal – i.e., how large of a population do we want to conserve?

There are several ways that we might delineate the desired K (and thus, the desired N if we set a goal of N > K/2) for Florida scrub-jays. At the most ambitious level, we could define K to be the number of jays (quantified as the number of breeding groups) that would be present if all potential habitat were occupied. This might be termed Kmax. It has been quantified for each of the populations and is used in the PVA model as an upper limit to the number of breeding groups. At the least ambitious level, we could use a K (maybe termed Kmin) that matches the population size that would be projected to persist in the current amount and quality (Strong, Weak, and Sink) of available habitat. A problem of using such a definition is that it would define K to be very small (and maybe 0) for populations that have so little Strong habitat that the population is projected to decline toward extinction. An intermediate concept of K that might be useful for scrub-jay management would be to determine first the percent of Strong habitat necessary to achieve a demographically and genetically stable population, and then to define K as the population size that would be sustained in such habitat (perhaps termed Kviable). There is some circularity in defining K based on aspects of viability and then using that K in some metrics of viability, but we can work with several concepts of K and see what provides the most useful way to assess prospects for management success.

Figures 42, 43, and 44, below, compare projections for an isolated population with 400 potential territories that range from 30% to 100% Strong, with the remaining territories being evenly split between Weak and Sink. Populations with about 50% or more Strong stabilized at population sizes that are approximately the number of Strong territories (Fig. 42). Populations with less than about 50% Strong declined slowly but steadily to occupy less than the number of Strong territories. Probability of extinction is minimal with 40% (160) or more Strong potential territories, but with 30% Strong (120 territories) the probability of extinction approximates 10% (Fig. 43). The decline in population size and possibility of extinction with the lesser amounts of Strong habitat seem to occur because the accumulated inbreeding, while not above the 10% threshold, still rises to levels that will cause significant declines in fitness (Fig. 44). For example, with the impacts of inbreeding on scrub-jays estimated by Chen et al. (2016), inbreeding of F = 0.05 (just slightly less than 1st cousin matings) would cause a reduction of 17% in survival. Although this might seem to be severe effects of inbreeding, the inbreeding depression that we have modeled in Florida scrub-jays is less than what has been reported in studies of inbreeding depression in other bird species (e.g., Niskanen et al., 2020).

These models suggest that a reasonable concept of carrying capacity, aligned with concepts of viability, might be that for a given population demographic stability often requires about 50% or more of habitat to be Strong, and such habitat will support about as many breeding groups as there are Strong potential territories, so that a management goal for K might be to aim for a number of breeding groups that is at least 50% of the number of potential territories. Conveniently, perhaps, this goal would match with a viability criterion of N>(Kmax/2). It should be noted, however, that describing complete occupancy of existing scrub-jay habitat as being Kmax does not imply that it might not be possible to achieve an even higher K by adding newly restored and managed scrub habitat.

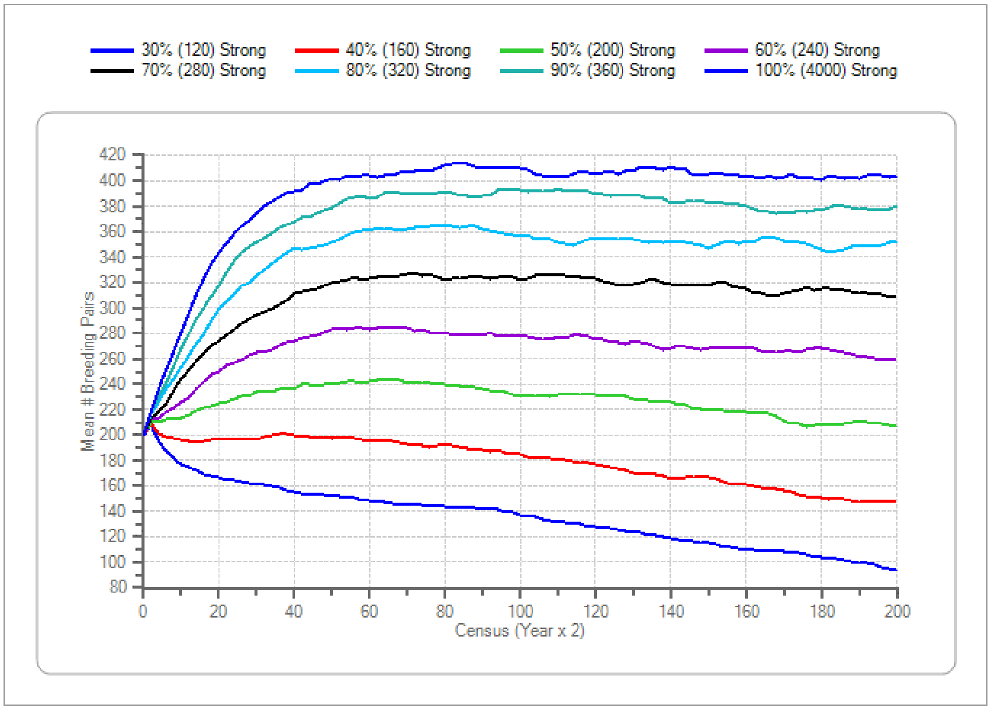

Figure 42. Projected number of breeding groups for a population with 400 potential territories, with the proportion in Strong habitat varying from 30% to 100%. Numbers in parentheses in the legend show the number of Strong potential territories in each case.

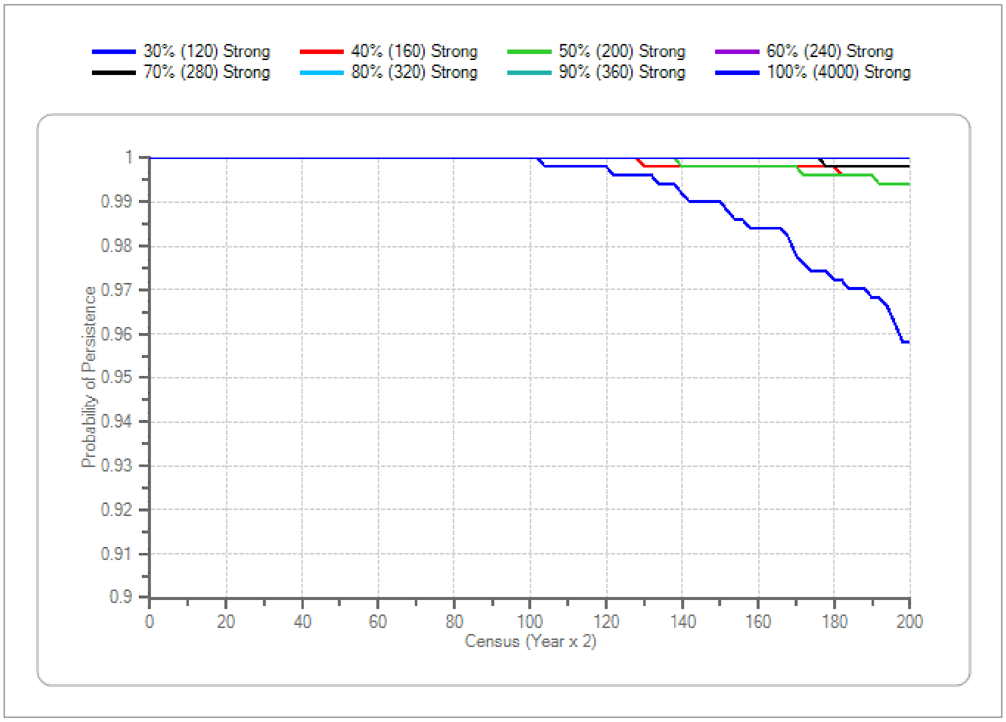

Figure 43. Probability of population persistence for a population with 400 potential territories, with the % in Strong habitat varying from 30% to 100%. Note that the y-axis starts at 90%. Only the line for 30% Strong is easily distinguished from the other scenarios.

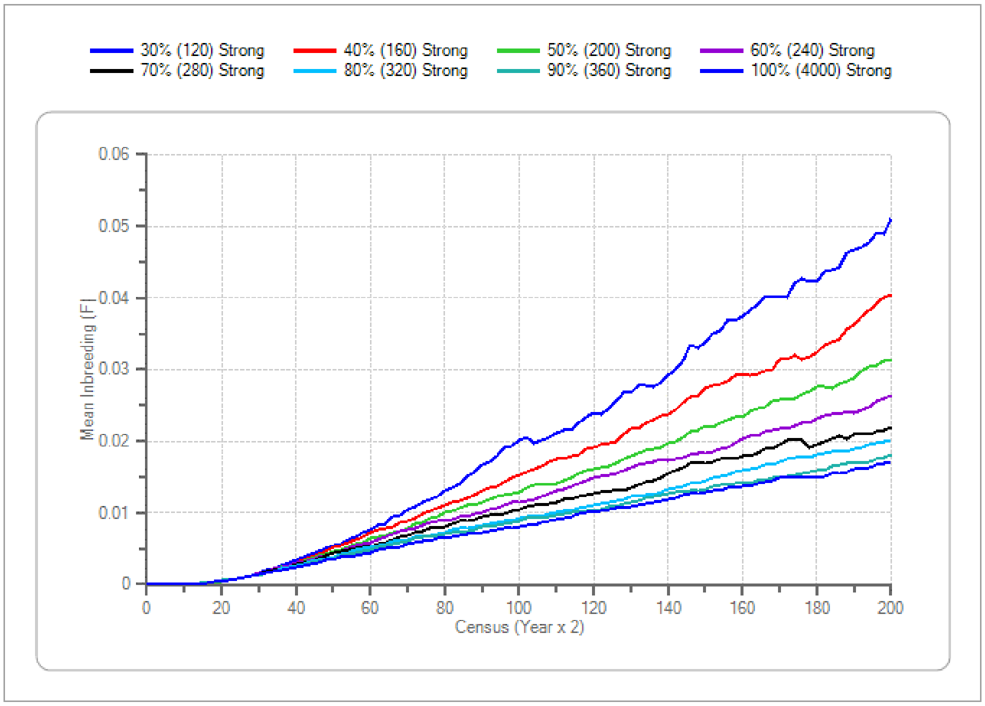

Figure 44. Mean accumulated inbreeding for a population with 400 potential territories, with the % in Strong habitat varying from 30% to 100% (top to bottom).

Given the above considerations, when evaluating results from management scenarios, we might consider a metapopulation to be "viable" if it sustains a population size that occupies more than 50% of potential territories, keeps accumulated inbreeding below 0.10, and has a probability of extinction over 100 years of less than 5%. When a possible management scenario is applied to a population that is projected to be in decline (not viable), we can examine the extent to which the management action would further damage or instead enhance prospects for the population, even if that management action alone would not ensure viability.

Metapopulations

In the next phase of the PVA work, we developed metapopulation models that represent the observed configuration of local populations on the landscape. A metapopulation is identified as a cluster of local populations that occasionally exchange dispersing individuals. There is very limited or no dispersal between the four designated metapopulations of FSJs in the Brevard County region, and they are likely now functioning as demographically and genetically independent metapopulations. We therefore assessed each of the metapopulations independently. Very rare dispersal might occur between the metapopulations, and these will be incorporated into the PVA as unrelated jays arriving from outside the metapopulation ("supplements" in the Vortex model). Any jays dispersing out of a metapopulation would be losses to the population and are treated as deaths in the PVA.

Tallies have been made of the observed movements of jays between local populations within each metapopulation. On the Brevard mainland, no movements of jays between the north and south sets of local populations have been recorded. Over the past decade, there have also not been recorded any movements of jays between north and central or south and central populations. Occasional dispersal between populations within each metapopulation cluster have been documented (see below). At KSC, there has been very limited dispersal between the core subpopulations. In the FSJ population inhabiting the Lake Wales ridge scrub community, studied at Archbold Biological Station, movements greater than 8 km have not been seen, and genetic data suggest divergence starts to be detected at about 4 km distance. We used these data to specify connectivity between local populations. We also ran simulations with greater connectivity between populations, as likely would have been the case 40 to 50 years ago before the habitat became as reduced and fragmented as it is today, and as might occur again with restoration of habitat between the current population boundaries.

Delineating local populations and metapopulations

Metapopulation models are being used to test the viability of each of the disjunct metapopulations and the individual local populations that comprise them. Local populations within each metapopulation were identified as those areas separated by more than two territory widths at their closest proximity. This results in areas within which about 90% of the birds remain within their local population. Clusters of breeding groups were defined to be within the same local population if the habitats were separated by less than 667 m from each other, with exceptions for some pairs of populations that are separated by less distance but separated by barriers to dispersal. Populations modeled within each metapopulation are listed below, but some of these populations include adjacent habitat not encompassed within the reserve, park, or other management unit for which the population is labeled. Some jays likely exist outside of these populations, but not in sufficient numbers within any area to be considered as a functional breeding population.

KSC/MINWR

Populations comprising the Kennedy Space Center/Merritt Island National Wildlife Refuge metapopulation are Shiloh, Happy Creek, Schwartz Road, and Tel4.

CCSFS

Populations comprising the Cape Canaveral Space Force Station metapopulation are Beach (plus North), Central, Phillips, and Delta. The “Beach” local population might be part of the KSC/MINWR metapopulation, but the small Beach population is more closely connected to the CCSFS population than to the KSC populations. The KSC/MINWR and CCSFS metapopulations might exchange some individuals via the proximity (6 km) of Happy Creek (in KSC) and Beach, and some models were run to test KSC/MINWR and CCSFS functioning as a single metapopulation.

The CCSFS populations and their habitats have not been monitored regularly following the same protocols as have the KSC/MINWR and the mainland populations. Since we lack fully comparable data on the demography of the CCSFS populations, we have assumed that the demography of those populations can be represented by the same demographic rates and relationships to habitat characteristics that have been determined for the KSC/MINWR populations. Additional field studies on the CCSFS populations could provide data that might allow PVA modeling with rates more specific to that metapopulation.

North Mainland

Populations comprising the North Mainland Brevard metapopulation (with abbreviations used in our models and reports) are Buck Lake Conservation Area (BUCK), Enchanted Forest (ENCH), Fox Lake Conservation Area (FOXL), Grissom megaparcel (GRIS), Indian Mound (INDM), Salt Lake Wildlife Management Area (SALT), Scottsmoor Sanctuary East (SCOTE), Scottsmoor Sanctuary West (SCOTW), and Titusville Wellfield (WELL), which includes the Dicerandra Scrub Sanctuary.

South and Central Mainland

The main populations comprising the South and Central Mainland Brevard metapopulation are Viera (including Viera mitigation area, Capron Ridge, and Cruickshank scrub sanctuaries) and Wickham Park (WICK) in Central Mainland; Malabar scrub sanctuary (MALA), Liberty Park (LIBE), Jordan Scrub Sanctuary (JORD), Valkaria scrub sanctuary and megaparcel (VALK), Babcock (BABC), Micco scrub (WMIC, including northern Sebastian Buffer Reserve), Palm Bay (PBAY), Corrigan Sebastian Buffer Reserve (CORR), Coracii Sebastian Buffer Reserve (CORA, including N Sebastian Conservation Area), North Fork Sebastian Buffer Reserve (NFOR), Carson Platt Sebastian Buffer Reserve (CP), Wabasso scrub (WABA, including Pelican Elementary School). The last 12 populations listed above are all within the South Mainland Brevard region. The two Central Mainland populations have exchanged few jays with the 12 South Mainland populations in the last 30 years. The S Mainland and C Mainland populations are included in our models as being part of the same metapopulation, but with low rates of dispersal between them.

Determination of functional relationship between distance and dispersal rates between populations

Matrices of all pairwise distances between local populations within each metapopulation were measured in km, between the closest points the habitats occupied by the populations. Dispersal rates were assessed for the populations in South and Central Mainland metapopulation over the time period of 1997-2008. Dispersal rate was quantified as the number of banded helper jays observed to move from one (source) population to another destination population (where they attempted to became breeders), as a proportion of the total bird-years of observation of banded helpers at the source.

Regression models were used to determine what function best fit the relationship between distance (D) and dispersal rate (R). Regression models that we tested included a simple linear model ($R = a + b \cdot D$), an inverse distance model ($R = a + b/D$), an inverse-squared model ($R = a + b/(D^2)$), an inverse square-root model ($D = a + b/(\sqrt{D})$), and a non-linear model that also fitted the exponent ($R = a + b \cdot D^c$). The three models with an inverse D relationship were tested also without the constant ($a = 0$), on the assumption that at very large distances the dispersal rate would necessarily approach 0. The inverse square-root model, without the constant term, provided the best fit to the observed dispersal rates, with a regression equation of $R = 0.0275/(\sqrt{D})$, ($SE(b) = 0.0051$; $P < 0.00001$, $R^2 = 0.1845$). The more flexible model that also fitted the exponent yielded the same relationship ($b = 0.0275$, $c = -0.50$, $R^2 = 0.1845$), indicating that no other exponent is a better fit than the inverse square-root. The plot of data points and the fitted line is shown below.

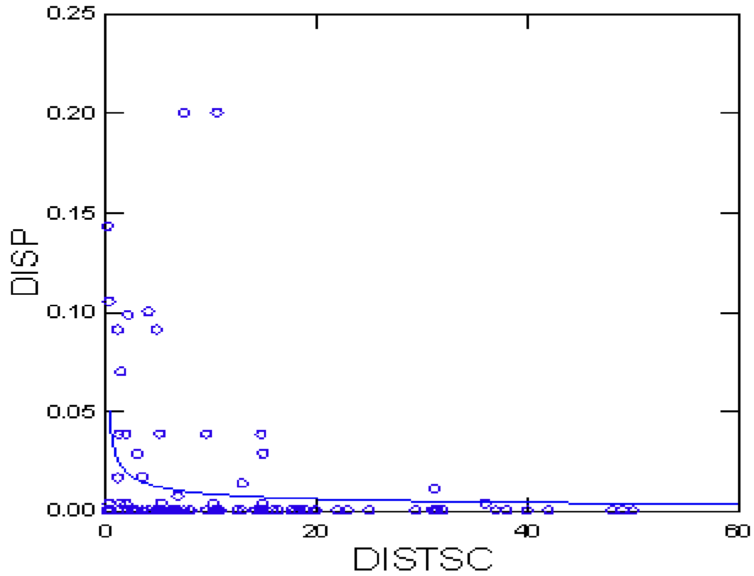

Figure 45. Curve describing the relationship between pairwise distance (DISTSC, in km) and annual dispersal rate of Helpers (DISP), based on data points for S and C Mainland populations

This curve is very similar to relationship of genetic identity-by-descent to distance reported in Aguillon et al. (2017) and is consistent with the conclusion of that study that the genetic patterns were as expected if there is isolation-by-distance.

The large scatter around the line is not surprising, because factors other than distance will influence dispersal rates, and because the dispersal data were based on only a few dispersal events (ranging from 1 to 13) from each population, and a total of 54 observed dispersals out of 835 jay-years of banded helpers. For the PVA metapopulation models, the annual probability of dispersal by a helper to each other local population was the predicted dispersal rate for the pairwise distance, using the inverse square-root relationship above. Rates 3x, 5x, and 10x of the predicted rates were also tested in order to examine both the sensitivity of the population dynamics to dispersal rates and the effectiveness of management strategies that increased dispersal via greater connectivity of habitat or translocation of jays.

Too few data exist on dispersal for the North Mainland and KSC/MINWR metapopulations to permit statistical analysis like the above. It might be expected that dispersal between N Mainland populations would be different than among similarly distant SC Mainland populations, because the N Mainland populations are generally much smaller, in more limited habitat, with fewer nearby populations (Breininger 1999). Very few (<5) banded jays in the KSC/MINWR metapopulation have been observed to disperse between the 4 local populations, and it is likely that between-population dispersal between the KSC/MINWR populations is lower than between mainland sites. Lacking data on dispersal rates in the N Mainland and KSC/MINWR metapopulations, we tested models that used the dispersal-distance relationship determined from the SC Mainland metapopulation, with the same range of multipliers for testing alternative possible rates.

The pairwise distances between the four local populations in the KSC/MINWR metapopulation range from 2 to 27 km, which leads to estimates of annual dispersal rates of helpers (based on the above curve) of 1.9% to

0.5%. For the SC Mainland metapopulation, the range of pairwise distances of 0.2 to 59 km leads to estimated dispersal rates of 6.2% to 0.4%. For the N Mainland metapopulation, the range of pairwise distances of 1.3 to 33 km leads to estimated dispersal rates of 2.4% to 0.5%.

There have been no observed dispersal events of banded jays moving between the three metapopulations, and it is likely that any such natural dispersal is so infrequent as to be unimportant to population dynamics. (Models that examine possible translocation management scenarios use the Supplementation option in Vortex to add some birds from outside the system.)

Validation of the FSJ PVA model

Vortex has been extensively tested as it has evolved over the past three decades, and it has been confirmed to produce correct population projections from the birth and death rates, variability in rates, and trends in rates. From the field studies of D. Breininger and others, we have estimates not only of the mean demographic rates, but also the differences in those rates between different habitat quality ("Strong", "Weak", and "Sink" territories in our model) and as functions of helper vs breeder status (for survival rates) and the number of helpers in a breeding group (for components of reproductive success). However, the model of the FSJ requires also a complex set of relationships to be inserted into Vortex in order to describe the probability of helper to breeder transitions, the dependency of this transition of status on territory availability and breeding opportunity, and the probability that a dispersing jay seeking breeding opportunities will locate the best available habitat. Given the complexity of the FSJ PVA model – which is necessary in order to represent the complex ways in which the FSJ social system influences population dynamics – it is important to validate that the model is producing projections that reflect accurately the structure of the populations that we are modeling.

We conducted model validation by comparing several key outputs of simulation models to data obtained from the field surveys. Model representations of the FSJ social system can be checked against the percent of adult jays that are breeders vs helpers; and from the ratio of 1st year juveniles to adult birds. Model representations of habitat selection by scrub-jays can be checked by comparing the percentages of breeding groups using Strong, Weak, and Sink habitat, and the percent of each type of habitat that is occupied.

The most complete data on these aspects of population structure are available for the four populations within the KSC/MINWR metapopulation, and good data are available also for most of the larger populations in the South Mainland metapopulation. The proportions of breeders vs helpers and juveniles vs adults varies among local populations and across years, and much of that variation is likely due to random and short-term fluctuations. Therefore, for model validation we compared model estimates to mean values across local populations and over time. Within the PVA model projections as well, the population structure varies over time, first as the initial conditions of the model shift to more equilibrium levels, and then as the population either grows or declines, and occupies more or less of the optimal and suboptimal habitat. Because the population structure and habitat use changes with density of breeding groups in each local population, for the tests of model validation we examined scenarios in which the populations were initialized with all potential habitat occupied, and then compared field data to the model projections for the populations after the numbers of breeding groups in the model dropped to the observed current population size (year 10 for KSC/MINWR; year 12 for S Mainland).

Table 6 compares the population structure between observed census data and the model predictions, for the two larger metapopulations and for data combined across both. We ran the metapopulation scenarios that set the dispersal rates by using the distance-dispersal function (see above). We compared results for simulations with two values of the preference (or accessibility) parameter that describes how effectively jays forming new breeding groups access the best of the available habitat in their local population.

We do not expect a perfect match between field data and the model results, because of the variability between sites and over time, and because the time of census each year in the field (in July, the approximate time of nutritional independence of juveniles) does not match the time of censuses in the PVA model (just before the breeding season). Even so, the data show reasonable correspondence between field census and model measures, giving us confidence that the PVA model is representing these aspects of the FSJ population dynamics adequately. The PVA model is projecting that a larger percent of the jays are breeders and fewer are helpers than has been tallied in the field surveys. This might be a consequence at least partly of the fact that the census in the model is taken at the end of the year for each cohort, so the proportion of helpers will have declined due to the higher annual mortality of helpers vs breeders. It is also possible that in our model we have too high of a transition rate from helper to breeder status. A consequence of that would be that the model would be a little over-optimistic with respect to the projected rates of population growth, and this might explain also the small over-estimate of the proportion of juveniles in the population. It will be useful if future field studies and statistical analyses can better define the determinants of helper to breeder transition, after which we can adjust this aspect of the PVA model as necessary and then re-examine the projected percentages of breeders, helpers, and juveniles. The value of the Pref parameter had very little effect the proportions of breeders, helpers, and juveniles in the model, as would be expected since that model parameter influences habitat choice rather than breeding status transition.

Table 6. Comparison of observed percentages of breeders, helpers, and juveniles to population structure generated by the PVA models.

Metapopulation	**Observed or Model**	**%Breeders**	**%Helpers**	**%Juveniles**
KSC/MINWR	Observed	63	22	15
	Model: Pref=6	68	13	20
	Model: Pref=4	67	14	19
S Mainland	Observed	61	20	19
	Model: Pref=6	70	11	19
	Model: Pref=4	70	10	20
KSC + S Mainland	Observed	62	21	17
	Model: Pref=6	68	11	19
	Model: Pref=4	70	10	19

Comparison of PVA model results with multi-state capture-recapture models

Recently updated analyses by D Breininger and colleagues at KSC of capture-recapture data using multistate models provide more detailed descriptions of average population structure and determinants of that structure. They reported mean family sizes of 2.7, lower than reported for FSJs in the stable, optimal habitat of Archbold Biological Station. Mean family size in the PVA model varies over time, as the population structure first shifts from initial assumed conditions to a more stable structure, and then as the populations decline over later years in the simulation. However, in our validation scenario, mean family size stabilizes by year 15 to be approximately 2.7, in accord with the field data.

A non-breeder-to-breeder transition probability of 0.46 was estimated from multi-state modeling (Breininger et al. unpublished manuscript). Transitions from helper to breeder status might be influenced by opportunities for jays to replace breeders that die. Such responses to breeding opportunities might add stability or resilience to the population, with the helpers forming a readily available pool for replacement of breeders that die. The multistate capture-recapture models show that breeder mortality is a significant determinant of helper to breeder transition probability. Other factors, such as family size and population density had weaker and less consistent effects in those models. The observed relationship of transition probability and breeder mortality was approximately linear, with a slope of approximately 1.3.

In the PVA model, a functional relationship of helper to breeder transition to breeder mortality will occur because helpers are modeled to transition to breeder status whenever they are needed to replace a breeder that dies. To compare the functional form and strength of the relationship generated by the model to that observed in the KSC/MINWR populations, we created a scenario for the KSC/MINWR metapopulation in which we tallied (as state variables) each year the proportion of female and male helpers that transition to breeder status and the mortality rate of female and male breeders. The tallies were done separately for each of the four local populations and separately each year. We examined the relationships across years 5 through 20, to avoid effects of initial conditions in the first few years, and patterns that might change after simulated populations become much smaller in size after a few decades. The relationship of helper to breeder transition probability (HtoBr) to breeder mortality (BM) during the prior year fit a linear regression well, with the relationship of HtoBr = 0.45 + 0.97 * BM for females and 0.32+1.35*BM for males – reasonably close to the observed relationship described in the above paragraph. Very similar regressions were obtained when year and local population were removed as cofactors. As with the other validation tests, we do not expect a perfect match between field trends and model results, because the relationships between variables can change across years, vary among levels of habitat quality, and vary with population density. Even so, the approximate concordance with observed helper to breeder transition probabilities helps to confirm that the PVA reasonably well represents the actual population dynamics.

Habitat occupancy

We next compared the percent of pairs occupying Strong, Weak, and Sink habitat in the model projections and the field observations. This comparison might be less reliable as a test of the model, however, because the proportion of pairs in each type of habitat will depend on the relative abundance of potential territories of each type, the density of occupancy of the potential territories, and the constancy of habitat quality in each territory. For example, if the local potential habitat is nearly saturated with breeding groups, then the ratio of occupancy of each of the three levels will necessarily approach the ratio of habitat quality in potential territories. Conversely, when a local population is at low density relative to the total potential territories, then most of the jays can exploit the Strong habitat and very few would be pushed into Sink habitat. Moreover, if the population is currently in decline or growing, or if habitat quality is changing, the occupancy of each level of habitat would often not be at the long-term equilibrium value that might be projected in the PVA model. However, to get a sense of whether the PVA model was simulating well the occupancy of Strong, Weak, and Sink territories, we compared the field census data to model predictions at a year in the model in which the overall number of breeding groups matched the current field census data.

In the following table, the top number in each cell gives the percent of breeding pairs in Strong, Weak, or Sink territories, and the second number in each cell gives the percent of the potential territories of that quality that are occupied by breeding groups. Table 7 shows that in our models, typically a higher proportion of the pairs occupied Strong habitat than has been observed in field censuses, and a lower proportion occupied Sink habitat. Similarly, more of the potential Strong territories, and fewer of the Sink potential territories, are occupied in the model than observed in the field. Models with the lower Pref parameter, specifying that jays less consistently settle in the best available habitat when setting up new breeding groups, produce patterns of habitat use that are closer to the field data, but still predict more in Strong and fewer in Weak than has been observed. The higher occupancy of potential territories classified as Sink in the census data as compared to the model projections might arise from pairs remaining in their territories even if the territory quality degrades over years, or it might reflect that our ability to identify the characteristics that indicate

Table 7. Comparison of distribution of breeding groups in Strong, Weak, and Sink habitat observed in the field vs generated by the PVA model.

Metapopulation	**Observed or Model**	**%Breeders in Strong** **Strong %Occupancy**	**%Breeders in Weak** **Weak %Occupancy**	**%Breeders in Sink** **Sink %Occupancy**
KSC/MINWR	Observed	47	10	43
		92	31	24
	Model: Pref=6	53	25	22
		100	80	13
	Model: Pref=4	50	23	27
		96	73	15
S Mainland	Observed	47	15	38
		65	61	31
	Model: Pref=6	68	15	17
		95	58	15
	Model: Pref=4	64	15	21
		88	58	17
KSC + S Mainland	Observed	47	11	42
		82	38	26
	Model: Pref=6	57	22	21
		100	75	13
	Model: Pref=4	54	21	25
		93	70	15

optimal habitat do not perfectly match up with the habitat characteristics that attract the jays, or it might arise from the jays seeking breeding territories being less able to locate and access the best territories in the populations than we have assumed in the models. These factors would lead to our model predictions for the metapopulations being optimistic, because more of the jays are currently inhabiting Sink habitat where demographic rates have been documented to be lower. These possibilities can be explored further as we obtain more data on dispersal patterns and after we develop linked habitat-population projection models.

Overall, the above tests of model predictions against field census data indicate that the current PVA model is a plausible model of the FSJ population dynamics, but it perhaps is biased toward projecting better population viability than is occurring with the current habitat quality and spatial distribution. This should be kept in mind when using the PVA results for planning conservation and management measures. Management plans should use a precautionary approach (with extra margin for error), and actual consequences of management actions should be monitored closely so that management can be adapted as needed.

Metapopulation viability

KSC/MINWR

Figure 46 shows the projected population size for the KSC/MINWR metapopulation with various levels of connectivity among local populations. Connectivity is quantified by the percent of helpers that disperse from any given population to another given population each year. Even with high connectivity, the metapopulation is projected to decline to occupy mostly Strong habitat (and not all Strong habitat, which amounts to 138 territories) in the long term. With less connectivity, the metapopulation is projected to decline to lower levels. The projection when dispersal rates are set by the dispersal-distance relationship is also displayed on the graph, but it almost precisely overlaps the 1% dispersal line, as expected because that is the approximate mean pairwise dispersal estimated from the relationship.

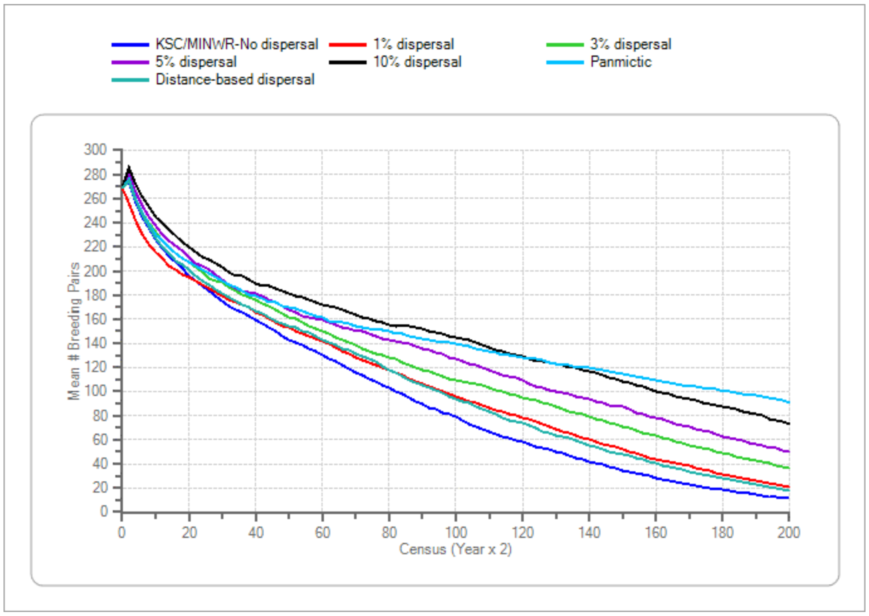

Figure 46. Projected population size of the KSC/MINWR metapopulation, with various dispersal rates.

However, the dispersal rates between local populations is only very imprecisely estimated, and it might change substantially with changing environmental conditions and habitat management. Figure 47 shows the projected population sizes with dispersal rates varying from 0 (totally isolated local populations) to 1x, 3x, 5x, or 10x the estimated current rates, or (as an extreme comparison) complete integration of the populations into one fully mixed (panmictic) population. The panmictic scenario shows a short-term depression in population size relative to 10x estimated dispersal, because some jays initially move from more optimal habitat to populations with less optimal habitat. However, in the long-term, the scenario with the highest rates of dispersal approximates a panmictic population. Notably, even a 3-fold or 5-fold increase in dispersal above the estimated current rates do not result in a metapopulation as robust as one with more complete connectivity. This suggests that dispersal between local populations is currently much lower than what would allow for maximal metapopulation viability. With higher rates of dispersal than currently estimated, the local populations would be mutually reinforcing demographically (e.g., providing resilience to local declines) and genetically (reducing or reversing accumulated inbreeding).

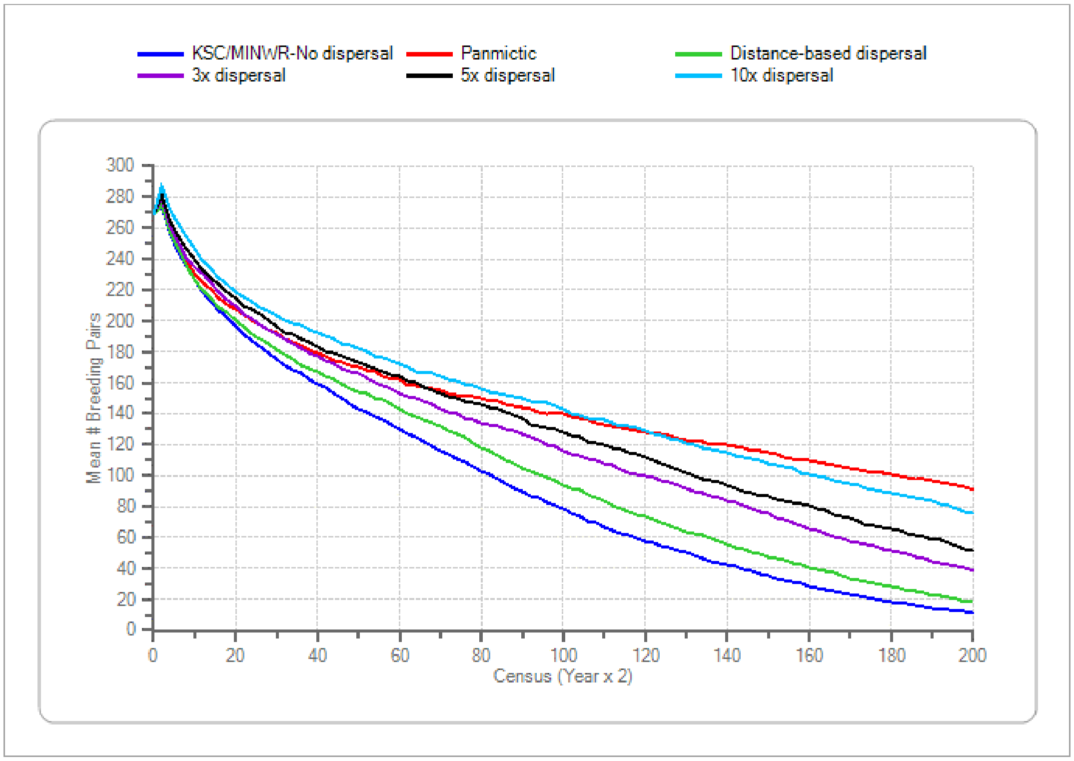

Figure 47. Projected population size of the KSC/MINWR metapopulation with dispersal at levels up to 10-fold above estimates based on distance, or with complete panmixia of the metapopulation.

The next graph (Fig. 48) shows the probability that the metapopulation will persist (with at least one breeding pair) under the various levels of connectivity. If dispersal is 10-fold higher than estimated currently, and if habitat remains as it is, then the metapopulation has more than a 90% chance of persisting 100 years into the future. With lower dispersal rates, the accumulated inbreeding eventually leads to significant probabilities that the population will be extirpated. The subsequent graph (Fig. 49) shows that inbreeding has accumulated to about 0.05 to 0.10 when the extinction probability rises above about 10%. Such a level of inbreeding might be considered a critical indicator that a population is in genetic and demographic peril.

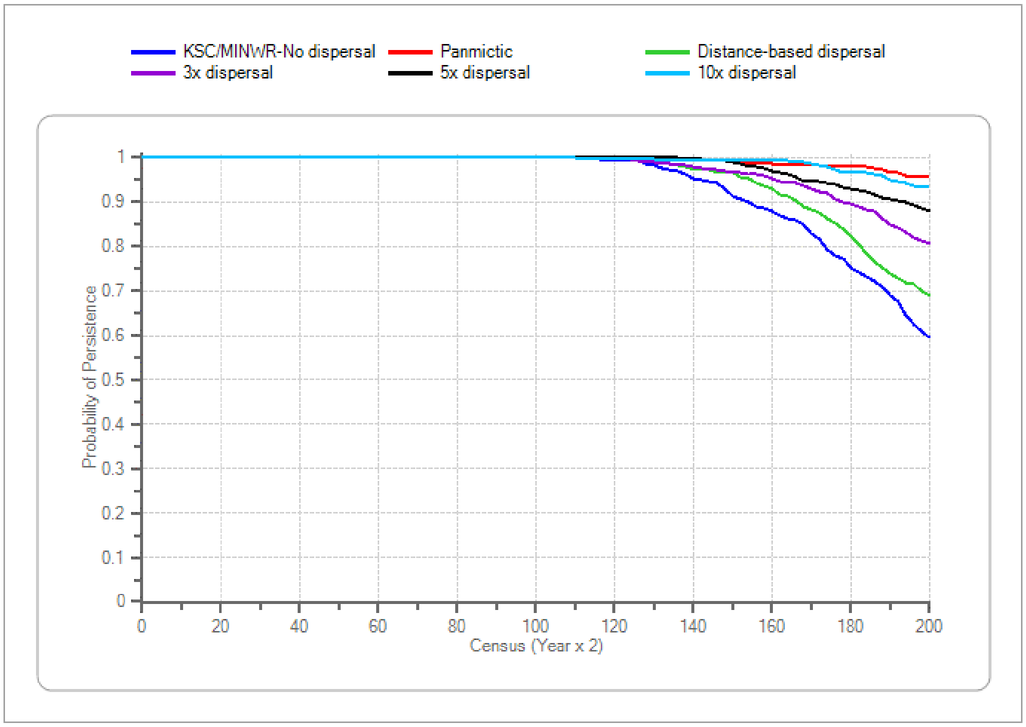

Figure 48. Probability of persistence of the KSC/MINWR metapopulation with dispersal at levels up to 10-fold above estimates based on distance, or complete mixing.

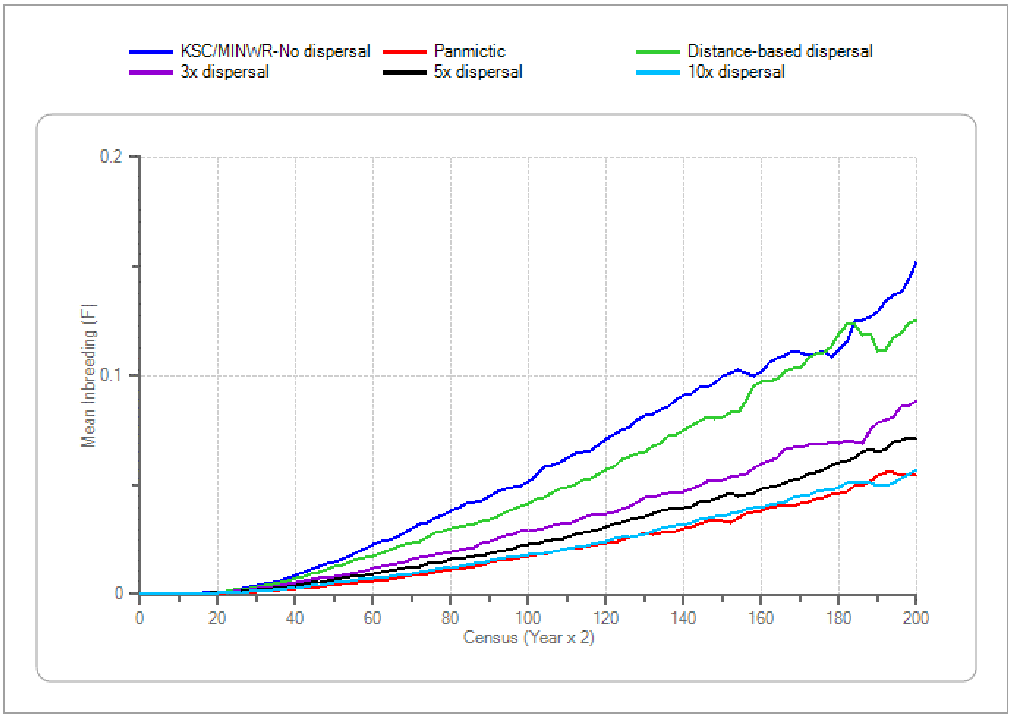

Figure 49. Accumulation of inbreeding in the KSC/MINWR metapopulation under various dispersal rates.

The accumulated inbreeding could be a result of unstable and declining populations, or it could be a cause, or both – in a feedback process. Figure 50 shows the mean population trajectory, with either the estimated dispersal or with complete connectivity, when inbreeding has the impact on fitness estimated by Chen et al. (2016) vs if inbreeding is assumed to have no effect on individual fitness. The comparisons show that the impact of inbreeding drives down the population size under the estimated dispersal, but also has a noticeable long-term negative impact on the KSC/MINWR metapopulation even if the four local populations were to be fully interconnected into one large population.

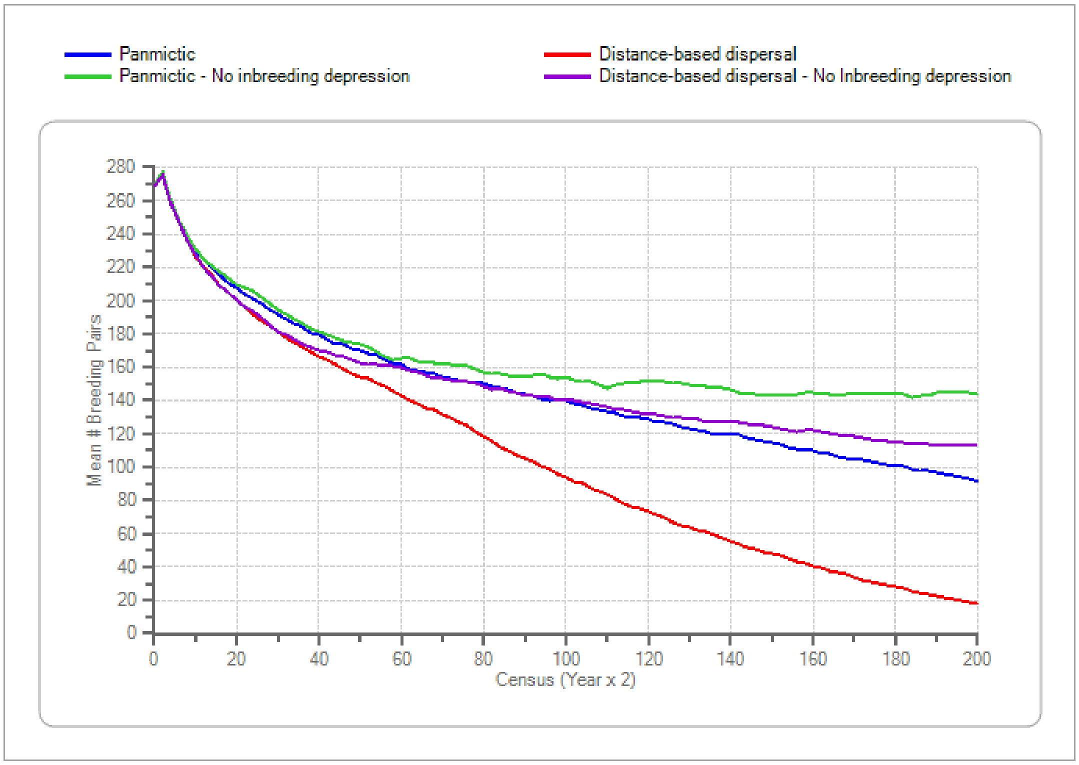

Figure 50. Projection population sizes of the KSC/MINWR metapopulation with estimated dispersal rates vs complete connectivity, and with vs without inbreeding effects included in the model.

Extinction is often defined (as is the case here) as the reduction of a population all the way down to no breeding pairs, it might be important also to document the probability that a metapopulation will decline below some size that is considered a threshold for an ecologically functioning population. Figure 51 shows the quasi-extinction curves – the probability that the metapopulation will fall below any given threshold – for the cases of various dispersal rates. For example, even with complete mixing of the local populations (red line), there is a 50% probability that the population will fall below N = 200, which would be about 75 breeding groups. With estimated rates of dispersal (green line), there is a 50% probability that the metapopulation will fall below N = 14, and a 14% chance it will fall below N = 100. Thus, the relatively low probabilities of complete extinction, as shown above in Figure 48, might be misleading. The metapopulation can be in serious decline long before the final extinction occurs. If ecological research and management goals can define a size that would be considered functionally extinct, such quasi-extinction curves for any given time period can be used to illustrate the risk of failing to sustain an ecologically functioning metapopulation.

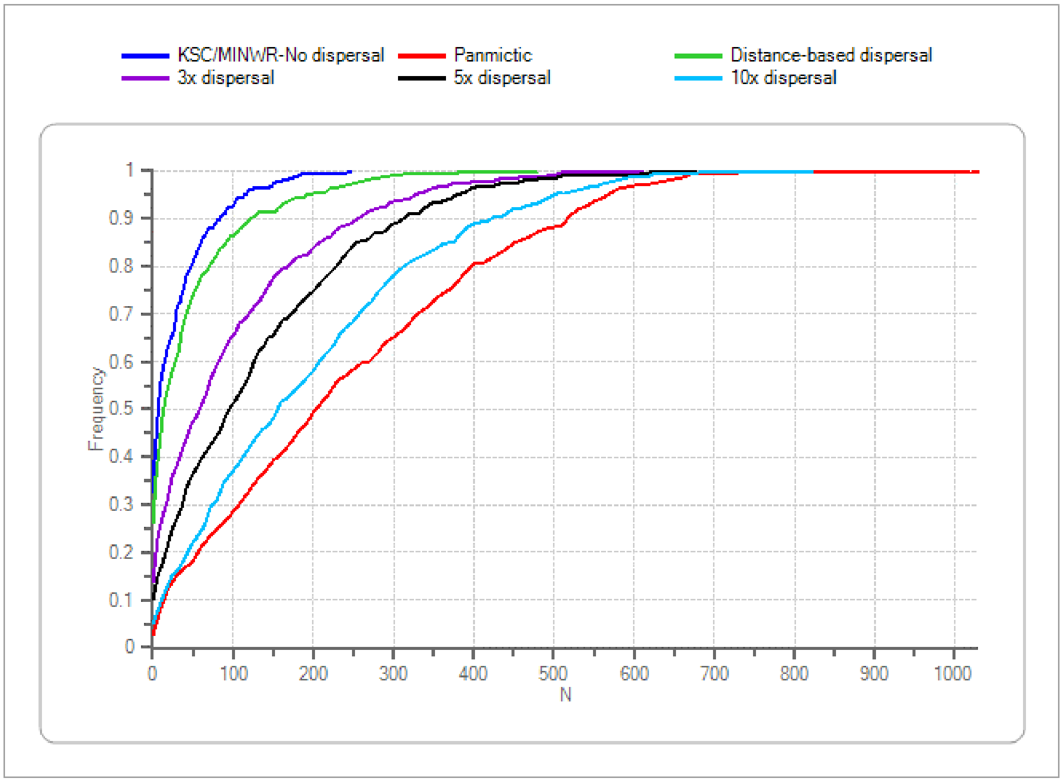

Figure 51. Quasi-extinction curves of the KSC/MINWR metapopulation with dispersal at levels up to 10-fold above estimates based on distance, or complete mixing. Note that these curves show the probability of the metapopulation falling below threshold sizes that are given as the total number of scrub-jays. This will be about 2.7x the number of breeding groups.

Figures 52 and 53 show the predicted mean trajectories and probabilities of extinction of the individual populations within the KSC/MINWR metapopulation, under the assumption of dispersal as estimated from distances between the local populations. These can be used as baseline projections when we examine management scenarios (below) that seek to improve the status of specific local populations. Although with high rates of dispersal, the overall KSC/MINWR metapopulation could have a low probability of extinction, and even with estimated dispersal rates the probability of metapopulation persistence is about 70% (see Fig. 48, above), none of the four largely isolated local populations is assured of persistence beyond about 50 years, and all have at least a 50% chance of extirpation within 100 years (Fig. 53).

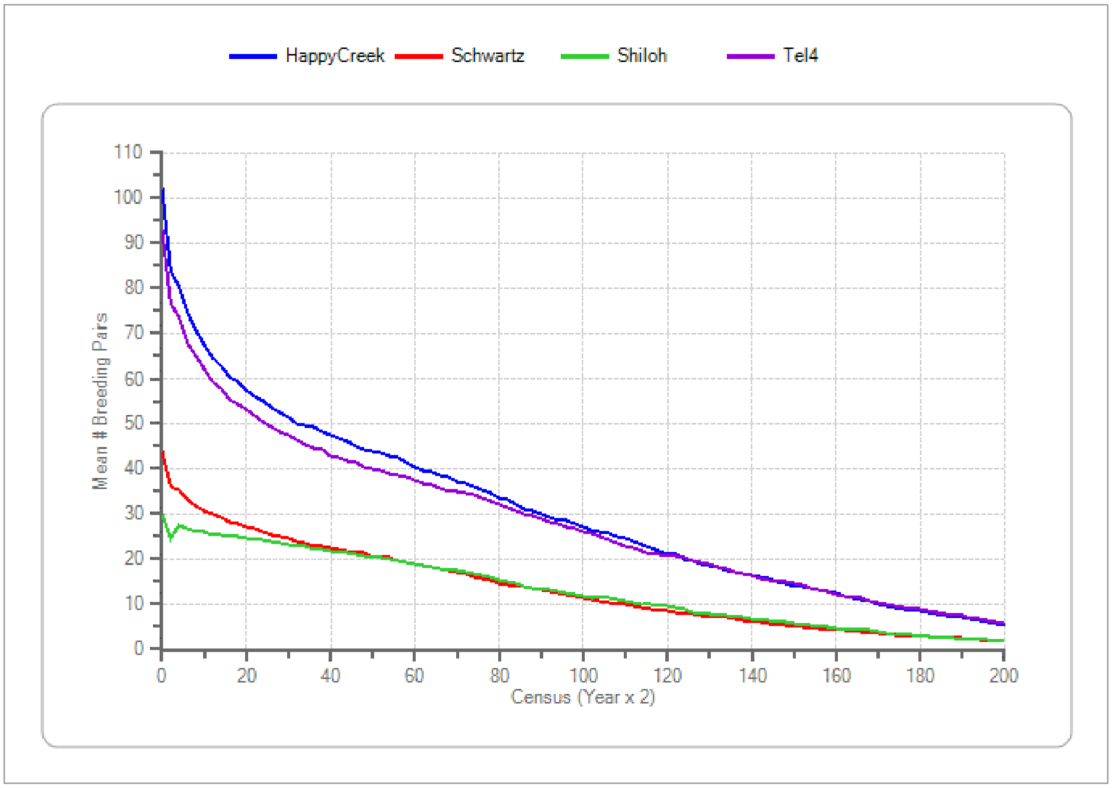

Figure 52. Projected sizes of the four local populations in the KSC/MINWR metapopulation.

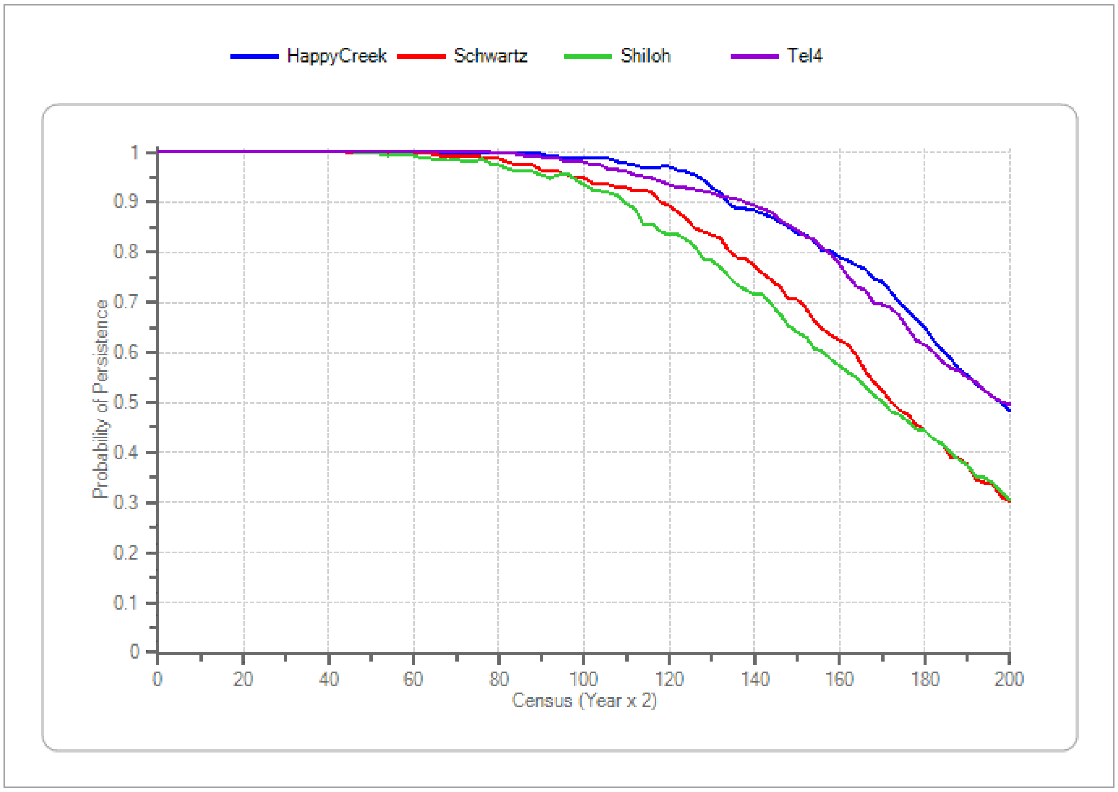

Figure 53. Probabilities of persistence for the local populations in the KSC/MINWR metapopulation.

CCSFS

We have not yet incorporated demographic rates from the Cape Canaveral Space Force Station (CCSFS) populations as such data were not collected according to the same protocols as the data collected on the KSC/MINWR and Mainland metapopulations. If we assume that the demographic rates in comparable habitats are similar, then only 13 out of 256 potential territories in CCSFS populations would be classified as Strong, 6 are Weak, and the remaining 237 are Sink habitats. Consequently, the CCSFS populations are projected to decline rapidly, regardless of interpopulation dispersal rates (Fig. 54), and the metapopulation is projected to go extinct in about 30 to 60 years (Fig. 55). Inbreeding rises rapidly (Fig. 56), but because of the rapid decline to small numbers, rather than as an initial cause of decline.

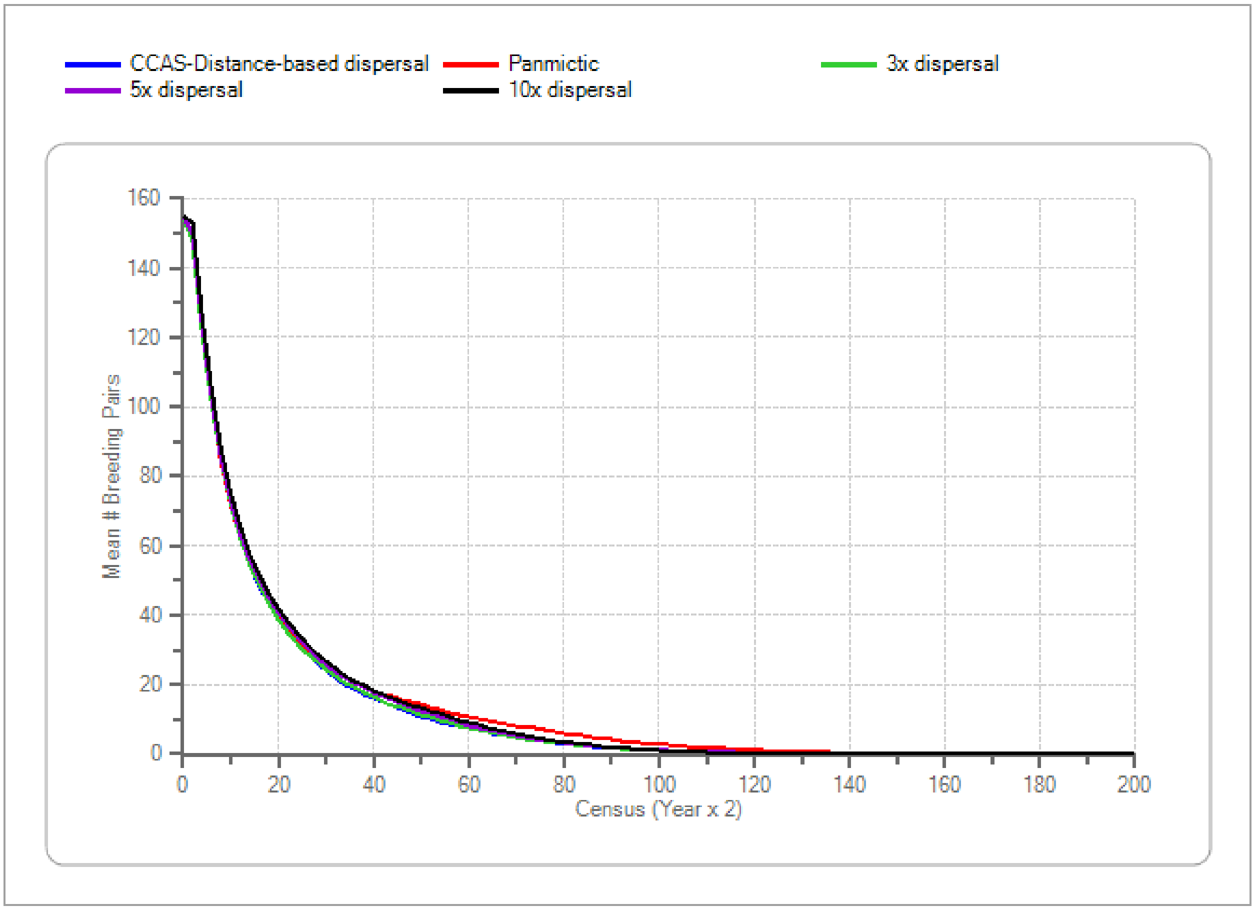

Figure 54. Projected population size of the CCSFS metapopulation with dispersal at levels up to 10-fold above estimates based on distances, or complete mixing.

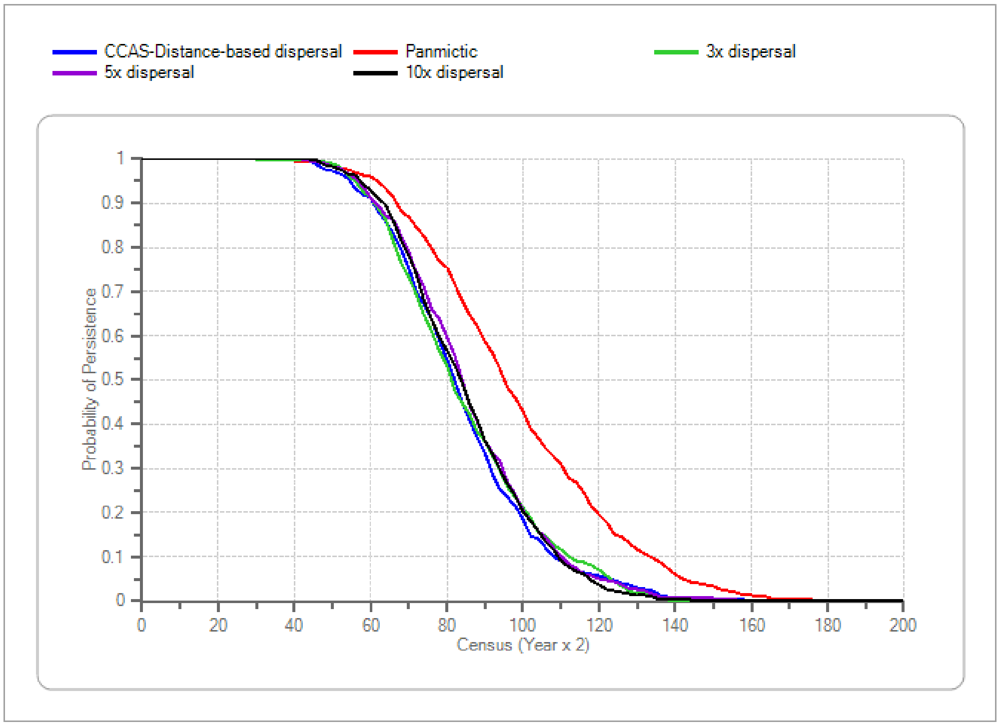

Figure 55. Probability of persistence of the CCSFS metapopulation with dispersal rates up to 10-fold above estimates based on distance, and for a completely panmictic population.

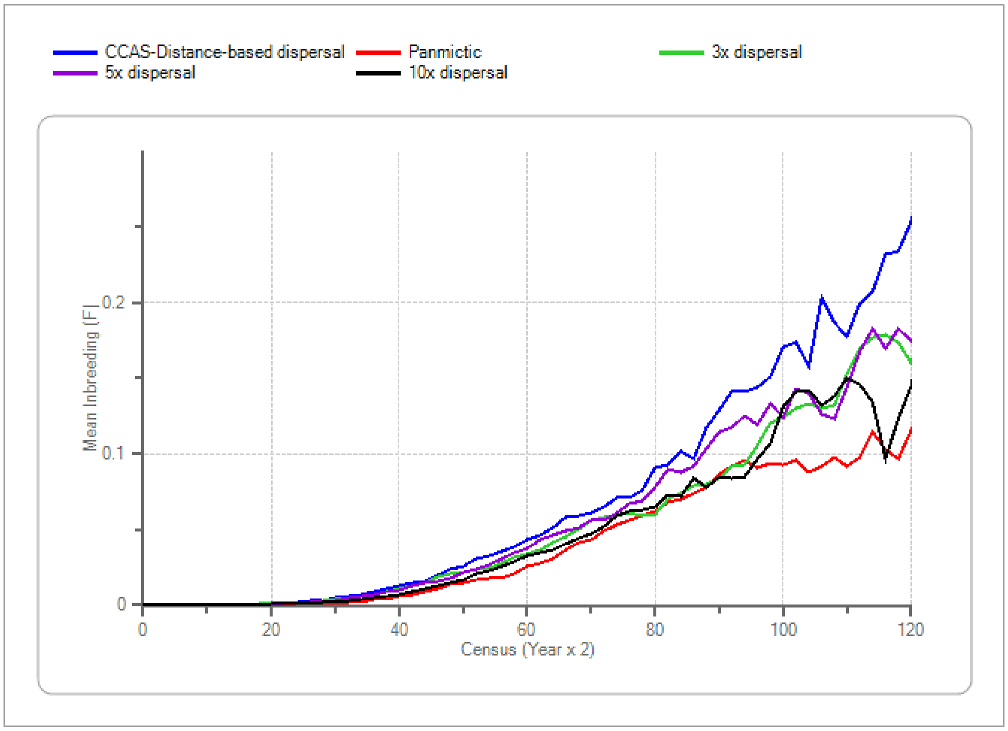

Figure 56. Accumulation of inbreeding in the CCSFS metapopulation with various dispersal rates. X-axis ends at year 60, because mean inbreeding after that is not meaningful because the populations were usually nearly or completely extinct.

Scenarios were modeled to test if the CCSFS populations might add to the stability of or be stabilized by dispersal to and from the KSC/MINWR populations. It was assumed that dispersal was possible between the Happy Creek population of KSC and the Beach-North population of CCSFS (with the rate determined by distance), but not to and from other populations of KSC to populations of CCSFS. For comparison, a model was also tested in which the entire KSC/MINWR plus CCSFS region was assumed to function as a completely interconnected (panmictic) population. Figure 57 shows the projected population sizes for these models, compared to models of only KSC/MINWR and only CCSFS. Combining the two regions – either with some dispersal between Happy Creek and Beach, or as a single panmictic population – is seen to provide a boost in population size over that of just KSC/MINWR on its own, but only until the CCSFS populations disappear. Over the long-term, the combined metapopulation harbors only a few more FSJs (Fig, 57), extinction rates are minimally slowed (Figure 58), and inbreeding accumulates almost as fast (Figure 59) compared to the KSC/MINWR metapopulation alone. For example, the middle set of lines on the graphs compare the population performance of KSC/MINWR alone (dark blue lines) to the combined KSC/MINWR plus CCSFS metapopulation (black lines) for the case of dispersal rates estimated from distances between populations.

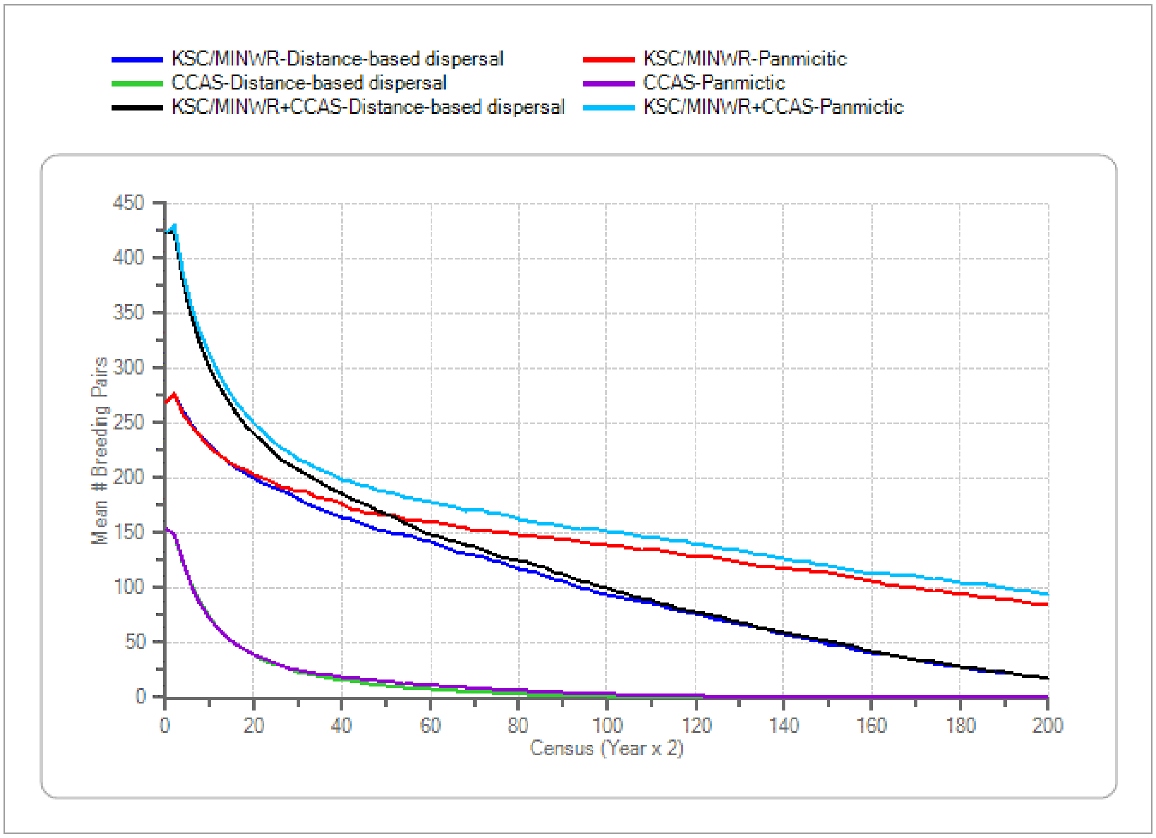

Figure 57. Projected population sizes for CCSFS populations alone (bottom two lines), KSC/MINWR populations alone (red and dark blue lines), and combined KSC/MINWR plus CCSFS populations (black and light blue lines), with either limited dispersal (bottom line of each pair) or completely panmictic populations (top line of each pair).

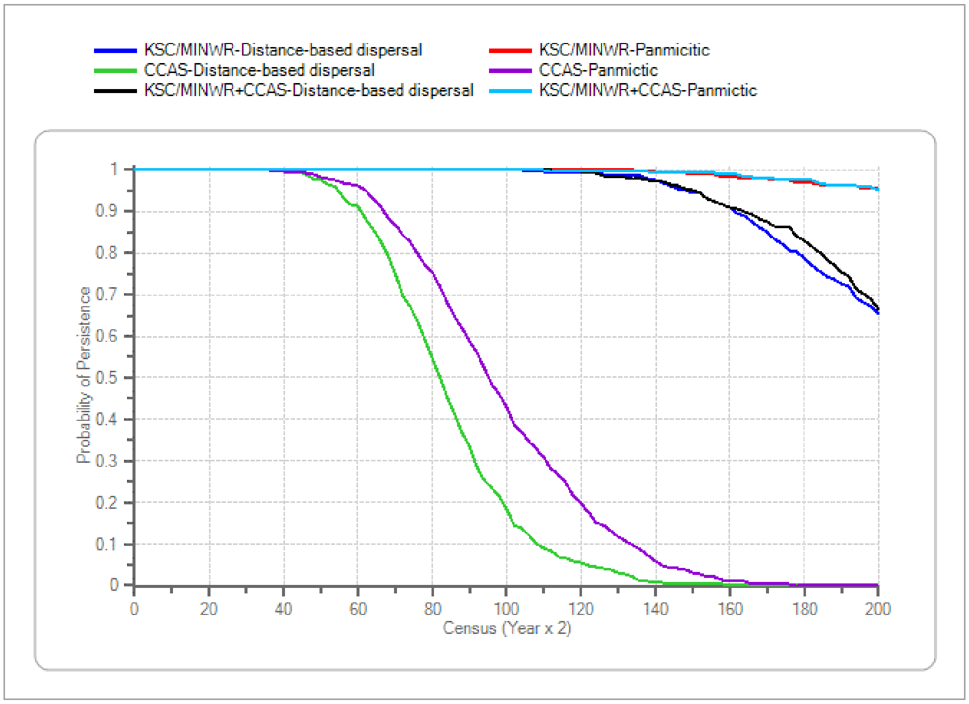

Figure 58. Probabilities of persistence of CCSFS populations alone, KSC/MINWR populations alone, and combined KSC/MINWR plus CCSFS populations, with either limited dispersal or completely panmictic populations.

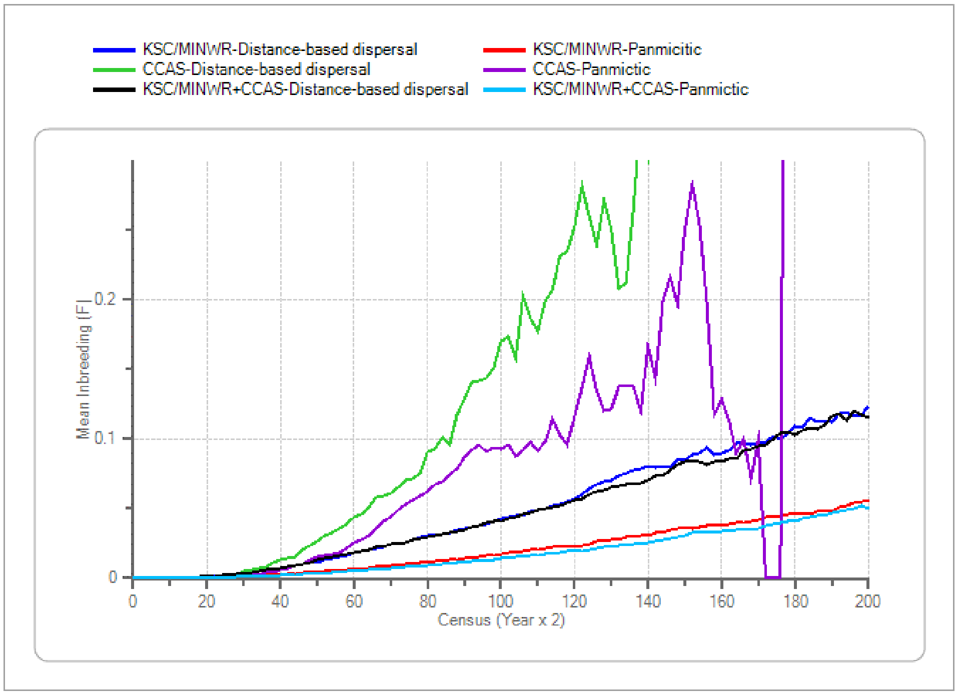

Figure 59. Accumulation of inbreeding in CCSFS populations alone (top two lines), KSC/MINWR populations alone, and combined KSC/MINWR plus CCSFS populations, with either limited dispersal or completely panmictic populations. Note that the values for CCSFS become meaningless after about year 70 because the metapopulation is usually extinct.

Although the model predicts that the CCSFS populations have too few potential territories in Strong habitat to sustain the populations (see Figures 54 and 55, above), it is possible that the CCSFS populations are sustained (or could be sustained) by immigration from KSC or elsewhere. Figure 60 compares population projections when the CCSFS populations are supplemented each year by 2, 4, 8, or 12 jays. Such supplementation prevents extinction of the CCSFS metapopulation, but the population size declines to fill not much more than the 13 Strong potential territories (with 2 immigrants per year), or those plus the 6 Weak potential territories and a few of the Sink territories. Thus, even regular immigration – which would prevent the accumulation of inbreeding and support the population demographically – is not projected to keep the CCSFS population from declining to about 10% to 20% of its current size.

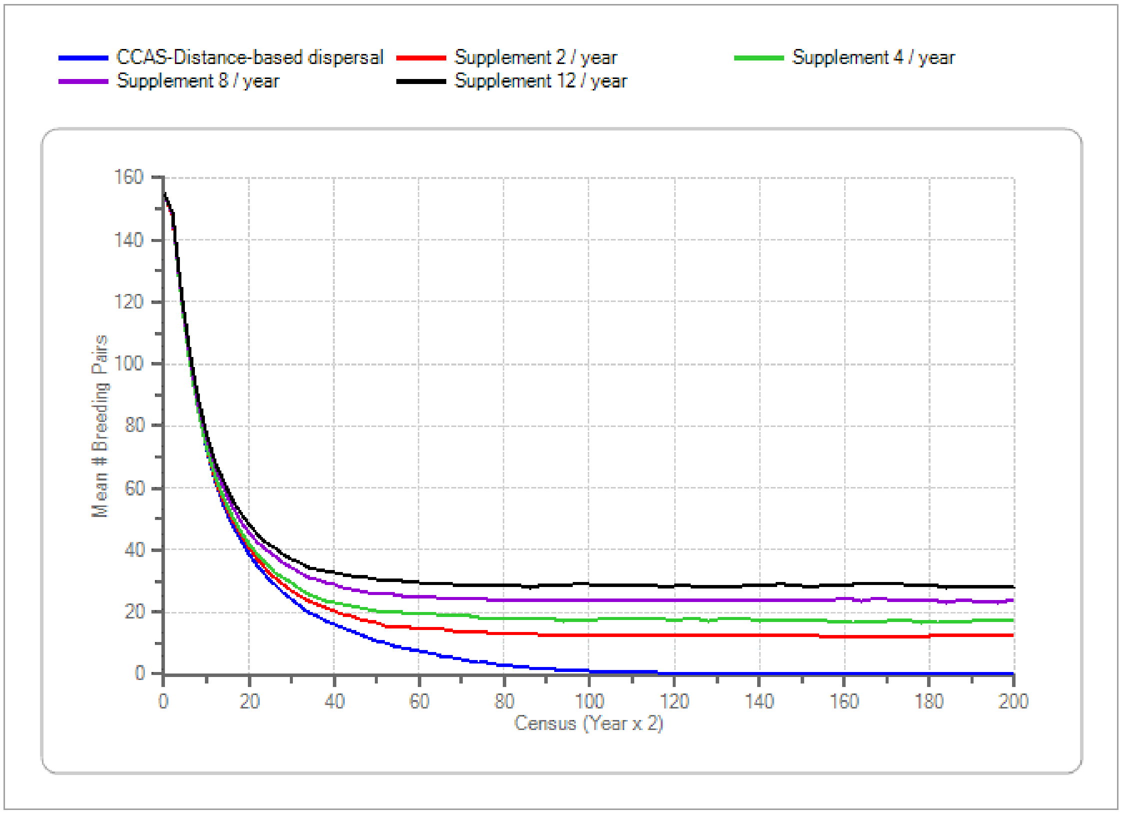

Figure 60. Projected population size of the CCSFS metapopulation if it is supported by 0, 2, 4, 8, or 12 immigrants per year (from bottom to top lines, respectively).

SC Mainland

The next two graphs show the mean projected population size for the SC Mainland metapopulation with various levels of connectivity among local populations – quantified either as a percent of helpers dispersing (Fig. 61) or as a factor of the dispersal rates estimated from the dispersal-distance function derived from the data on observed movements in this metapopulation (Fig. 62). If the metapopulation were to be fully interconnected (panmictic), the metapopulation is projected to decline to occupy mostly Strong habitat in the long term. The fragmentation of the metapopulation, even if there are high rates of dispersal of between local populations, leads to the metapopulation declining to much lower levels (and often to 0).

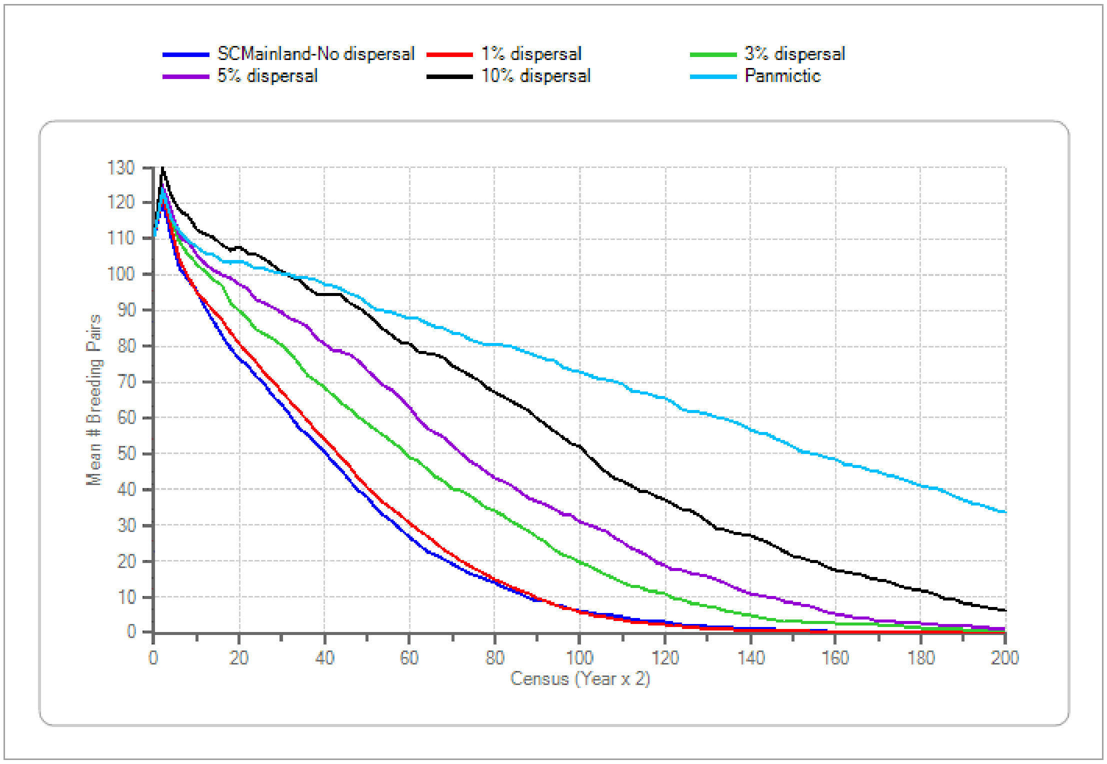

Figure 61. Projected size of the SC Mainland metapopulation, with various dispersal rates.

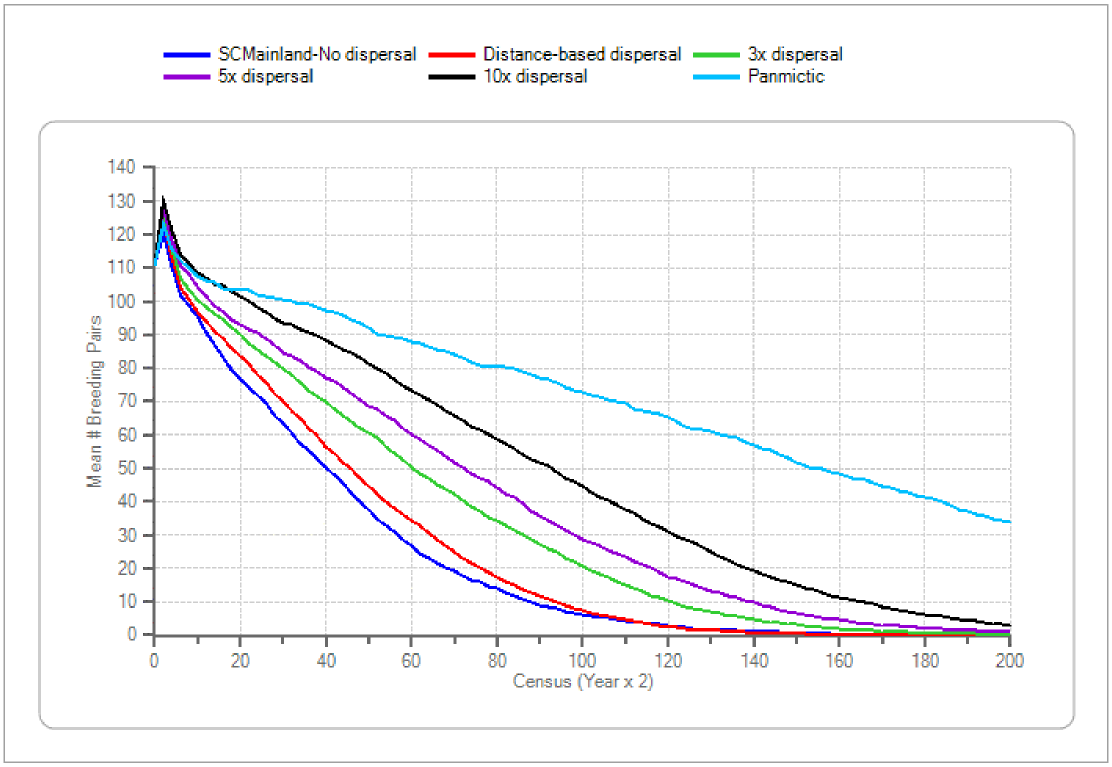

Figure 62. Projected population size of the SC Mainland metapopulation with dispersal at levels up to 10-fold above estimates based on inter-population distances, or complete mixing.

The next graph (Fig. 63) shows the probability that the metapopulation will persist under the various levels of connectivity. Even if dispersal is 10-fold higher than estimated currently (and if habitat remains as it is), then the metapopulation has an 80% chance of extinction within 100 years, with extinction being possible starting in about 40 years. With lower dispersal rates, the accumulated inbreeding (Fig. 64) causes even more rapid and more certain extinction. (Inbreeding is erratic after most iterations of a scenario are nearly extinct.)

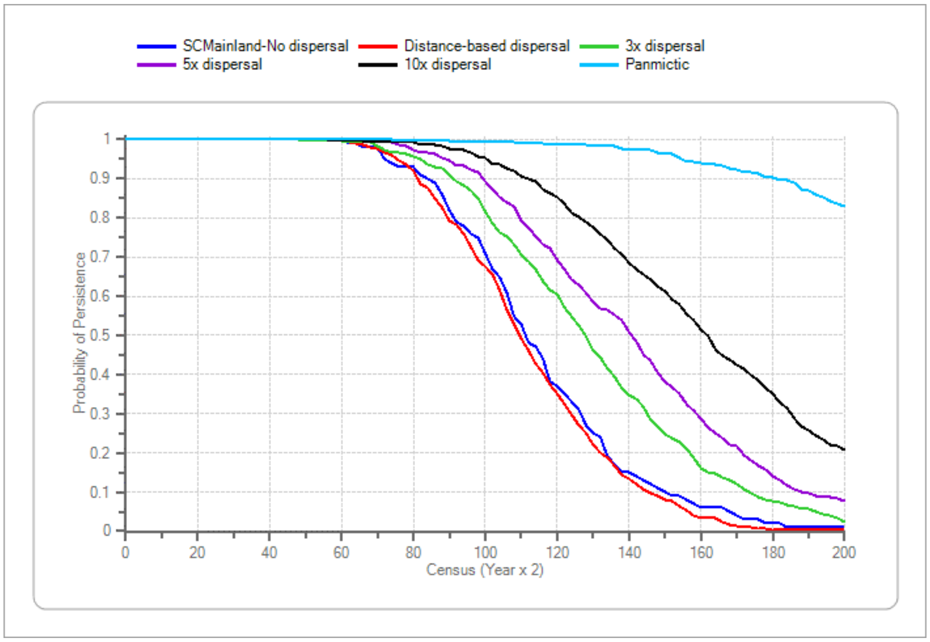

Figure 63. Probability of persistence of the SC Mainland metapopulation with dispersal at levels up to 10-fold above estimates based on inter-population distances, or complete mixing.

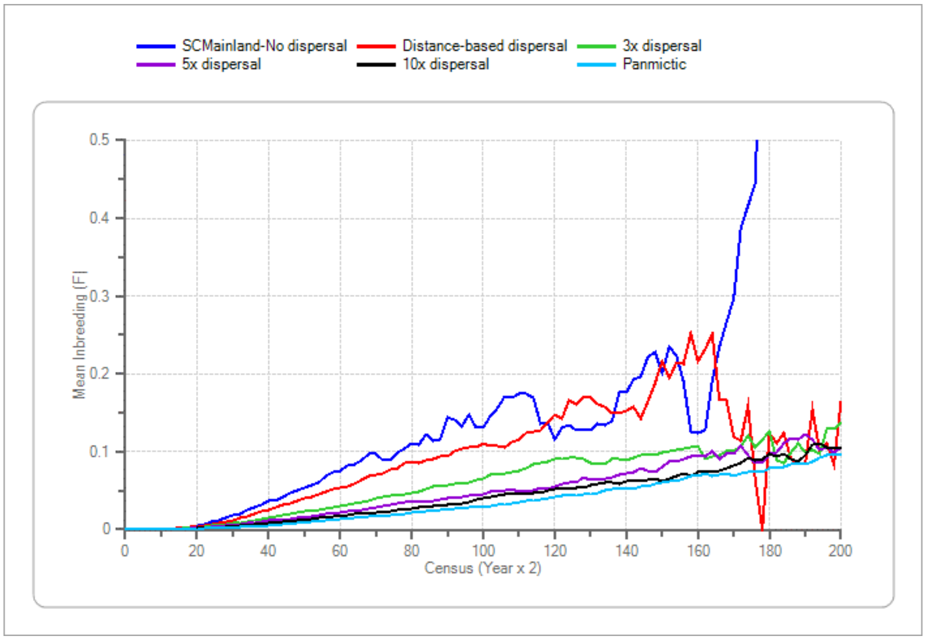

Figure 64. Accumulation of inbreeding in the SC Mainland metapopulation with dispersal at levels up to 10-fold above estimates based on inter-population distances, or complete mixing.

Figure 65 shows that if the SC Mainland populations were fully interconnected and if accumulated inbreeding had no impact on fitness (top line), then the metapopulation would stabilize at a size that is a little larger than the number that can be sustained in the available optimal habitat (80 Strong potential territories). However, the metapopulation is not large enough, overall, to avoid slow accumulation of inbreeding, resulting in ongoing population decline starting after about 20 years (red line). The high fragmentation of the metapopulation into about 14 local populations results in population decline, whether inbreeding depression impacts fitness, although the estimated effect of accumulated inbreeding accelerates the decline.

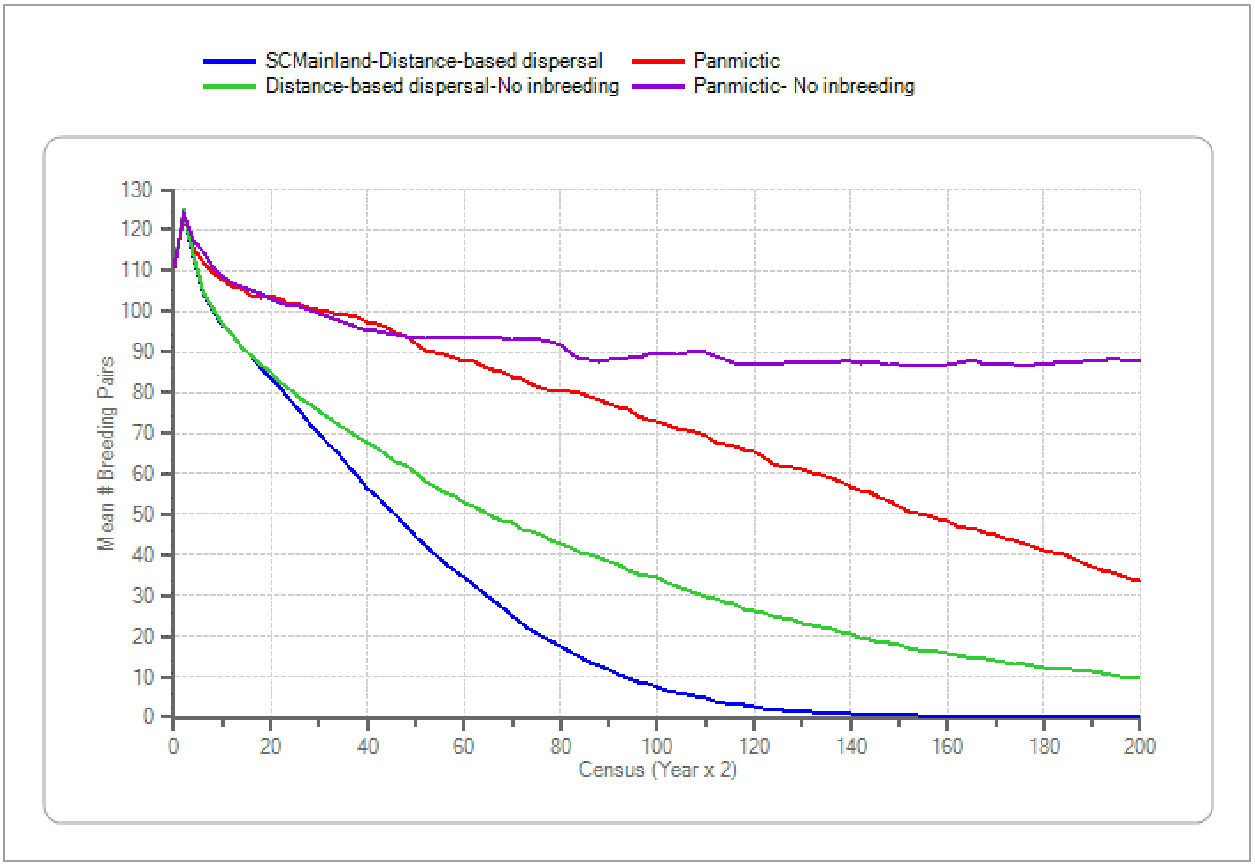

Figure 65. Projection population sizes of the SC Mainland metapopulation with estimated dispersal rates vs complete connectivity, and with vs without inbreeding effects included in the model.

Figure 66 shows the predicted trajectories of the individual populations within the SC Mainland metapopulation, under the currently estimated rates of dispersal between populations. All the local populations are projected to decline to extinction, although at varying rates due to different amounts of Strong habitat available for breeding groups. Carson Platt has the most potential Strong territories, and it has almost a 50% chance of persisting for 50 years. Viera currently has the most breeding groups, but 27 of its 28 potential territories are filled, with 17 out of 27 pairs in suboptimal habitat; it is therefore projected to decline in the next few years. Most of the local populations are projected to have a 50% probability of persistence for about 20 to 40 years (Fig. 67).

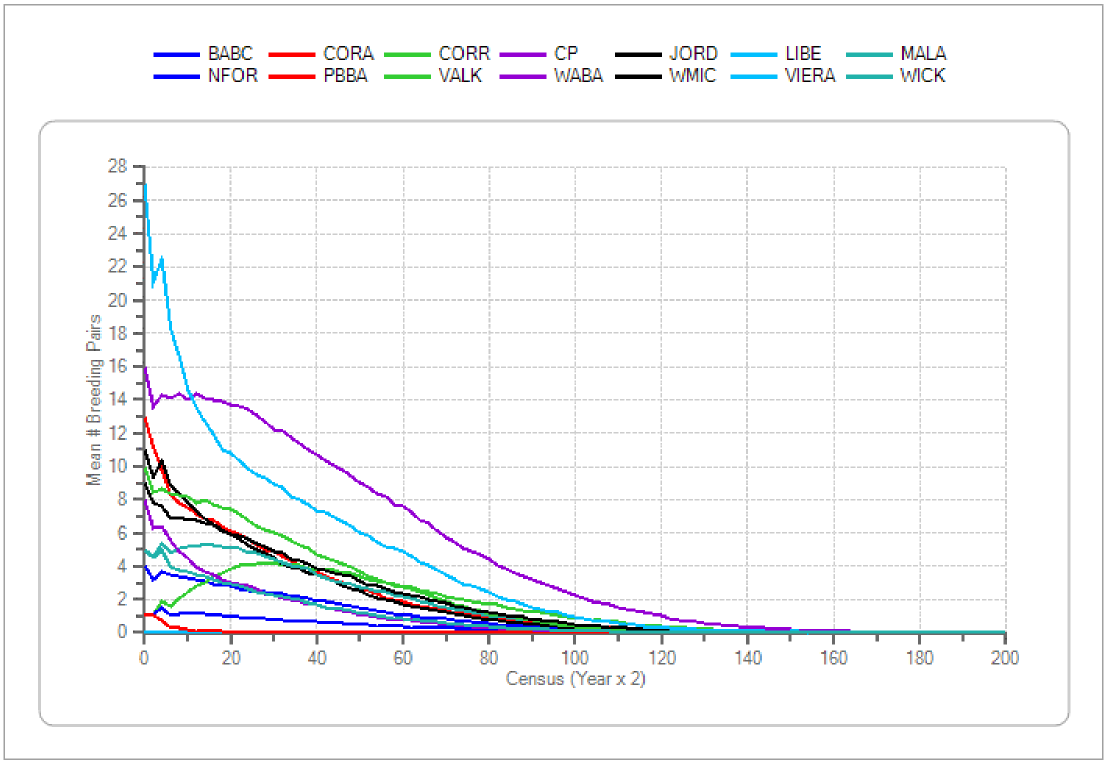

Figure 66. Projected sizes of the local populations that comprise the SC Mainland metapopulation.

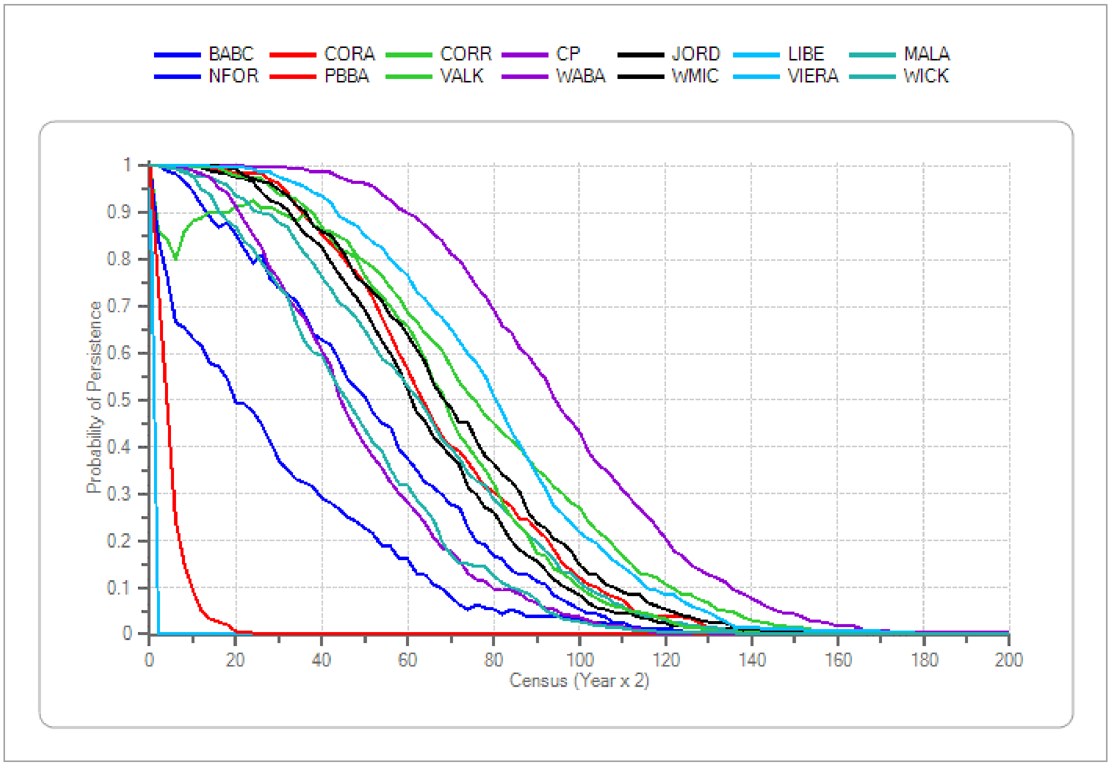

Figure 67. Probabilities of persistence for each of the local populations that comprise the SC Mainland metapopulation.

N Mainland

The next two graphs show the mean projected population size for the N Mainland metapopulation with various levels of connectivity among local populations – quantified either as a percent of helpers dispersing (Fig. 68) or as a factor of the dispersal rates estimated from the dispersal-distance function derived from the data on observed movements in the SC Mainland metapopulation (Fig. 69). Even if the N Mainland metapopulation were to be fully interconnected, the metapopulation is projected to decline to extinction. Increasing rates of dispersal among fragmented local populations provides (in itself) no benefit, because the very limited optimal habitat (only 10 Strong potential territories, out of a total of 113 potential territories, spread across 9 sites) is too little to sustain a breeding population.

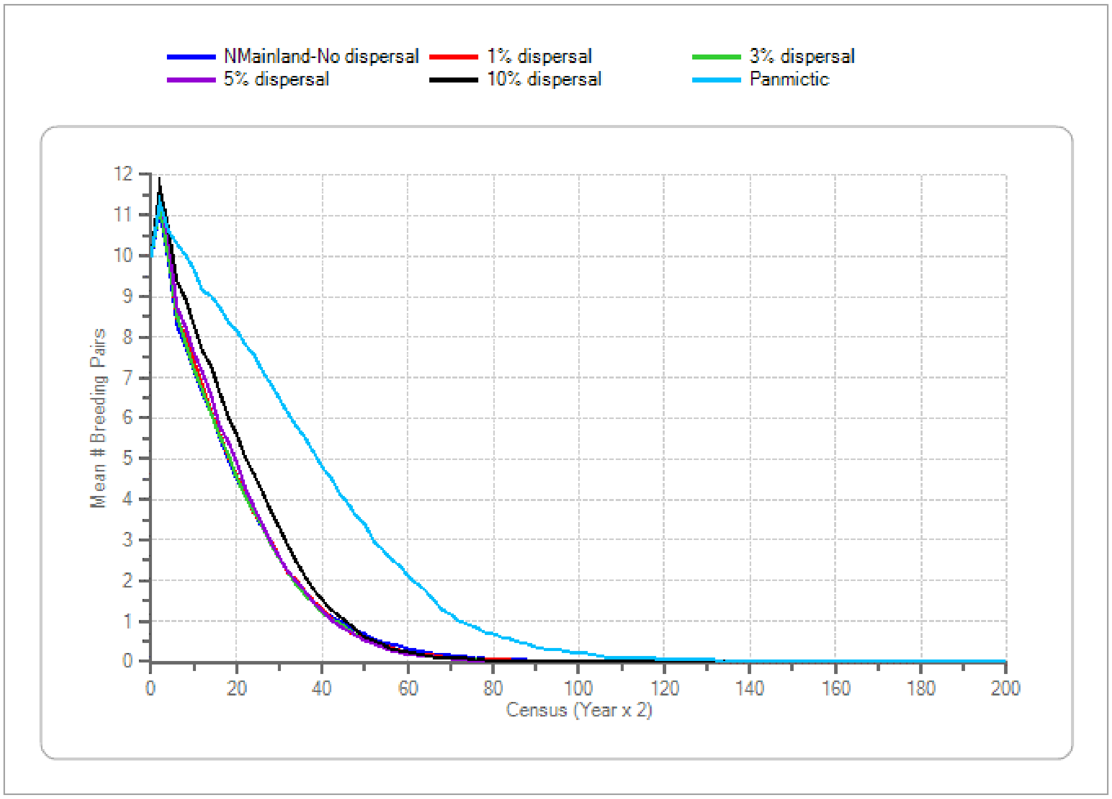

Figure 68. Projected population size of the N Mainland metapopulation, with various dispersal rates.

As shown in Figure 70, even under high rates of dispersal, the N Mainland metapopulation is projected to have a 50% probability of complete extinction within about 16 years. Extinction could be as soon as 10 years, or as late as about 30 years.

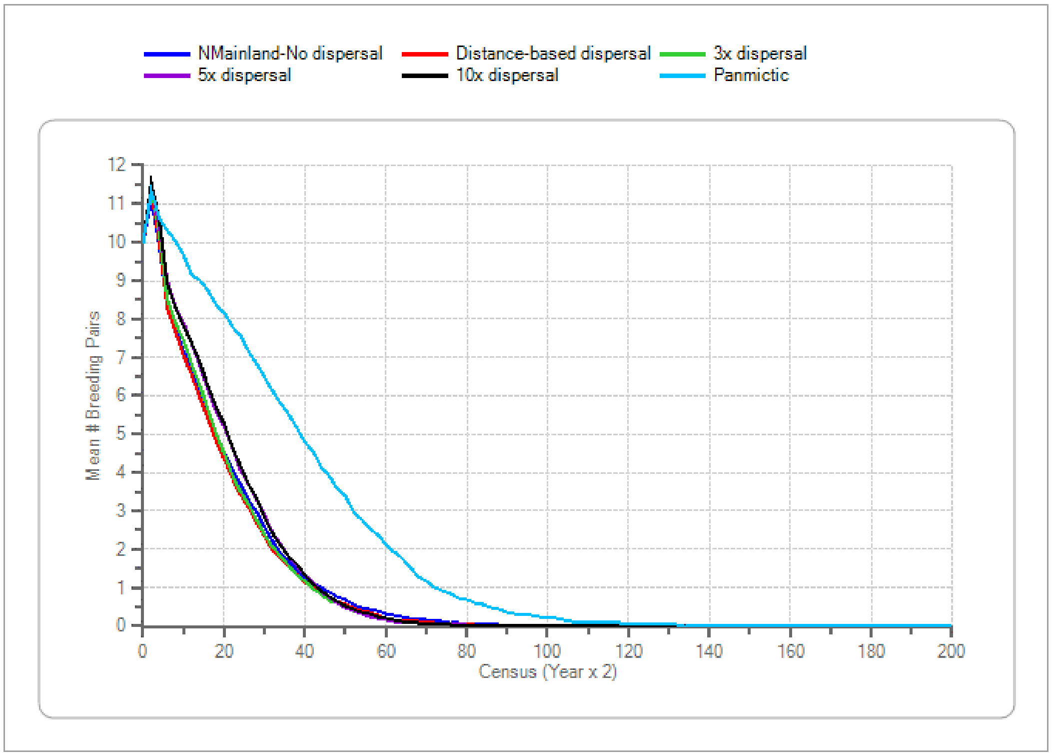

Figure 69. Projected population size of the N Mainland metapopulation with dispersal set at levels up to 10-fold above estimates, or complete mixing.

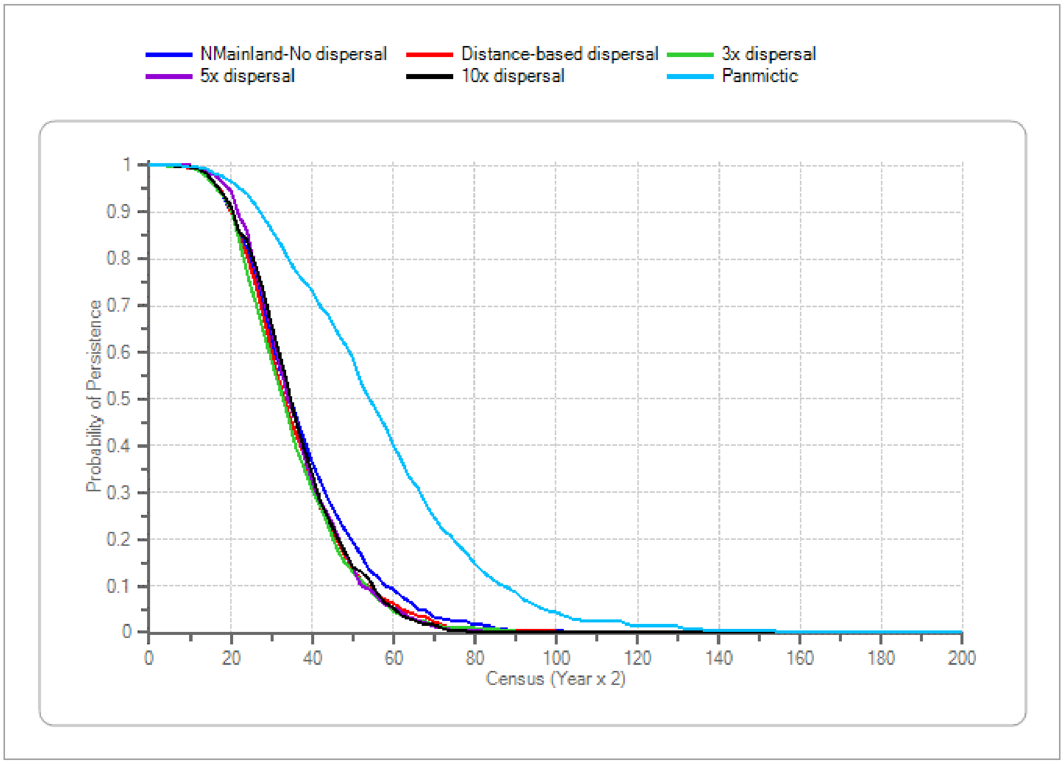

Figure 70. Probability of persistence of the N Mainland metapopulation with various dispersal rates.

Figure 71 shows the rapid accumulation of inbreeding in the small and fragmented N Mainland metapopulation, although the graph becomes meaningless after about 30 years because few of the simulated populations persist.

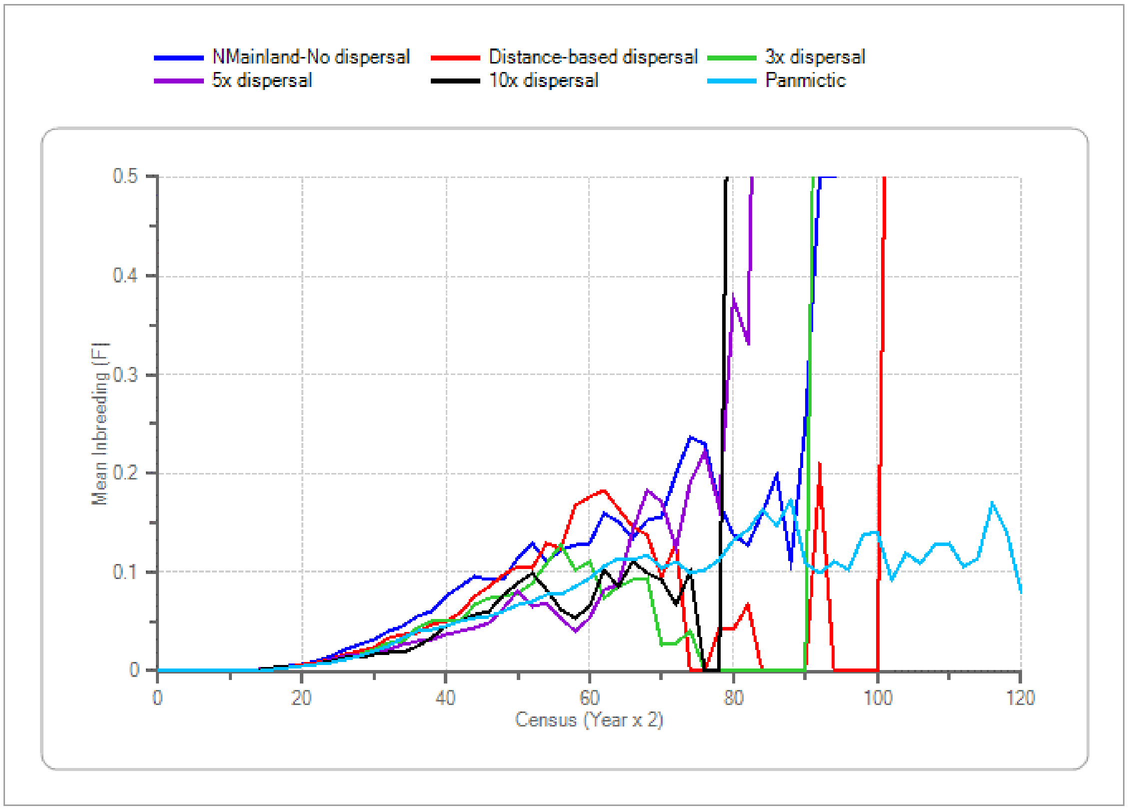

Figure 71. Accumulation of inbreeding in the N Mainland metapopulation under various dispersal rates.

Figure 72 shows that with or without the damage due to inbreeding, the N Mainland metapopulation is too small and fragmented to persist on its own. The decline would be slower if the metapopulation were not fragmented, but the metapopulation has too little optimal habitat to be sustainable.

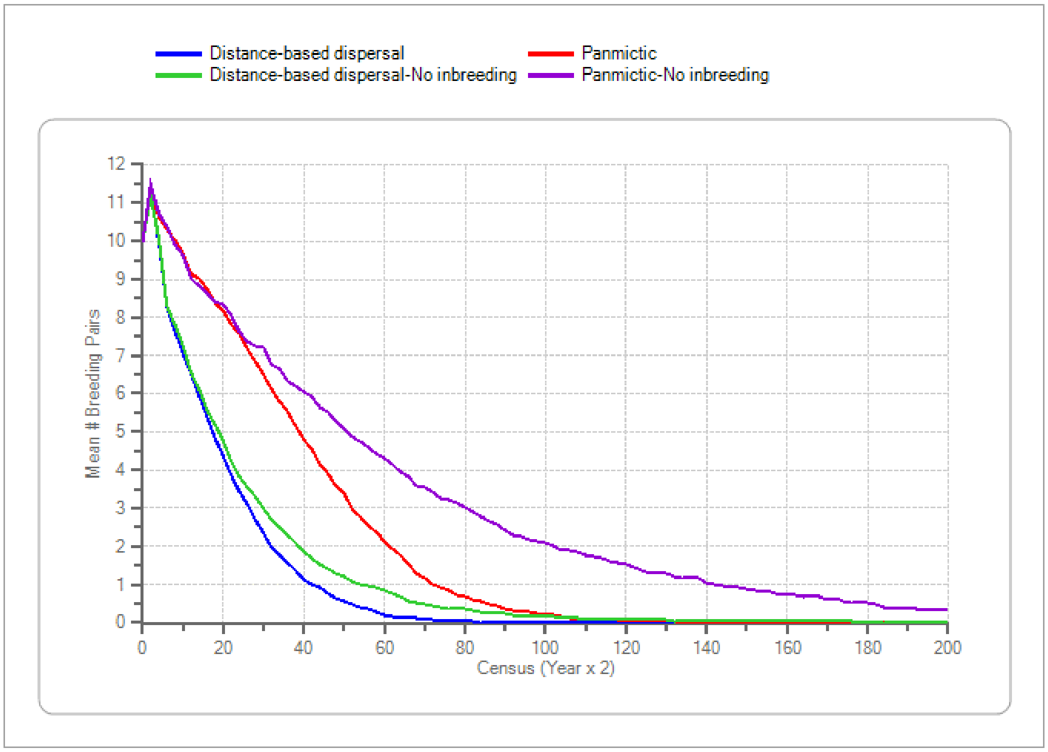

Figure 72. Projection population sizes of the N Mainland metapopulation with estimated dispersal rates vs complete connectivity, and with vs without inbreeding effects included in the model.

Figure 73 shows the predicted trajectories of the individual populations within the N Mainland metapopulation. SALT and SCOTW are the only local populations that have more than 1 Strong potential territory (with 4 and 3), but even SALT has a 50% chance of disappearing within 15 years (Fig. 74).

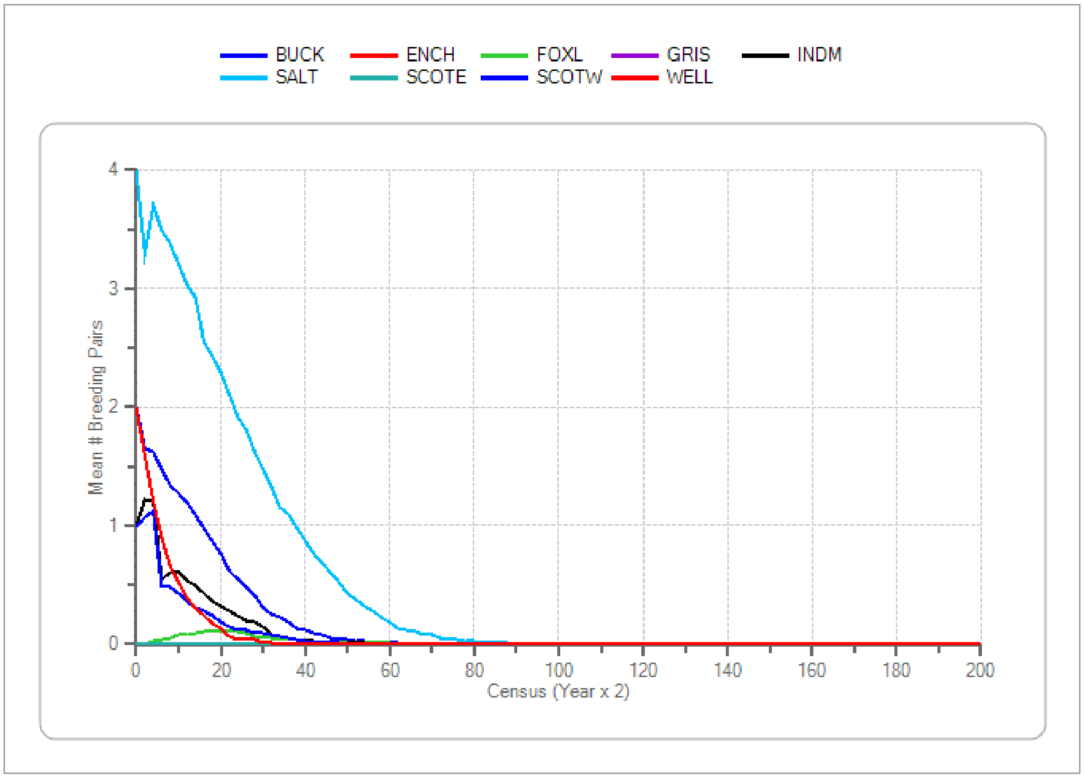

Figure 73. Projected sizes of the local populations that comprise the N Mainland metapopulation.

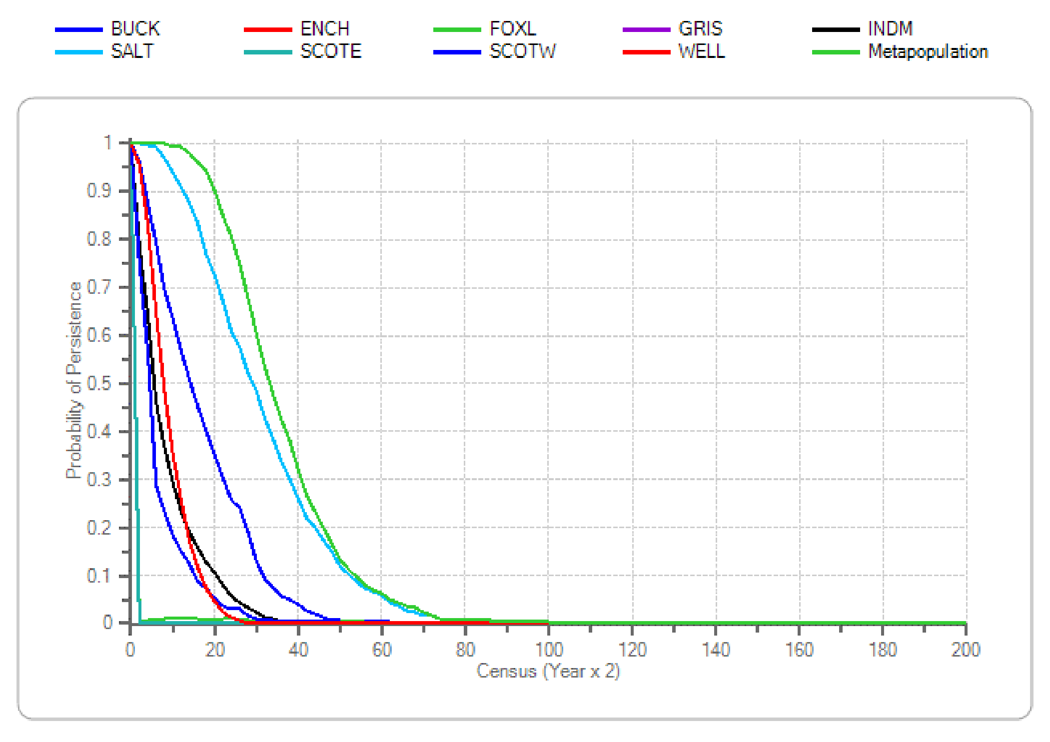

Figure 74. Probabilities of persistence for each local population in the N Mainland metapopulation.

Overall summary of metapopulation viability

The next two graphs show the predicted mean population trajectories (Fig. 75), with the uncertainty around these mean trajectories (vertical lines show +- 1 SD), and the probabilities of metapopulation persistence (Fig. 76). The general pattern is that the populations are expected to decline to occupy the Strong habitat, where reproduction is adequate to more than offset mortality. At that time, if the population is still large enough and interconnected to afford demographic and genetic stability, it would persist at that lower size breeding population. If the breeding population supported by Strong habitat is too small and disconnected from other populations, it will likely be unstable and go extinct, sooner or later.

Thus, although all three metapopulations are expected to contract to occupy, at most, primarily or only the Strong habitat, the three metapopulations are different in their vulnerabilities. The KSC/MINWR metapopulation is large enough, and each of its four constituent populations are large enough, so that it is likely to avoid complete extinction for at least 80 years. The SC Mainland metapopulation currently has only 41% of the population size of KSC/MINWR, and it is fragmented into 14 relatively isolated units. Therefore, it is projected to decline to extinction in about 40 to 70 years if nothing is done to increase optimal habitat and connectivity. The N Mainland metapopulation has too few breeding groups, too little optimal habitat, and is scattered among too many very small fragments to allow it to persist as a functional metapopulation.

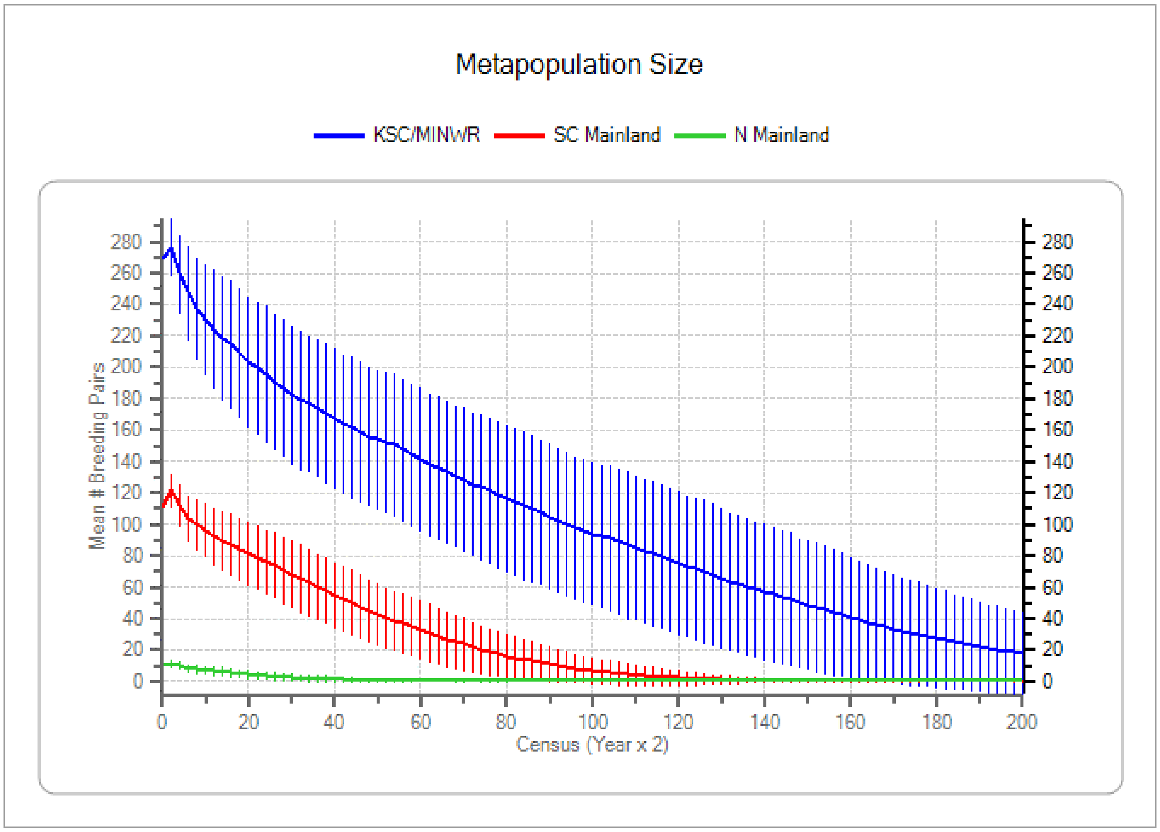

Figure 75. Mean (+- SD) metapopulation sizes, projected over 100 years.

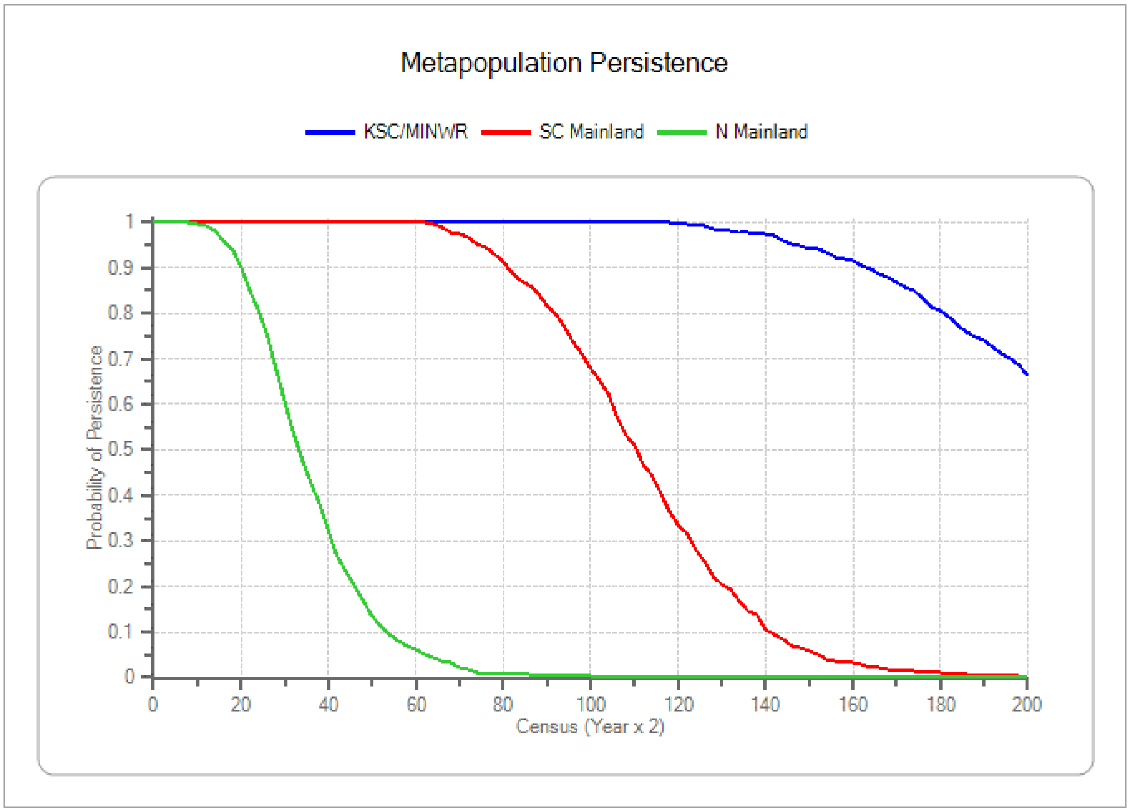

Figure 76. Probabilities of metapopulation persistence for each of the three metapopulations.

The above projections for the metapopulations indicate that the Florida scrub-jays in Brevard County are not likely to recover under current conditions. All three metapopulations are expected to decline, with only the KSC/MINWR metapopulation likely to persist, although at a smaller size. Management strategies that might reverse the declines, stabilize the metapopulations, or even achieve growth in numbers are explored in the subsequent scenarios.

Management scenarios

We used metapopulation models to test the viability of each of the disjunct metapopulations and the individual local populations that comprise them. The models exploring the current status of each metapopulation, the primary factors that influence that status, and the projections under various assumptions about uncertain parameters were presented in the prior sections of this report. The baseline model for each metapopulation under the assumption that dispersal between local populations occurs at the rates estimated from distances between population can be used a standard against which the efficacy of each tested management scenario is to be compared. Some of the management scenarios have been run also under assumptions of higher rates of dispersal, and these scenarios can represent either what might happen if dispersal is more than we first estimated, or what would happen if actions are taken to increase connectivity in addition to the other management actions being tested.

The management scenarios described in this report were developed in response to the suggestions made by managers during meetings at KSC and the Brevard Environmentally Endangered Lands program (EELs). The findings from these analyses have been presented to the scientists and managers of KSC, FWS, MINWR, CCSFS, EELs, Florida Fish and Wildlife Conservation Commission and other involved agencies. The initial management scenarios presented in this report mostly focus on requirements for metapopulation viability and generic management strategies (such as “How much does habitat quality need to be improved to ensure viability?”), rather than on specific actions at the local population level (such as “How many jays could be removed over the next 5 years from the Cruickshank scrub sanctuary without jeopardizing the future of the breeding population?”). The subsequent scenarios explore more location-specific and time-specific management actions. The results are presented not as definitive projections for any scenarios, but more as indications of expected trends and examples of the kinds of management scenarios that can be examined in the PVA. Additional scenarios representing other possible management actions or with different assumptions about the population and habitat dynamics can be run as those scenarios are identified in discussions with managers. Indeed, one primary purpose of this PVA project is to create a robust modeling platform that will support ongoing evaluation of status and options.

The results below follow a general format of describing the impacts on the metapopulations with respect to projected numbers of breeding pairs, mean inbreeding, and probability of population persistence. Further details about impacts on local populations (in addition to the metapopulation-level effects) and other measures of viability (population growth rates, extent of habitat occupancy, uncertainty or range of outcomes for measures of viability, etc.) can be provided for any scenarios of interest.

KSC/MINWR metapopulation management scenarios

The results from exploration of management scenarios for the KSC/MINWR metapopulation are summarized below.

What would be required, with respect to percent of habitat that is Strong, to keep the KSC/MINWR metapopulation persisting (probability of extinction < 5%), stable ($N > 0.5 \cdot Kmax$), and genetically healthy (inbreeding < 0.10)?

The next three graphs show the effect of increasing the percent of habitat that is Strong, for several scenarios of habitat management. Currently, the KSC/MINWR metapopulation is estimated to have habitat for 707 potential territories, with 20% in Strong habitat, 12% in Weak, and 68% in Sink. If 50% or 100% of current Weak habitat is improved to become Strong, and 50% or 100% of Sink is improved to become Weak (red and green lines), the population declines more slowly, but it still declines (Fig. 77); probability of extinction drops below 10% (with 50% improvement) or 5% (with 100% improvement) (Fig. 78); and inbreeding stays below 0.10 (Fig. 79). Population growth is not assured, because there is currently little Weak habitat to improve to Strong, and Sink habitat converted to Weak still leaves breeding pairs in those Weak territories with reproductive rates insufficient to achieve population growth.

Improving habitat to the species recovery goal of 70% Strong, which would require improving all Weak and more than half of the currently Sink habitat to Strong, could result in a population that grows to over 500 breeding groups (about 70% of Kmax) (Fig. 77, top line), extinctions would be prevented (Fig. 78), and inbreeding would be safely below 3% (Fig. 79). Habitat improvement would not be instantaneous, however. A scenario achieving 70% Strong over the next 20 years (black lines) projects slower approach to a stable size, but the population is still viable, with N > 450 breeding groups, no extinctions, and inbreeding < 0.04.

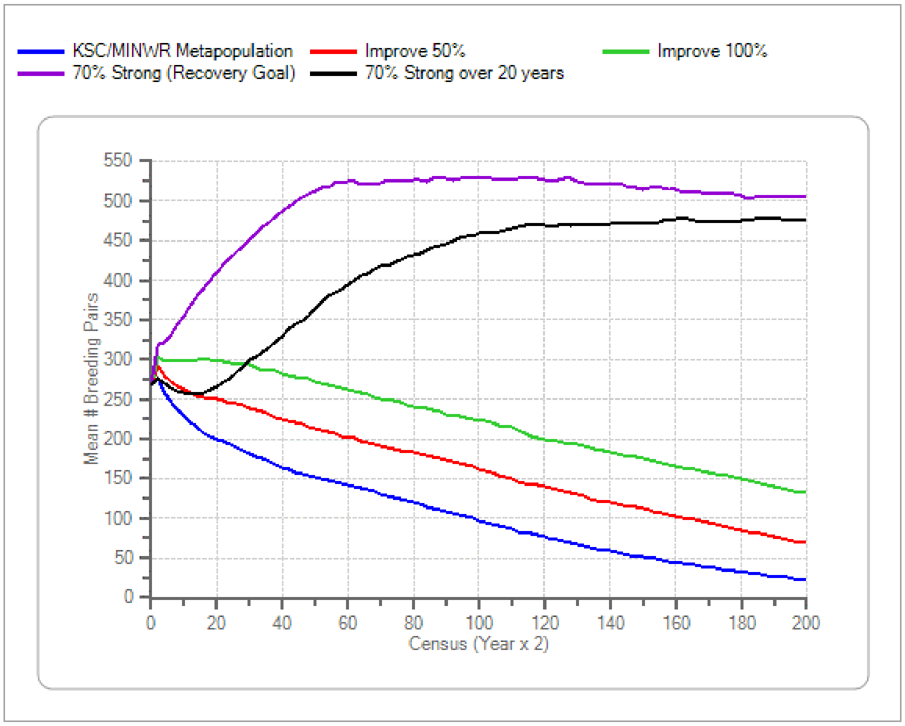

Figure 77. Projected number of breeding groups in the KSC/MINWR metapopulation under current distribution of habitat (blue line), with 50% (red) or 100% (green) of Weak improved to Strong and Sink improved to Weak, and scenarios with 70% Strong (and 20% Weak, 10% Sink) achieved either at the outset (purple) or over 20 years (black).

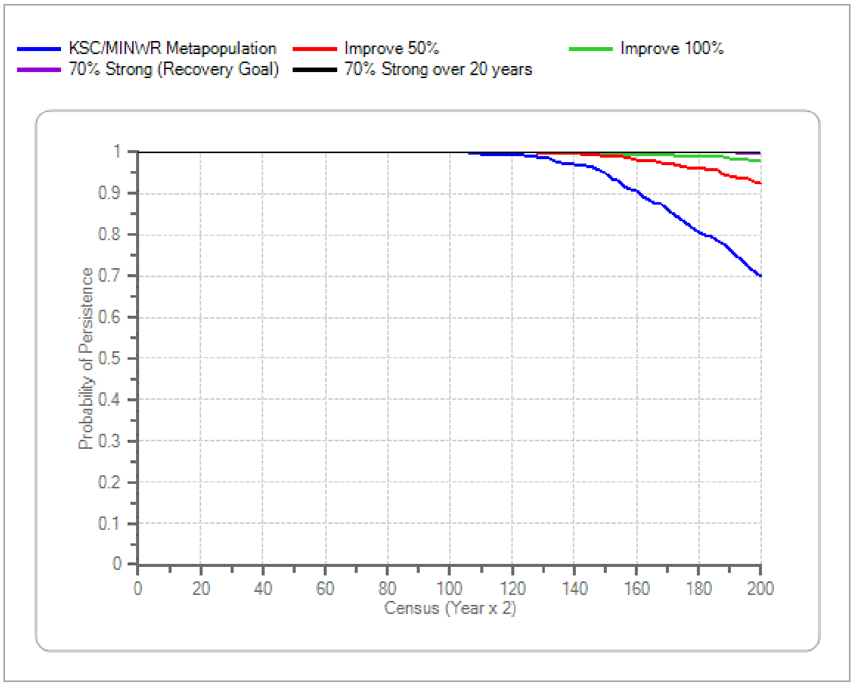

Figure 78. Probability of metapopulation persistence under current distribution of habitat (blue line), with 50% (red) or 100% (green) of Weak improved to Strong and Sink improved to Weak, or with 70% Strong (and 20% Weak, 10% Sink) achieved either at the outset (purple) or over 20 years (black).

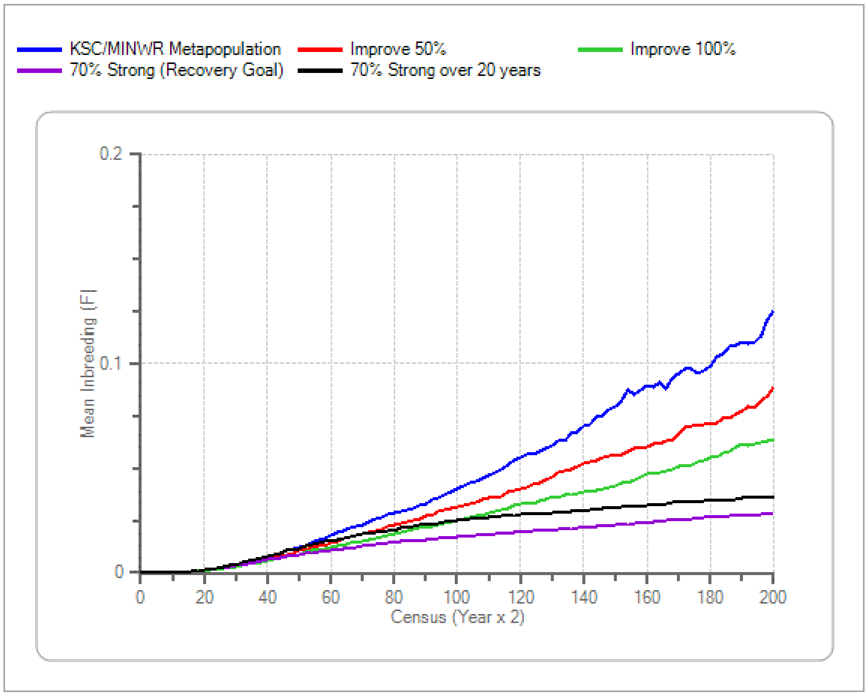

Figure 79. Mean inbreeding under current distribution of habitat (blue line), with 50% (red) or 100% (green) of Weak improved to Strong and Sink improved to Weak, or with 70% Strong (and 20% Weak, 10% Sink) achieved either at the outset (purple) or over 20 years (black).

How much Strong habitat is needed to achieve viability?

The amount of habitat that would need to be made Strong to ensure population viability was examined further by comparing scenarios with 30% up to 70% Strong habitat. To achieve a metapopulation that remains above Kmax/2 (i.e., N > 354) would require that more than 50% of the habitat be Strong condition (Fig. 80). However, even with as little as 30% Strong, probability of extinction of the KSC/MINWR metapopulation remains at 5% (Fig. 81) and inbreeding remains < 0.10 (Fig. 82).

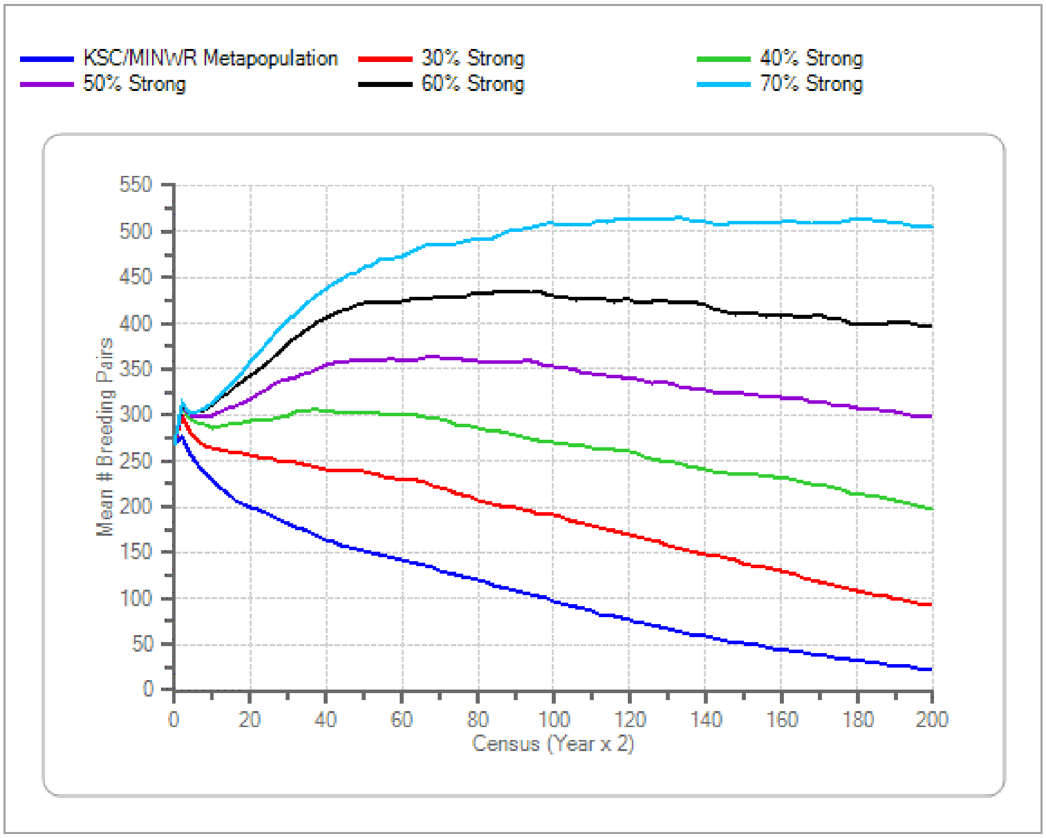

Figure 80. Projected number of breeding groups in the KSC/MINWR metapopulation under current distribution of habitat (20% Strong, blue line), or with 30% to 70% of habitat Strong.

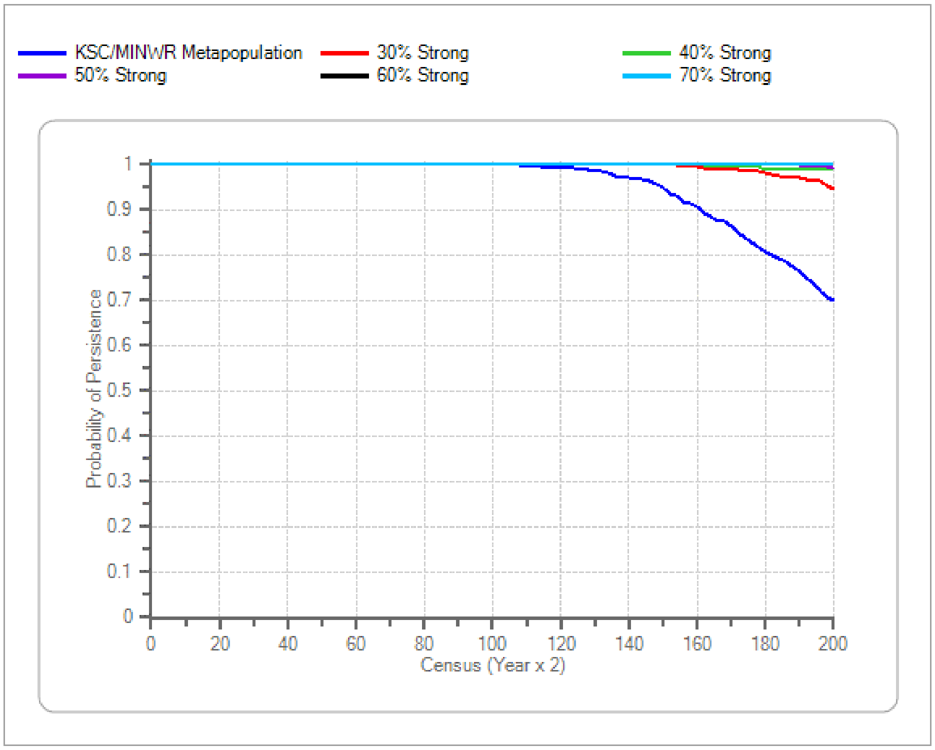

Figure 81. Probability of metapopulation persistence under current distribution of habitat (20% Strong, blue line), or with 30% to 70% of habitat Strong.

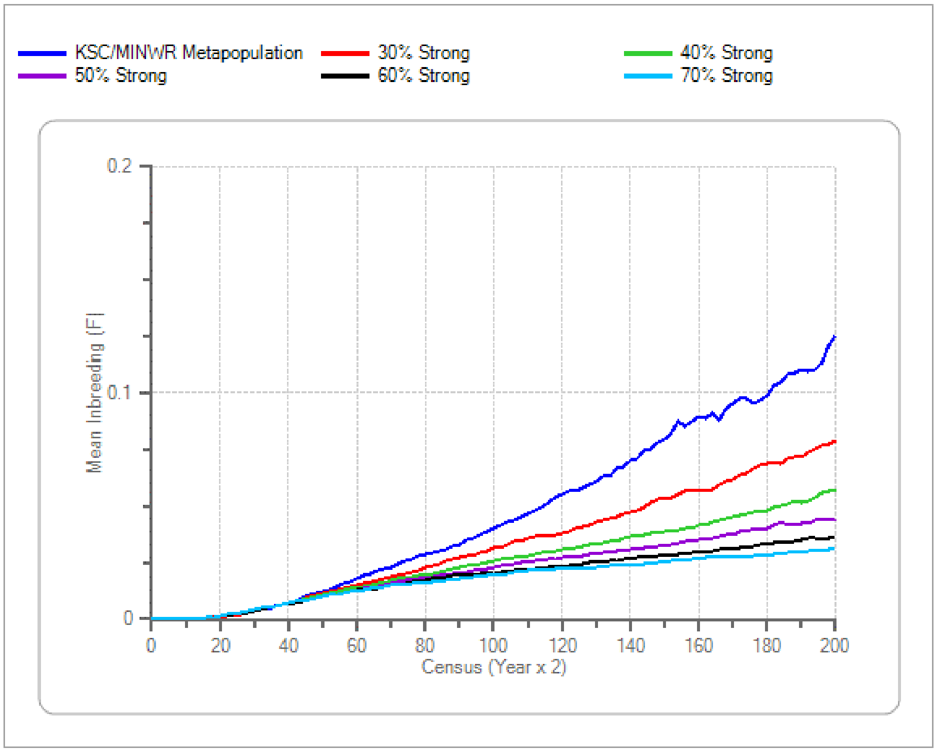

Figure 82. Mean inbreeding under current distribution of habitat (20% Strong, blue line), or with 30% to 70% of habitat Strong.

If the current habitat remains as is, would the population remain stable and viable if initial numbers were increased to fill all Strong habitat?

Currently, 92% of Strong habitat is occupied. (31% of Weak and 24% of Sink habitat is occupied.) Thus, if additional jays were added to fill the existing Strong habitat (11 breeding groups added to the current 127 in Strong habitat), there would be only a small improvement in population size and viability relative to the projections of the current metapopulation (models have been run, but graphs are not shown).

What if some or all Sink habitat was lost?

If existing Sink habitat degraded to the extent that it was no longer suitable for scrub-jays that might be detrimental to metapopulation viability because a buffer for holding excess jays would be lost, or it might be beneficial because new breeding pairs would not be attracted to establish territories in poor habitat. The next two graphs show the effect if 50%, 75%, or all the current Sink habitat (484 potential territories) was removed from habitat available for use by scrub-jays in the KSC/MINWR metapopulation. In the short-term (up to about 20 years), there would be a faster reduction in population size, as Sink habitat would not be available for use by the more than 100 breeding groups currently in Sink. In the long-term, however, removal of Sink habitat is projected to benefit the metapopulation, because jays seeking new breeding territories would be forced to use Strong or, less frequently, Weak habitat (Fig. 83). It is important to note, however, that these analyses did not consider that the loss of Sink habitat might also remove “stepping stones” that could contribute to connectivity among areas of Strong habitat. Thus, a possible negative impact of loss of Sink habitat has not yet been included in these projections. Moreover, converting Sink to Strong results in much better enhancement of population viability (see Figs. 74-79, above) than does removal of Sink.

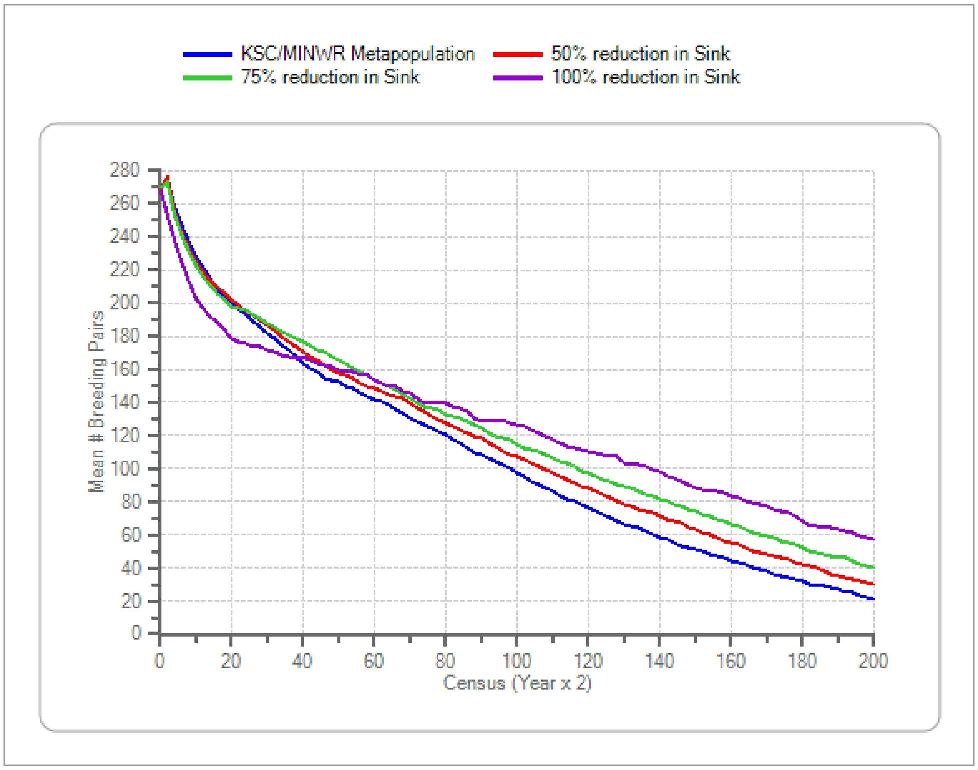

Figure 83. Projected number of breeding groups in the KSC/MINWR metapopulation under current extent of habitat (blue line), or with 50%, 75%, or 100% of Sink habitat removed.

Removal of some or all Sink habitat is also projected to reduce the probability of population extinction (Fig. 84). Again, however, these projections do not include any possible effect on connectivity and accessibility of Strong habitat. Even with that caveat, a general conclusion from the scenarios shown in Figures 77-84 is that scrub management regimes that leave a majority of potential habitat in Sink condition (as is the case presently) will not be expected to result in a metapopulation that is demographically and genetically healthy. Further scenarios comparing possible management regimes can be explored (especially after habitat models are developed and linked to the Vortex PVA model), but preliminarily these results suggest that 50% or more of habitat should be Strong at any given time.

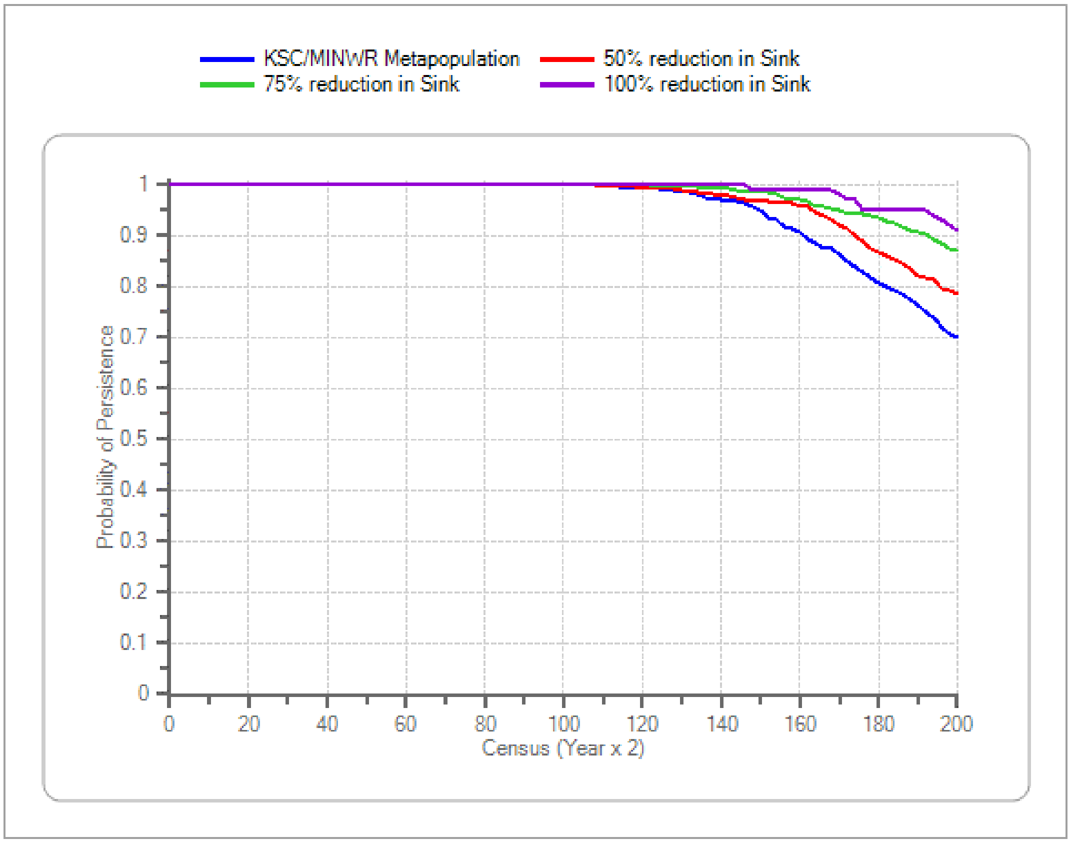

Figure 84. Probability of metapopulation persistence under current extent of habitat (blue line), or with 50% (red), 75% (green), or 100% (purple) of Sink habitat removed.

What if the Schwartz Road unit cannot be managed for scrub-jays and becomes all Sink habitat?

Currently, the Schwartz Road unit contributes 21 Strong potential territories (all of which are occupied), 24 Weak (4 occupied), and 116 Sink (19 occupied) to the KSC/MINWR metapopulation. The next two graphs show the impact if the habitat used by the Schwartz Road population is not managed for scrub-jays and becomes all Sink – either immediately or over the next 20 years. Loss of the Strong and Weak territories from Schwartz Road reduces the metapopulation size by about the number of breeding groups currently using Strong and Weak habitat (Fig. 85), but it would have only a small effect on the persistence of the entire KSC/MINWR metapopulation (Fig. 86).

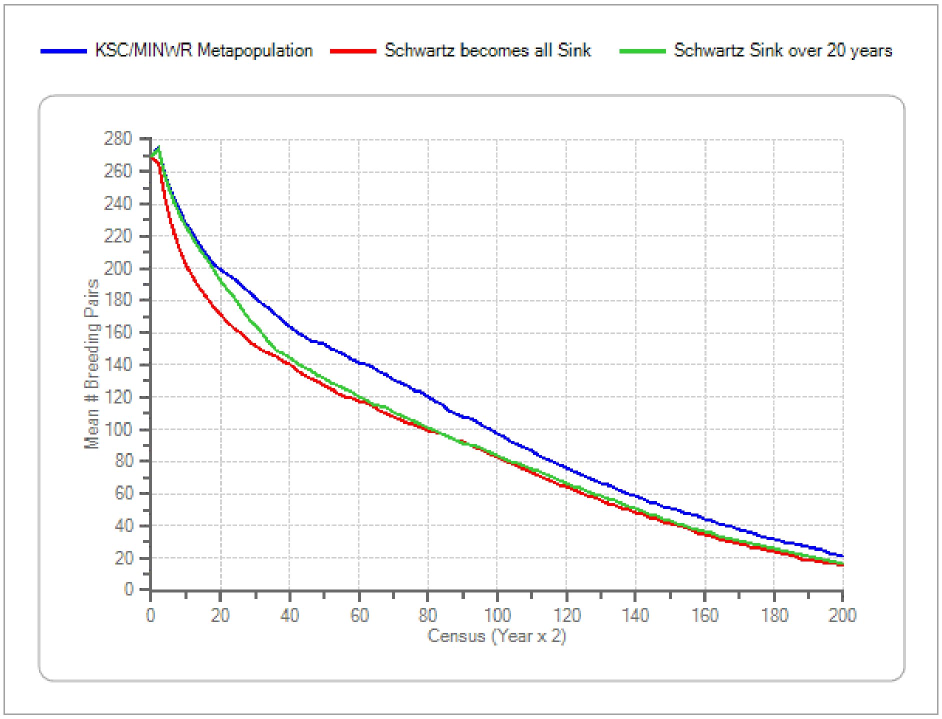

Figure 85. Projected number of breeding groups with the current habitat, or if the habitat used by the Schwartz Road population is not managed and degrades to become all Sink either instantly or over the next 20 years.

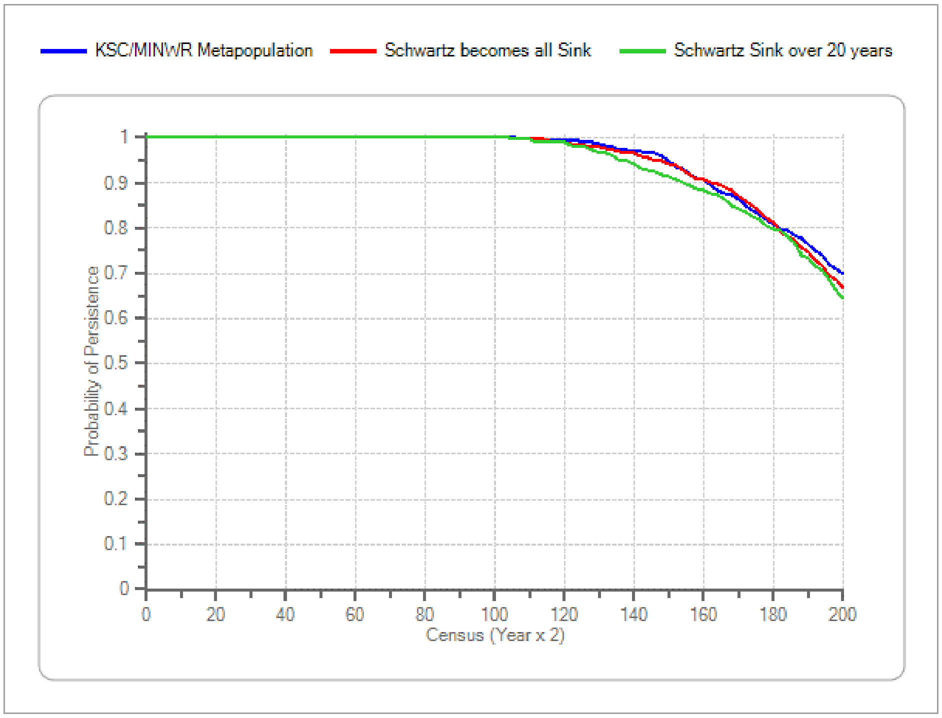

Figure 86. Probability of metapopulation persistence with the current habitat, or if the habitat used by the Schwartz Road population is not managed and degrades to become all Sink either instantly or over the next 20 years.

How much would it help if the Happy Creek and Shiloh populations were fully connected?

If Happy Creek and Shiloh populations could be fully connected, there would be a small increase in the mean projected number of breeding groups (Fig. 87, compare bottom two lines), and a more noticeable decrease in the probability of extinction (Fig. 88), because of reduced accumulation of inbreeding (Fig. 89). If, in addition, habitat is improved to become 70% Strong (top two lines), the small benefit of connectivity to total population size remains, there is no likelihood of extinction regardless of connectivity between Happy Creek and Shiloh, and the low expected inbreeding (mean F = 0.03) is reduced further. Thus, the primary effects of connecting Happy Creek and Shiloh is to moderately reduce the accumulation of inbreeding (shifting mean F from > 0.10 to < 0.10), resulting in improved population persistence, in scenarios where lack of habitat quality causes the populations to decline over time.

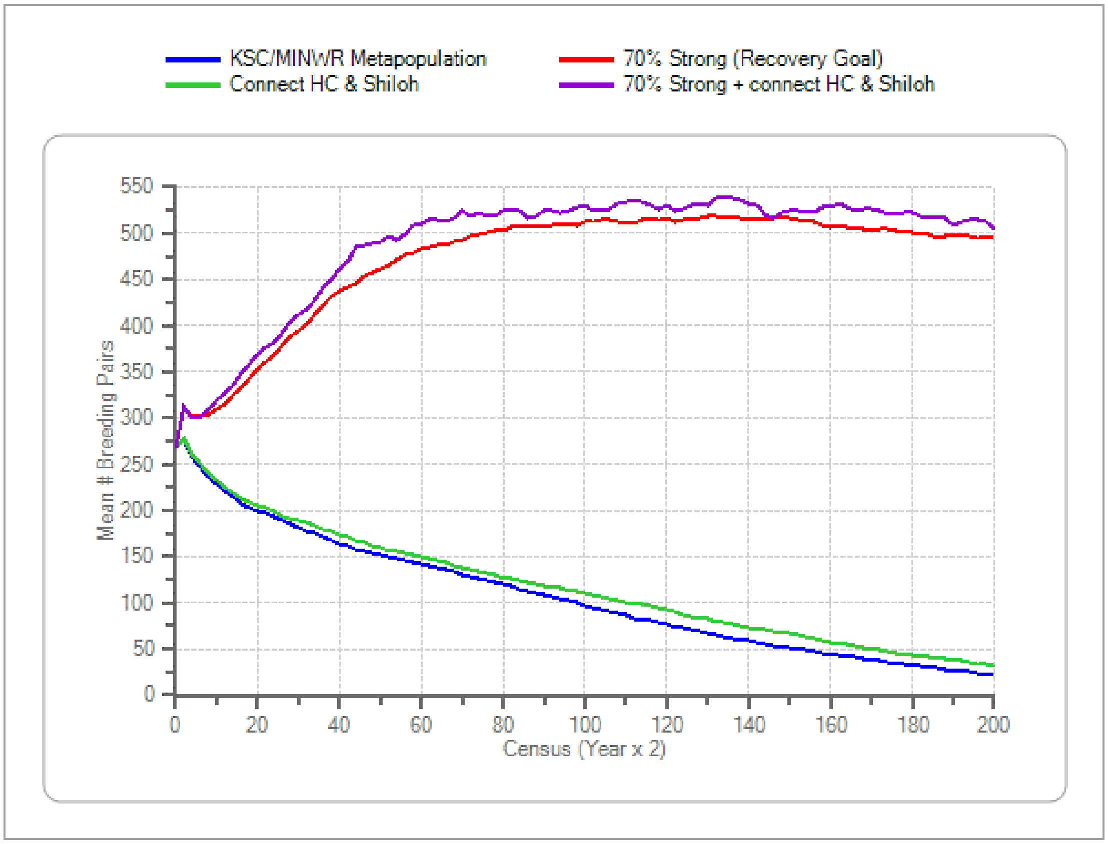

Figure 87. Projected number of breeding groups in the KSC/MINWR metapopulation with the current configuration of habitat (blue line), if Happy Creek and Shiloh populations are fully connected (green), if habitat is improved to be 70% Strong (red), or if Happy Creek and Shiloh are combined and habitat is improved to be 70% Strong (purple).

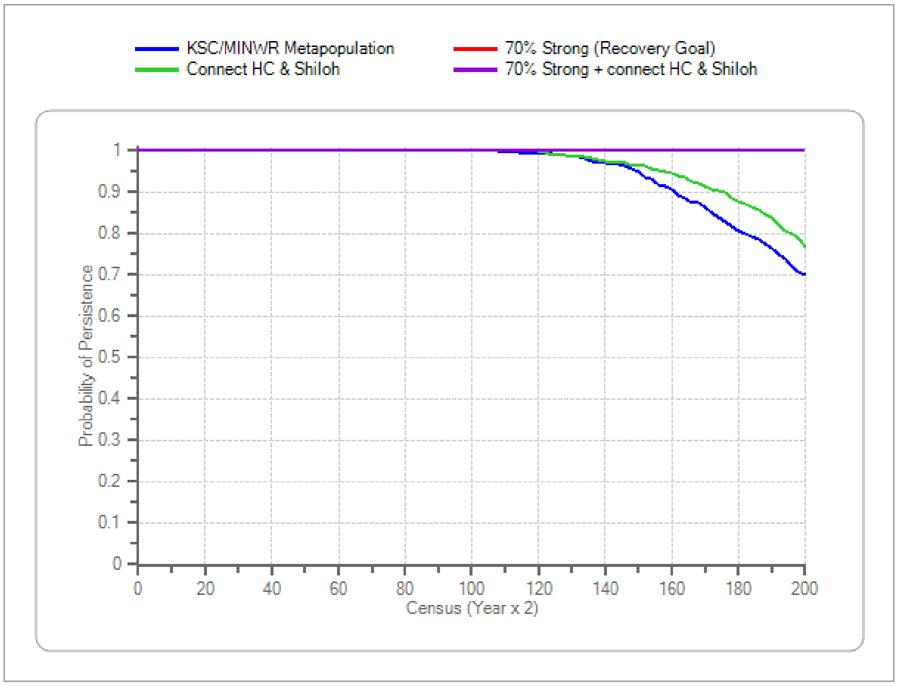

Figure 88. Probability of metapopulation persistence with the current configuration of habitat (blue line), if Happy Creek and Shiloh populations are fully connected (green), if habitat is improved to be 70% Strong (red, obscured under the purple line), or if Happy Creek and Shiloh are combined and habitat is improved to be 70% Strong (purple).

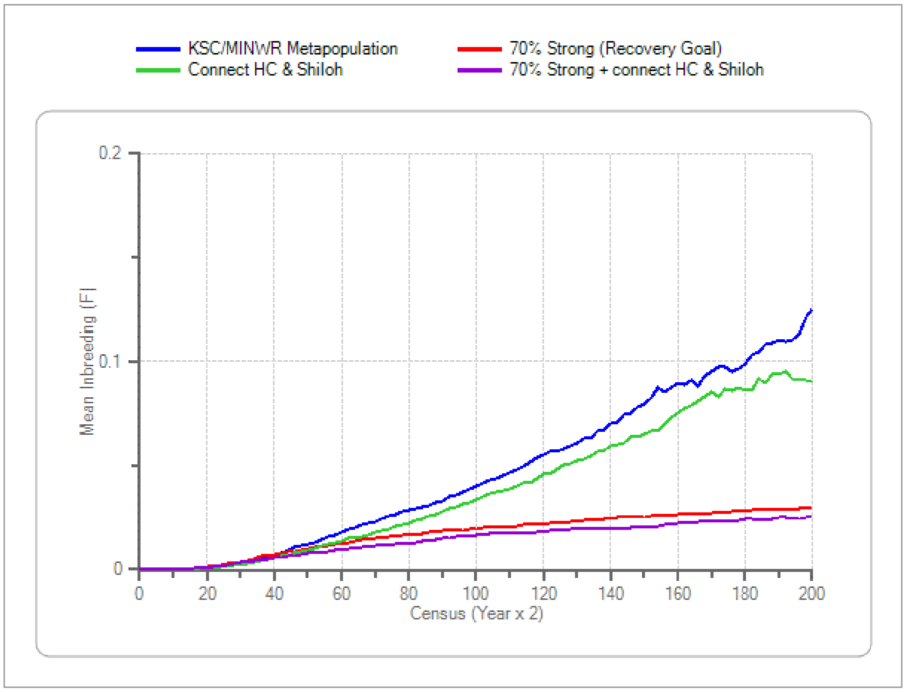

Figure 89. Mean inbreeding with the current configuration of habitat (blue line), if Happy Creek and Shiloh populations are fully connected (green), if habitat is improved to be 70% Strong (red), or if Happy Creek and Shiloh are combined and habitat is improved to be 70% Strong (purple).

If the population reaches capacity, how many scrub-jays are excess each year to the need for replacements to sustain the population?

If habitat is not improved to at least 50% Strong, then the population is projected to decline and never approach carrying capacity. At less than 50% Strong, the excess from Strong are fully absorbed by the Weak and Sink habitats, which do not support positive population growth, and there will be no excess jays if habitat is not improved. Therefore, the examination of the number of excess jays above what is needed to sustain the population has been tested, so far, only for the case of 70% Strong habitat.

Moreover, estimating or even defining the number that is excess at K is problematic with the structure of the population model we have constructed. That is because the population is limited by the number of potential breeding territories. When territories are saturated, no new breeding pairs are formed, the population stops growing, and the PVA model does not need to remove any birds to keep the population below K. I.e., limitation of population size is imposed by restrictions on reproduction rather than by removal of excess birds.

One meaningful way to examine the number of jays that might be removed each year without damaging population viability is to test different rates of removal to see how many can be removed, on average, while still allowing the population to persist with at least 50% of potential territories occupied. This was tested with the condition that removals did not start until half of the territories were used by breeding groups and thereafter were conducted only in years when N > Kmax/2.

Figure 90 shows the projected population sizes when habitat is improved to 70% Strong, and then 1 to 8 pairs are removed from each local population after any year when that population exceeds 50% occupancy of potential territories. When up to 3 or 4 pairs are removed per population, the long-term population size is suppressed. Above that level of harvest, there is no further effect on the population size. As shown in Figure 91, this is because with 4 or more pairs harvested per year, the local populations are typically constrained to grow to a size not much more than N = Kmax/2 while, on average, about 14 to 16 jays are removed per year. This might be viewed as the sustainable take that could be removed annually, but with the recognition that this level of harvest is possible only if the habitat is improved to 70% Strong. Scenarios cold be run to test how many jays could be removed each year if there was less Strong habitat (perhaps 50%, still enough to sustain growth up to K.)

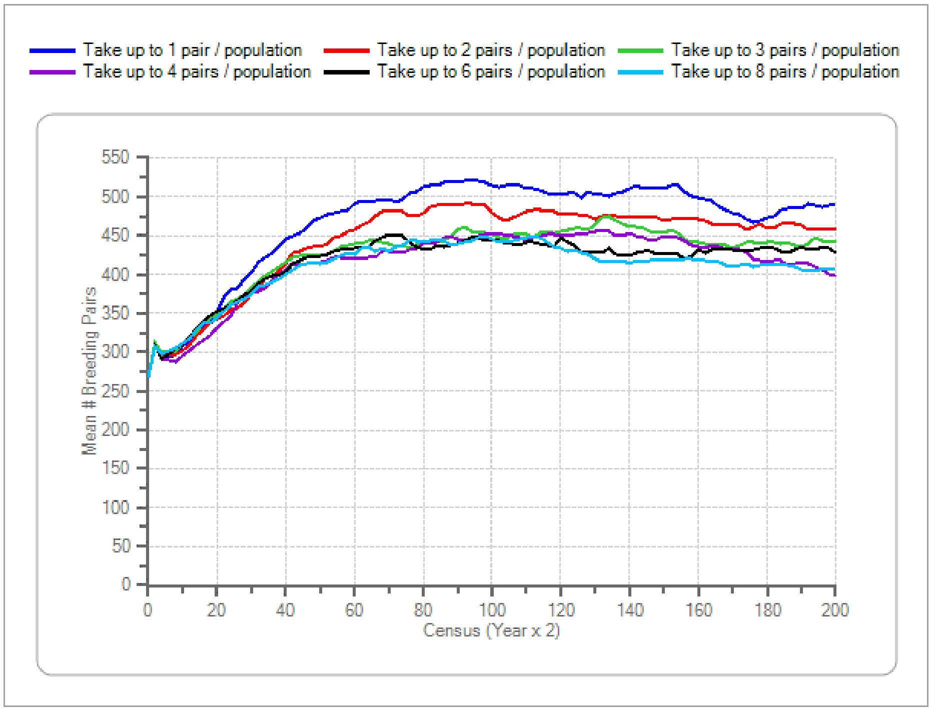

Figure 90. Projected number of breeding groups when habitat is improved to 70% Strong and then 1 to 8 pairs are removed from each local population subsequent to any year in which more than half of the potential territories were occupied.

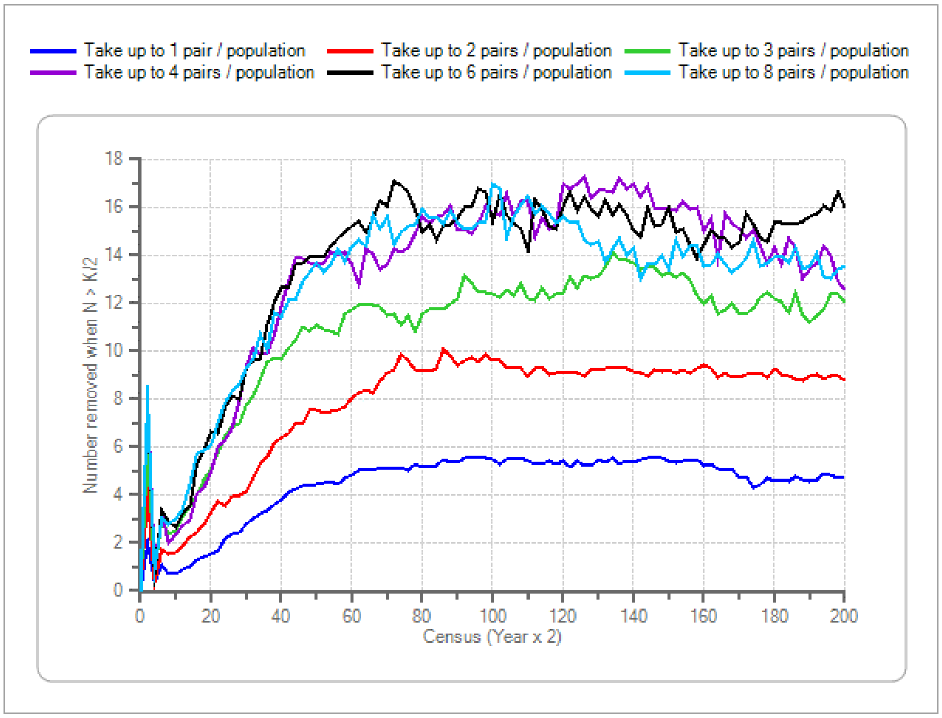

Figure 91. Mean number of jays that can be removed each year when habitat is improved to 70% Strong and then 1 to 8 pairs are removed from each local population any year in which more than half of the potential territories were occupied.

Does the KSC/MINWR metapopulation remain viable if jays are removed from Weak and Sink habitat (for translocation to support other sites)?

The impact of removing jays from Weak and Sink habitat was modeled both in scenarios with the current amount of Strong, Weak, and Sink habitat and in scenarios in which the habitat had been improved to become 70% Strong, 15% Weak, and 15% Sink.

If habitat is not improved, then the KSC/MINWR metapopulation is projected to be in decline, so it might not be meaningful to try to assess how many could be removed and still leave the population viable. However, we can ask how much the projected population size is reduced with varying levels of removals of jays from Weak and Sink habitats, to see if those removals cause considerable further damage to an already vulnerable population. If fewer than 1 pair of jays in Weak and 1 pair in Sink habitat are removed from each population per year, the decline in the metapopulation is accelerated, but not dramatically (Fig. 92, lines above the black line). With 1 to 4 pairs removed from Sink and from Weak habitat per year from each population, the reduction in population is more notable, up to 50%. However, after the first 30 to 40 years, little further damage is done by attempted removal of jays from each local population. This is because few jays remain in Weak and Sink habitats, so that the higher levels of removals are not implemented.

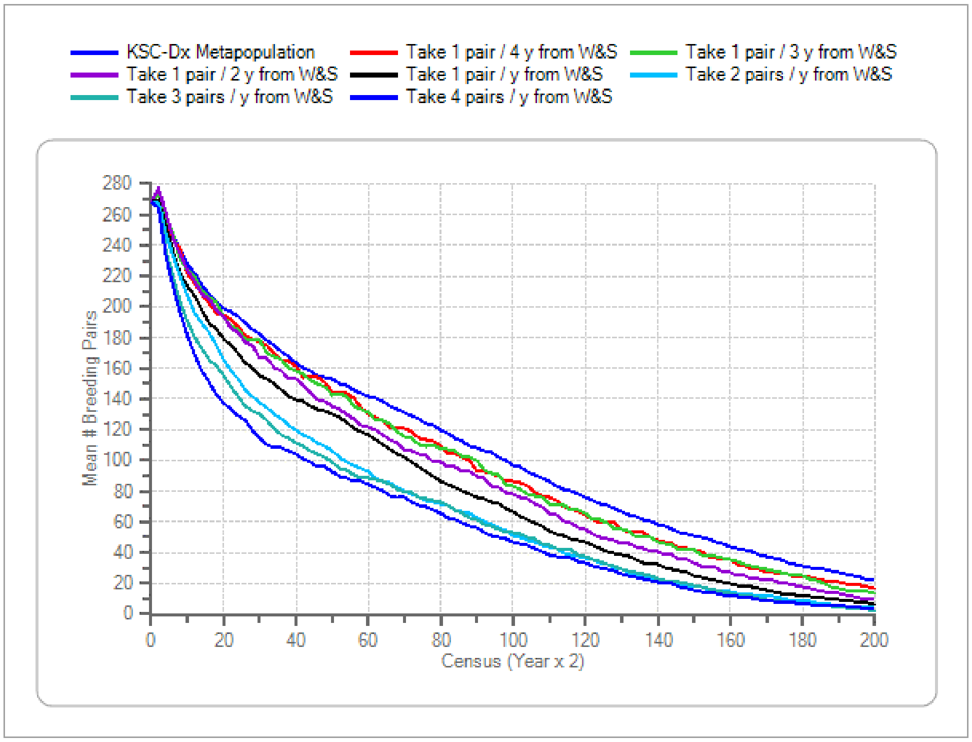

Figure 92. Projected number of breeding groups with the current configuration of habitat, when no jays are removed (top, blue line), or when jays are removed from Weak and Sink habitat at rates that vary from 1 pair from each of Sink and Weak habitat in each local population per 4 years (red line) up to 4 pairs from each of Sink and Weak per population per year (bottom line).

The number removed per year is shown in the next graph. With the higher rates of removals, the number that can be removed from Weak and Sink habitat declines rapidly over time, as Weak and Sink territories are rapidly emptied (Fig. 93). The mean number removed per year is harder to see when the removals occur only every 2, 3, or 4 years, but with the lower rates of removal the attempted numbers can be mostly sustained for about 50 years until the reduction in the overall population size is such that few pairs remain in Weak and Sink habitat.

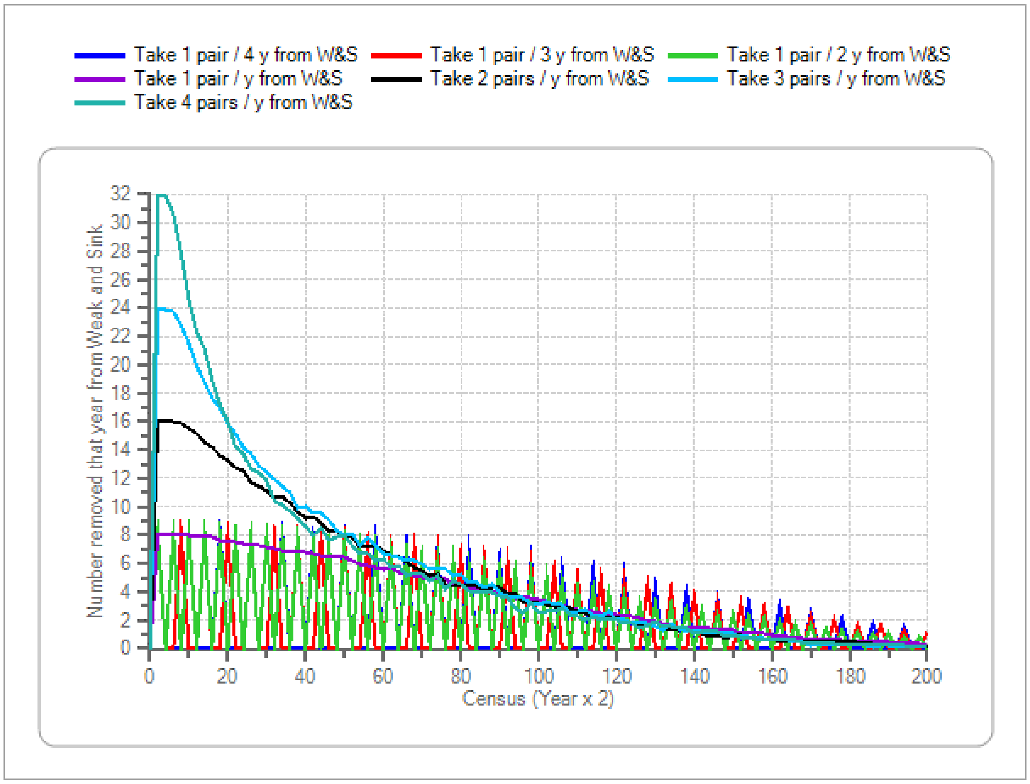

Figure 93. Number of jays that can be removed from the declining KSC/MINWR metapopulation, when jays are removed from Weak and Sink habitat at attempted rates that vary from 1 pair from each of Sink and Weak habitat in each local population per 4 years (red, 4-y cyclical line) up to 4 pairs from each of Sink and Weak per population per year (top line).

These projections suggest that if there is not habitat improvement, then harvesting more than about 1 pair from Weak and 1 pair from Sink per population each year would considerably accelerate the decline. In addition, after the population is reduced to having very few jays in Weak and Sink habitat, it would not be possible to obtain the desired number of birds. Removals over shorter periods of time can be tested, and it is likely that the population could sustain harvests from Weak and Sink habitats for several years with very little impact on the long-term metapopulation viability.

If the habitat is first improved to 70% Strong, then population size is reduced, but not dramatically, with removal of up to about 2 pairs per population from the Weak habitat and 2 pairs per population from the Sink habitat (Fig. 94). Attempts at removing more than that do not depress population size further, because the removals largely depopulate the Weak and Sink habitat. The numbers that can be removed per year from Weak and Sink habitat reach a maximum at about 14 to 16 jays (Fig. 95). This reinforces the conclusion from a previous case (Figs. 90 and 91) that the numbers that could be removed from the KSC/MINWR metapopulation without causing decline is about 14 to 16 pairs per year, if the habitat is improved to be 70% Strong.

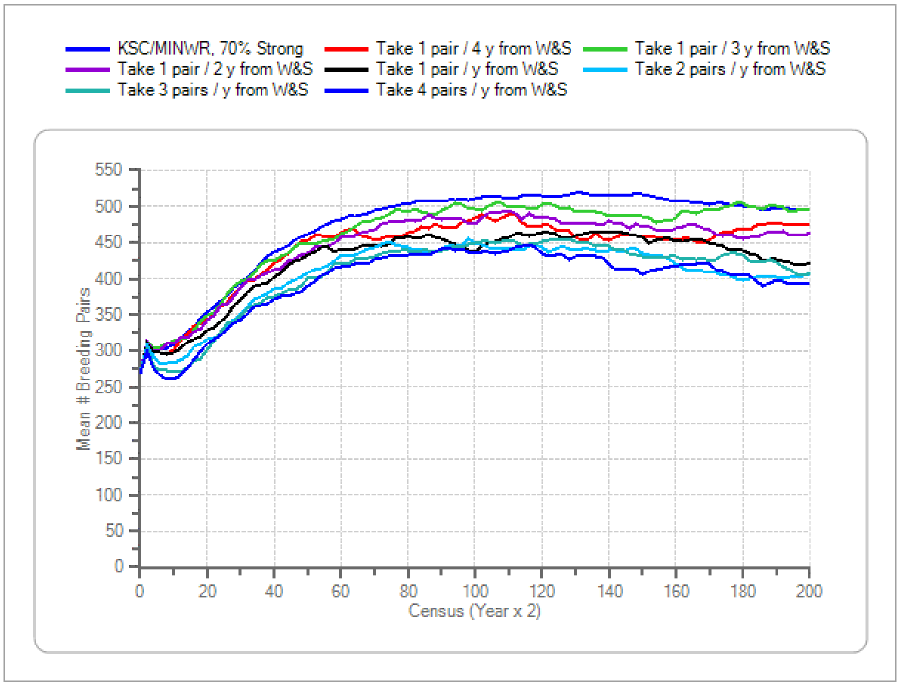

Figure 94. Projected number of breeding groups with habitat improved to 70% Strong, when no jays are removed (top, blue line), or when jays are removed from Weak and Sink habitat at rates that vary from 1 pair from each of Sink and Weak habitat in each local population per 4 years (red line) up to 4 pairs from each of Sink and Weak per population per year (bottom line).

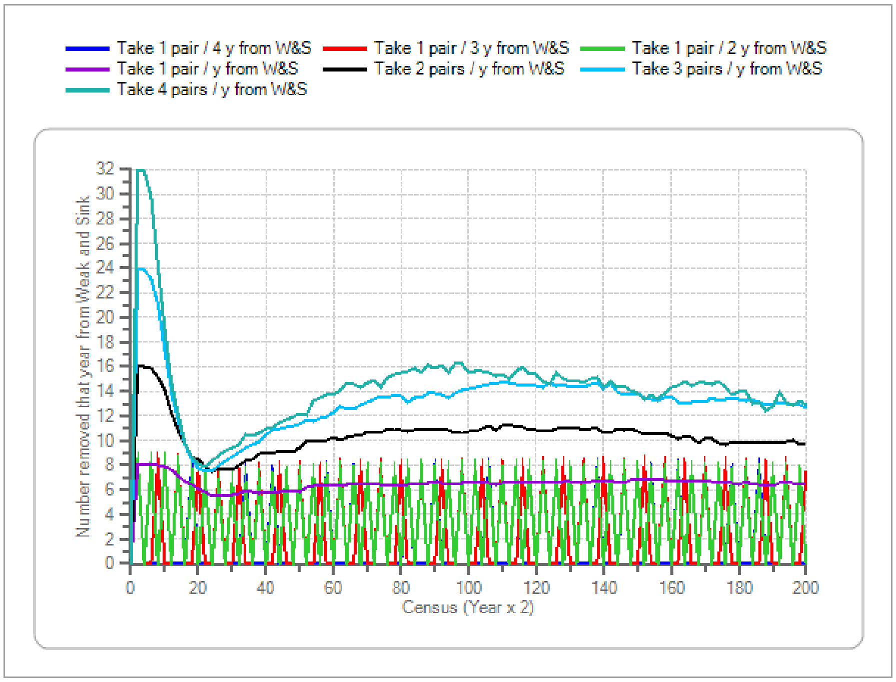

Figure 95. Number of jays that can be removed from KSC/MINWR if habitat is improved to 70% Strong, when jays are removed from Weak and Sink habitat at rates that vary from 1 pair from each of Sink and Weak habitat in each local population per 4 years (red, 4-y cyclical line) up to 4 pairs from each of Sink and Weak per population per year (top line).

What if all are removed from Sink? How many would be taken?

Removing all jays from Sink territories each year causes a moderate depression in metapopulation size (Fig. 96), although the effect is not large after the first few years if the habitat is not improved and therefore the population would be in decline. Figure 97 shows that initially about 200 jays would be removed from current Sink habitat, and thereafter up to about 4 jays that settle into Sink habitat would be removed each year.

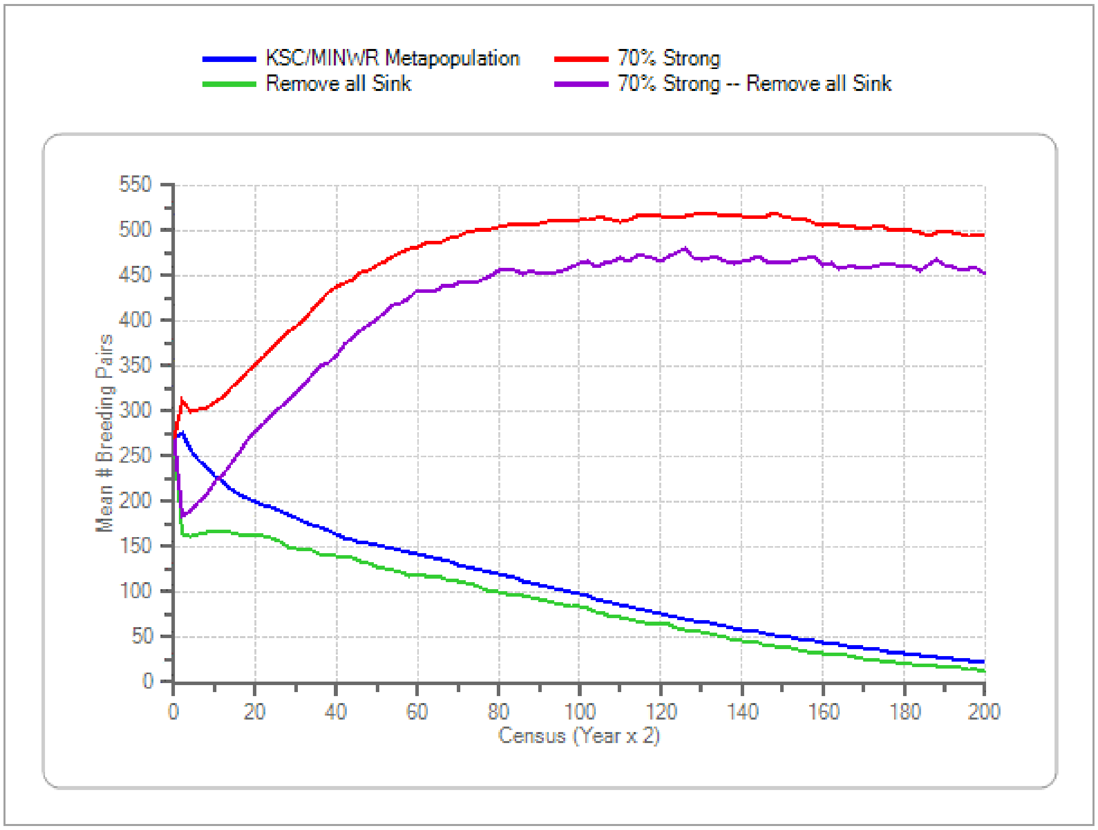

Figure 96. Projected number of breeding groups with current habitat (lower lines) or with habitat improved to 70% Strong (upper lines) when all jays in Sink habitat are removed each year (purple and green lines) or not (blue and red lines).

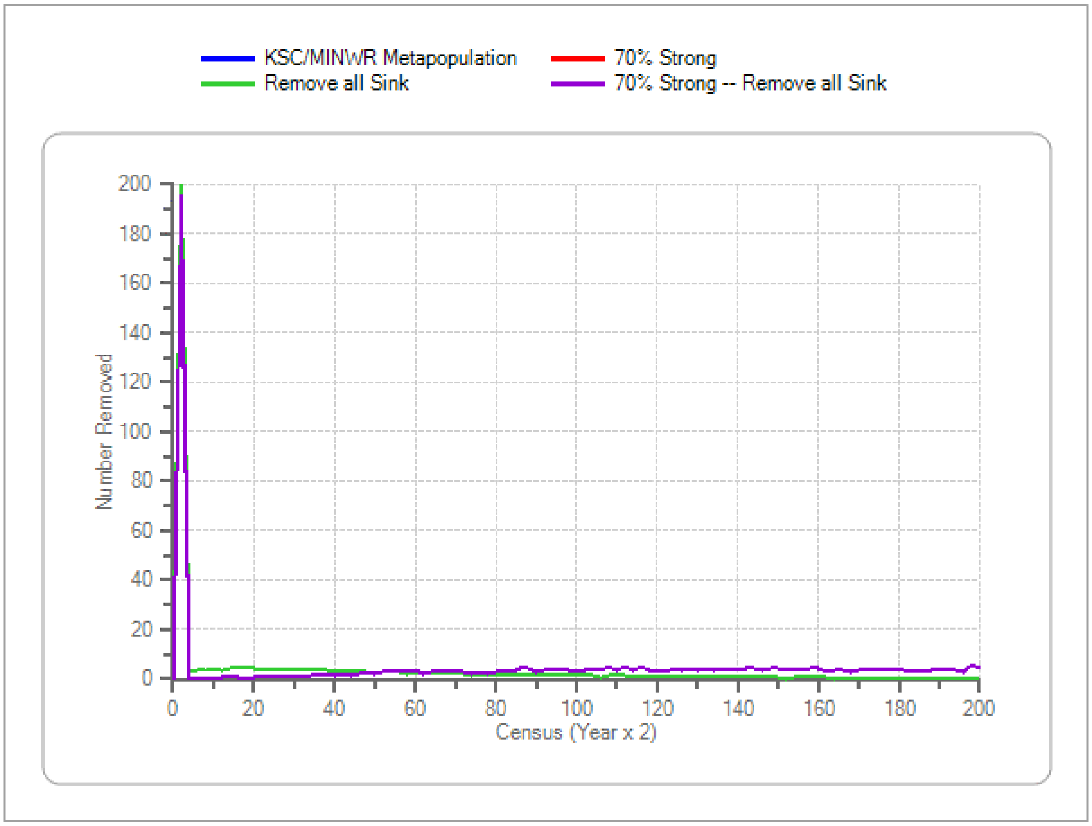

Figure 97. Number of jays removed each year with current habitat (blue line) or with habitat improved to 70% Strong (red line) when all jays in Sink habitat are removed each year.

Strategies that combine aspects of the above scenarios – e.g., initially removing a many (but not all) of jays currently in Sink habitat, and then periodically removing some jays from Weak and from Sink habitats – could be explored to determine what cumulative removals over time might be done without significantly damaging the viability of the KSC/MINWR metapopulation.

CCSFS metapopulation management scenarios

The results for management scenarios for the Cape Canaveral Space Force Station (CCSFS) metapopulation are summarized below.

What would be required to keep the metapopulation persisting (probability of extinction < 5%), stable (N > 0.5·K), and genetically healthy (inbreeding < 0.10)?

As shown in Fig. 98, below, the CCSFS population has too little Strong habitat to be expected to avoid a steady decline toward extinction, and it would contribute jays to a combined KSC/MINWR + CCSFS metapopulation only for a few decades until the CCSFS populations disappeared.

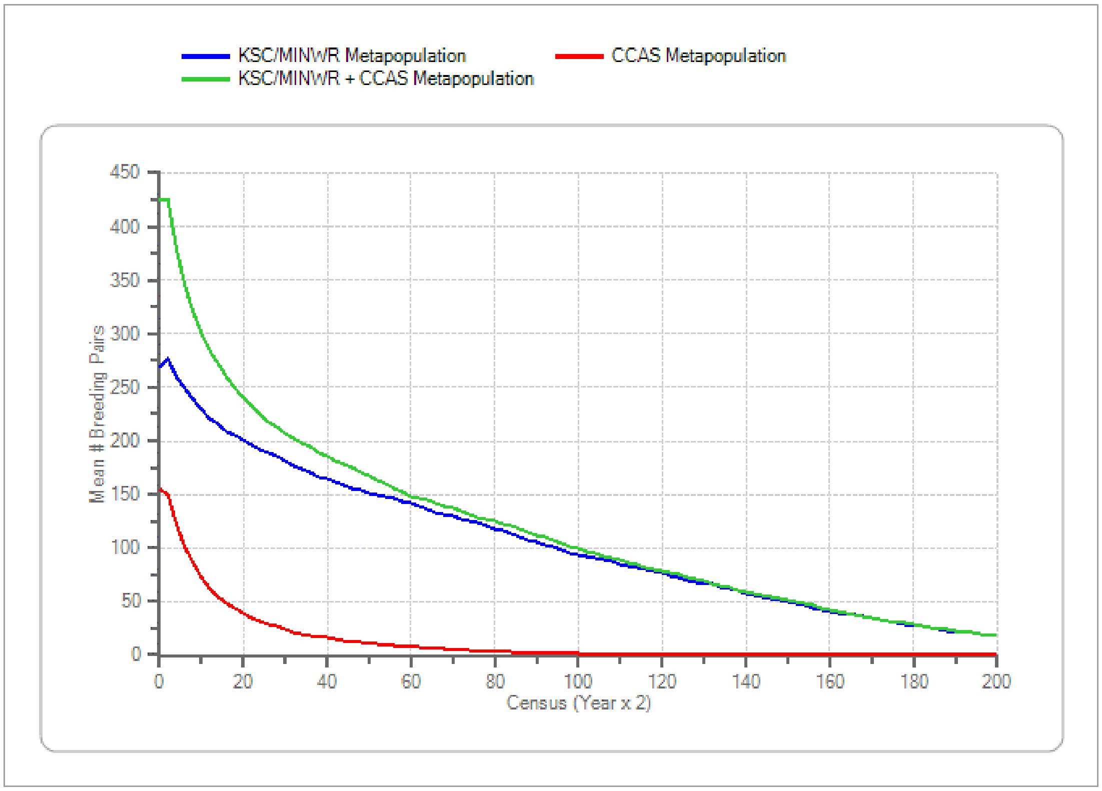

Figure 98. Projected number of breeding groups with current habitat in the KSC/MINWR metapopulation (blue), in the CCSFS metapopulation (red), and in the combined metapopulation with an estimated low rate of dispersal between Happy Creek (KSC) and Beach-North (CCSFS) populations.

Can the CCSFS metapopulation be sustained by immigration from KSC?

The CCSFS metapopulation could be sustained by steady immigration into Beach-North (either natural dispersal or via managed translocations), but only at population sizes that approximate the number of Strong habitat territories (13) plus the supplements from the prior year (Fig. 99). In these scenarios with regular supplementation, extinction is completely avoided, but could occur quickly if releases were stopped. Inbreeding is prevented by the steady in-flow of unrelated jays, but it would rise if the supplementation ceased.

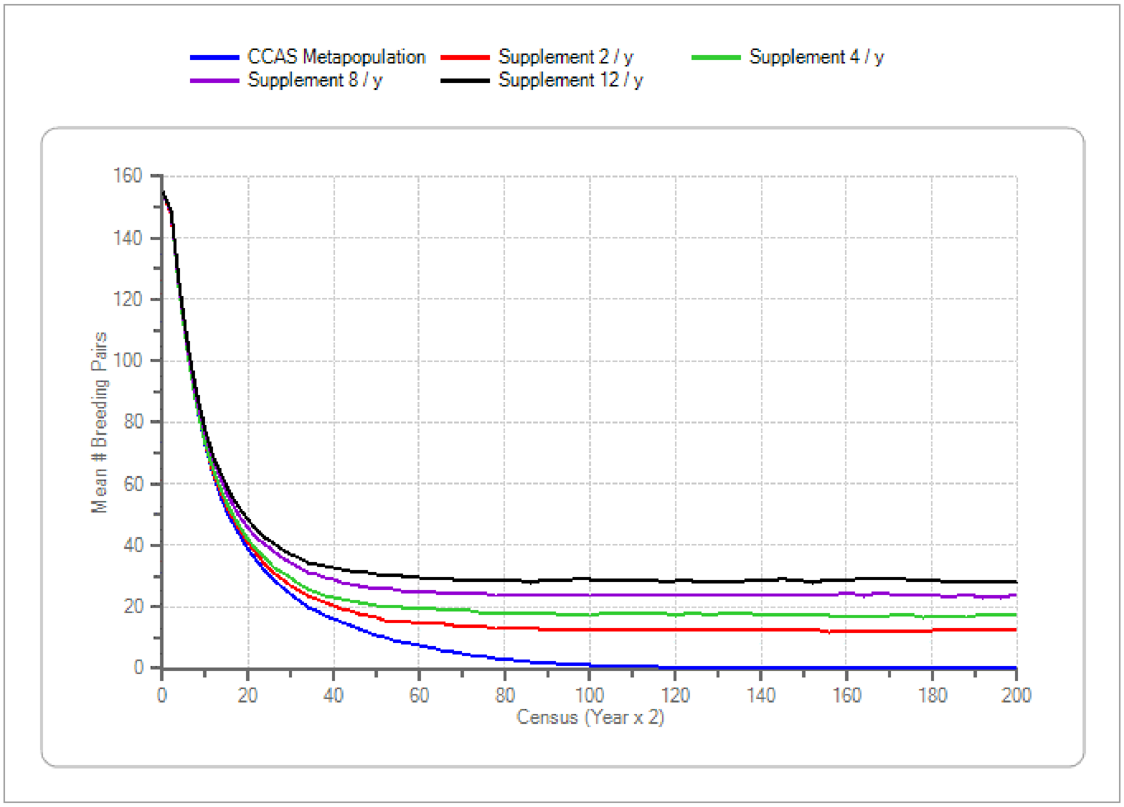

Figure 99. Projected number of breeding groups with current habitat in the CCSFS metapopulation, with 0 to 12 jays added per year to the Beach-North population.

How much habitat improvement is needed to achieve viability for CCSFS?

Presently, the CCSFS metapopulation is estimated to have only 13 territories in Strong habitat, 6 in Weak, and 237 potential territories in Sink habitat. All the Strong and Weak and 136 of the Sink territories are occupied. If habitat in CCSFS could be improved to become 50% to 70% Strong, then the projected decline in population size could be temporarily halted for about 30 years. Before decline resumed, if habitat were made 70% Strong, the population would be projected to plateau for several decades at a size that is about 50% occupancy of potential territories – thereby meeting one criterion for viability (Fig. 100). However, even with habitat improvement, in the long-term inbreeding would accumulate to levels that depress survival (Fig. 101), and that would cause a significant possibility of extinction (Fig. 102).

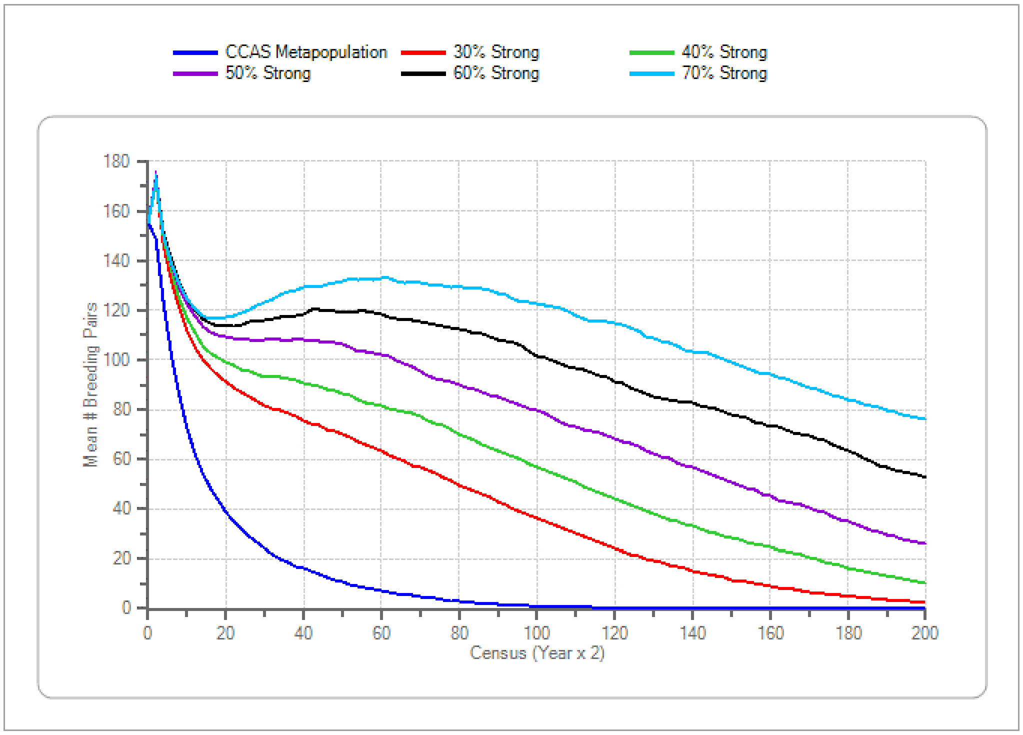

Figure 100. Projected number of breeding groups with current habitat in the CCSFS metapopulation (bottom, blue line), or with habitat improved to be 30%, 40%, 50%, 60%, or 70% Strong.

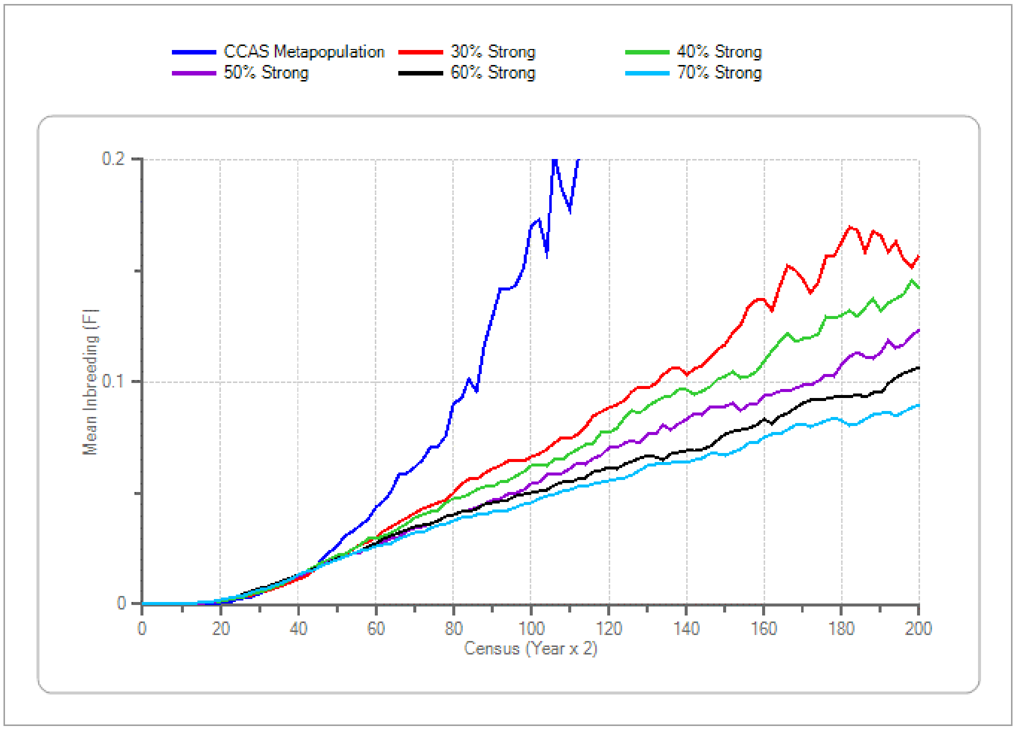

Figure 101. Accumulation of inbreeding with current habitat in the CCSFS metapopulation (top, blue line – going off the top of the graph as the population is going extinct), or with habitat improved to be 30%, 40%, 50%, 60%, or 70% Strong.

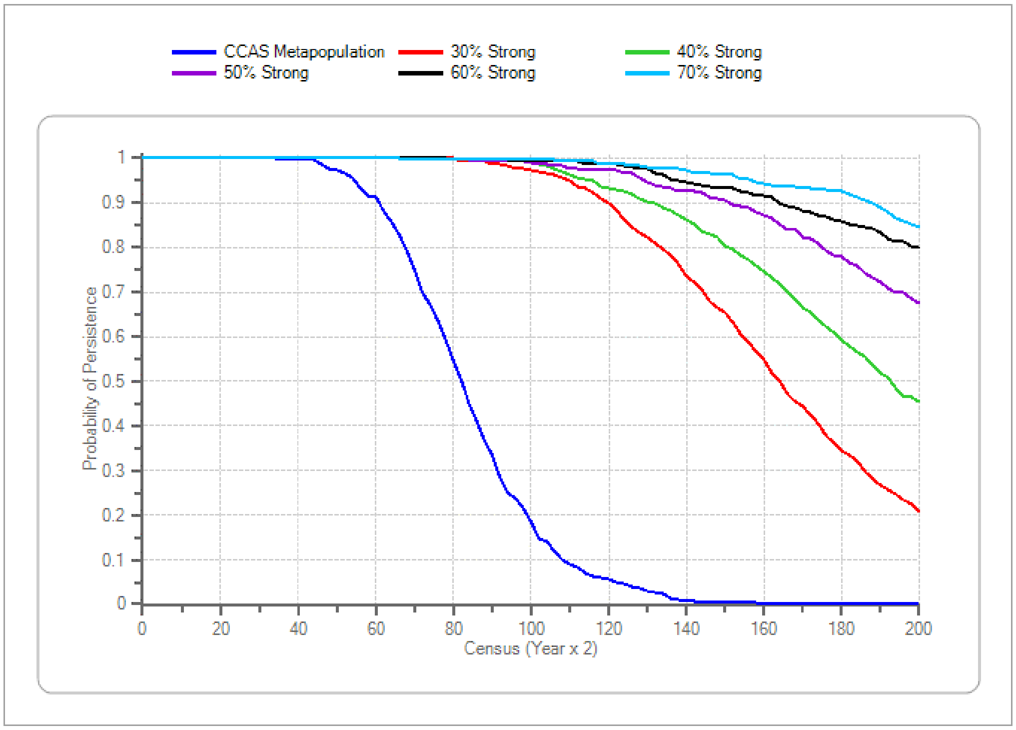

Figure 102. Probability of metapopulation persistence with current habitat in the CCSFS metapopulation (bottom, blue line), or with habitat improved to 30%, 40%, 50%, 60%, or 70% Strong.

Can a combination of habitat improvement and regular supplementation ensure CCSFS metapopulation viability?

If habitat is improved and there is regular reinforcement via immigrants (natural or via managed translocations) into the Beach-North population, then the CCSFS population could be largely stabilized at numbers that exceed 50% of habitat occupied in the case of 70% Strong (Fig. 103). Extinction would be completely avoided. Inbreeding would stay below 0.05 but begins to approach a level that depresses population growth in the long term (Fig. 104). The seemingly paradoxical lower inbreeding when there is supplementation, but no habitat improvement occurs because in that scenario the population collapses so that recent, non-inbred immigrants comprise a large part of the breeding population.

The overall conclusion from these initial models of possible management scenarios is that the CCSFS metapopulation could be sustained and viable if there is both considerable habitat improvement and regular immigration (even at low levels) from KSC or jays translocated from elsewhere.

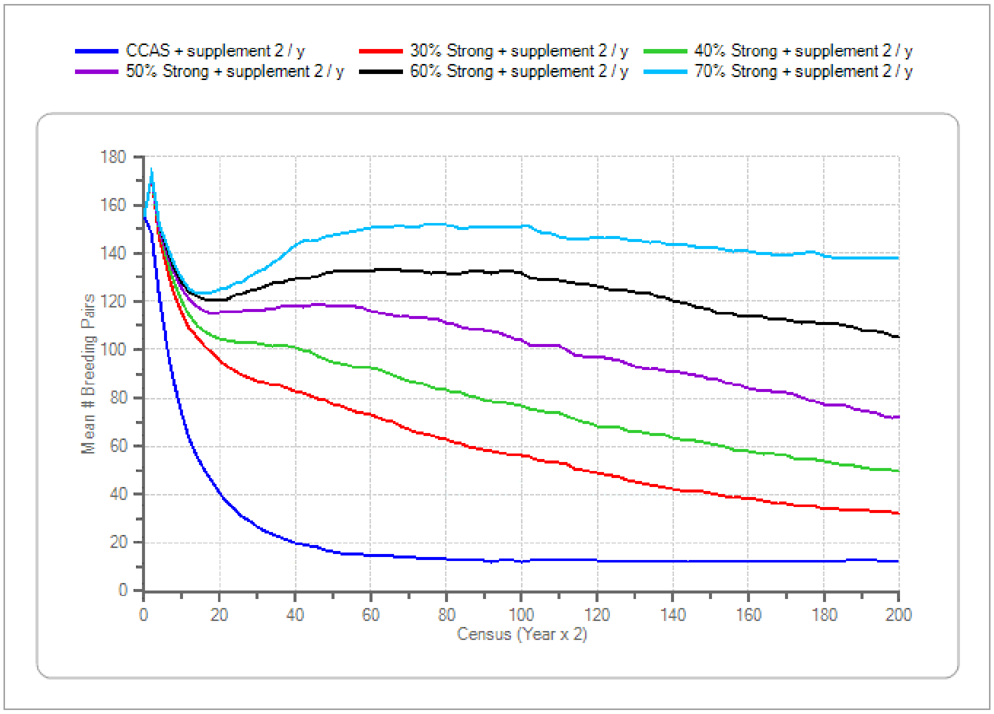

Figure 103. Projected number of breeding groups with current habitat in the CCSFS metapopulation (bottom, blue line), or with habitat improved to be 30%, 40%, 50%, 60%, or 70% Strong, and with 2 jays added to the Beach-North population each year.

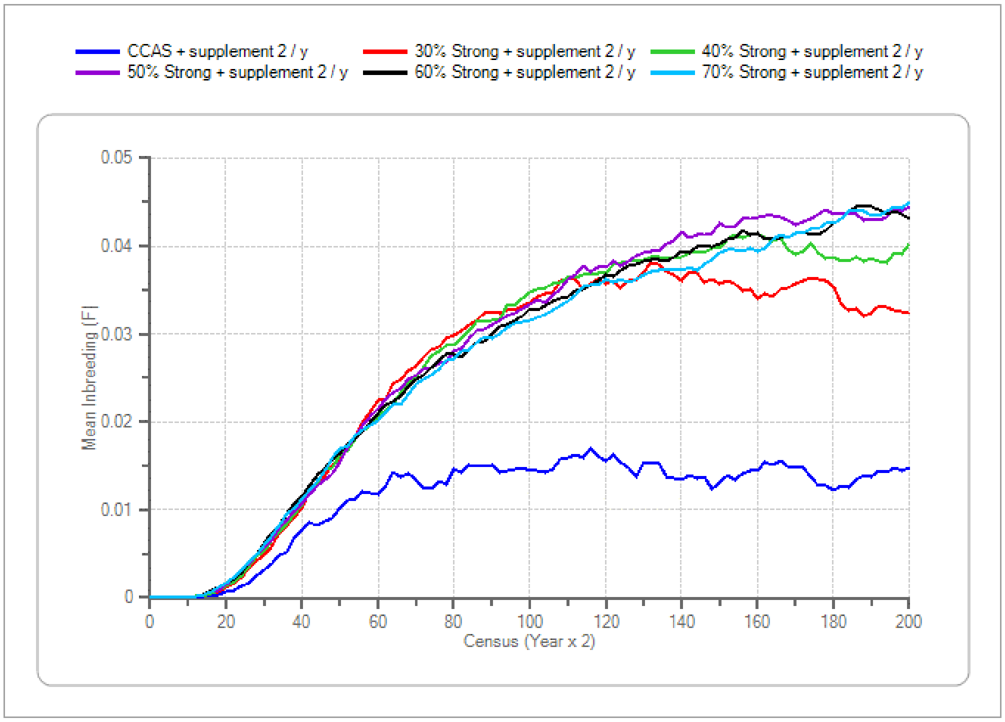

Figure 104. Accumulation of inbreeding with current habitat in the CCSFS metapopulation (bottom, blue line), or with habitat improved to be 30%, 40%, 50%, 60%, or 70% Strong, and with 2 jays added to the Beach-North population each year.

South and Central Mainland metapopulation management scenarios

The results for management scenarios for the South and Central Mainland Brevard metapopulation are summarized below.

What would be required to keep the metapopulation persisting (probability of extinction < 5%), stable (N > 0.5·K), and genetically health (inbreeding < 0.10)?

We analyzed the 12 populations in South Mainland and the 2 populations in Central Mainland as a single metapopulation. Some dispersal between South and Central has been observed, but the dispersal rate expected based on the distance separating South from Central is very low. As reported above (see section on *Overall Summary of Metapopulation Viability*), the SC Mainland metapopulation is fragmented into populations that are too small, too isolated, and have too little Strong habitat to ensure that the metapopulation will be viable. Below we explore management options that might achieve viability.

Would an increase in connectivity among local populations ensure viability?

The next three graphs show the projections if dispersal rates are as estimated from field data (blue lines), are 3x higher (red), are 5x higher (green), or there is panmixia across the metapopulation (purple). Although increased dispersal would considerably slow the decline, even with complete connectivity the population is projected to slowly decline (Fig. 105) because there are too few Strong potential territories (currently 80). Depending on the dispersal rate, the metapopulation starts to be vulnerable to extinction after about 30 or more years (Fig. 106), due to the accumulation of damaging levels of inbreeding (Fig. 107).

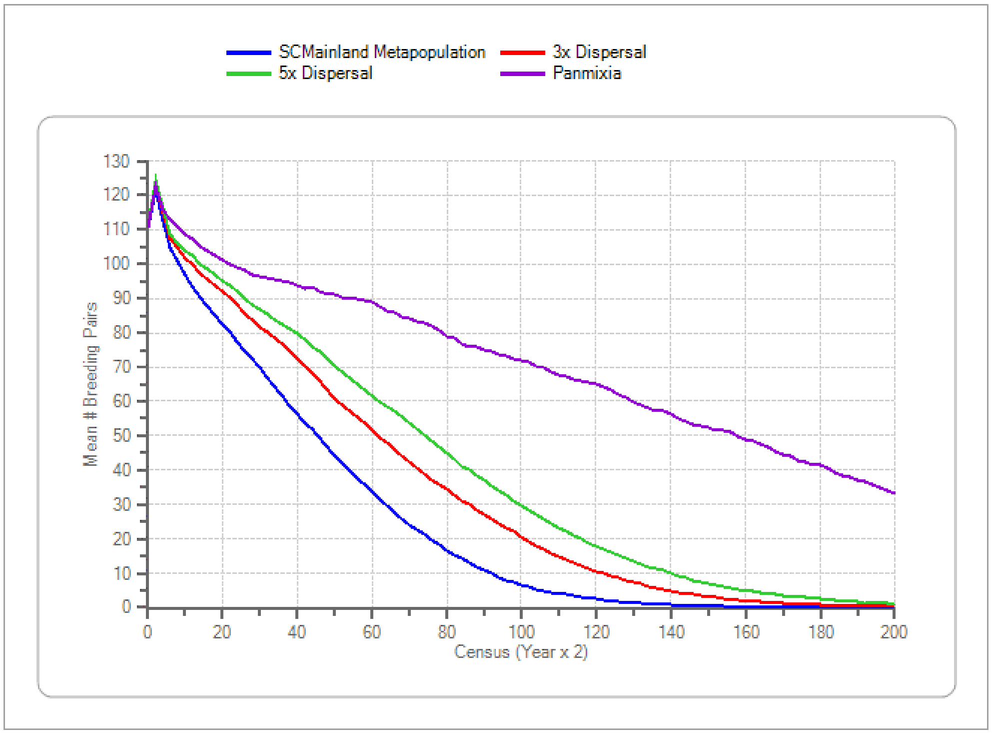

Figure 105. Projected number of breeding groups in the SC Mainland metapopulation with dispersal as estimated from distances between local populations, or with 3x or 5x higher dispersal, or under complete panmixia.

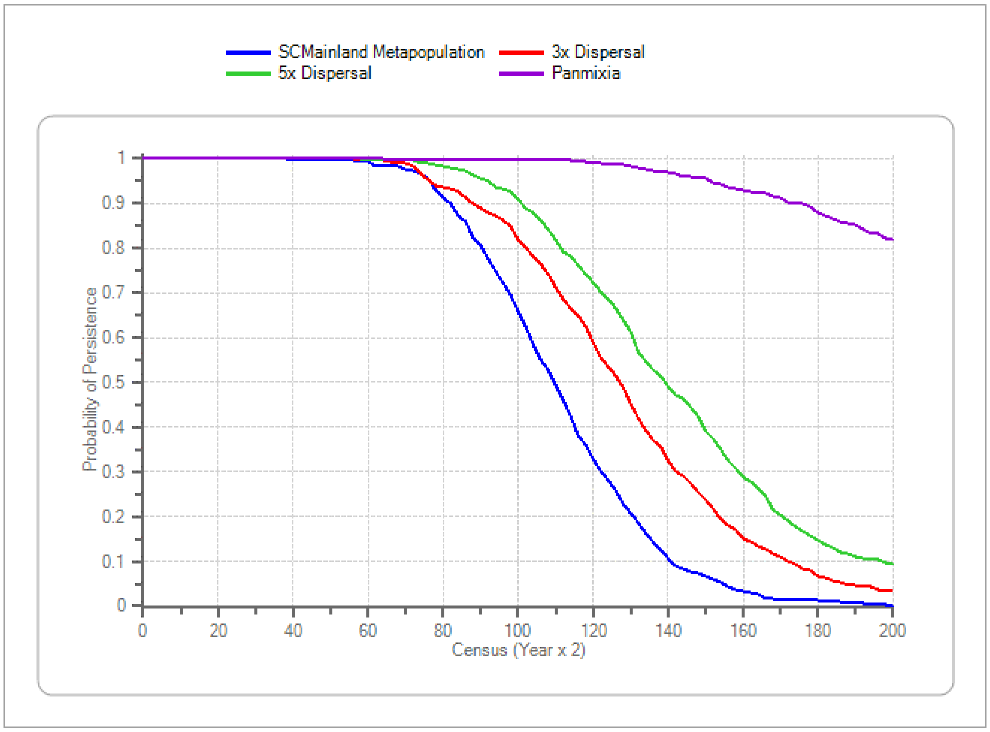

Figure 106. Probability of metapopulation persistence with dispersal as estimated from distances between local populations, or with 3x or 5x higher dispersal, or under complete panmixia.

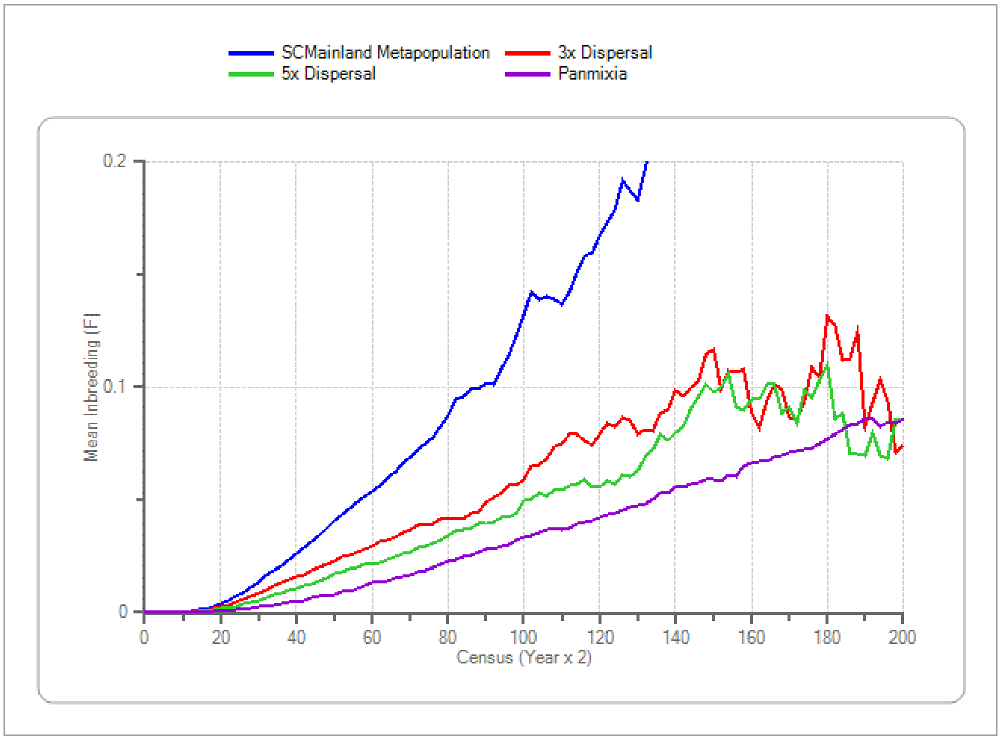

Figure 107. Accumulation of inbreeding with dispersal as estimated from distances between local populations, or with 3x or 5x higher dispersal, or under complete panmixia. The line for the estimated dispersal (blue) becomes undefined as the population goes toward extinction.

Would habitat improvement ensure viability?

The next three graphs show projections if habitat remains as is (80 Strong, 28 Weak, and 134 Sink potential territories; blue line), or if 50% of Weak is improved to Strong and 50% of Sink is improved to Weak, or if 100% of Weak is improved to Strong and 100% of Sink is improved to Weak, or if habitat is improved to become 70% Strong. Habitat improvement would slow the decline in numbers (Fig. 108), but it does not stop the decline nor prevent extinctions starting in about 30 to 40 years (Fig. 109), because the limited dispersal among populations results in inbreeding accumulating to damaging levels (Fig. 110).

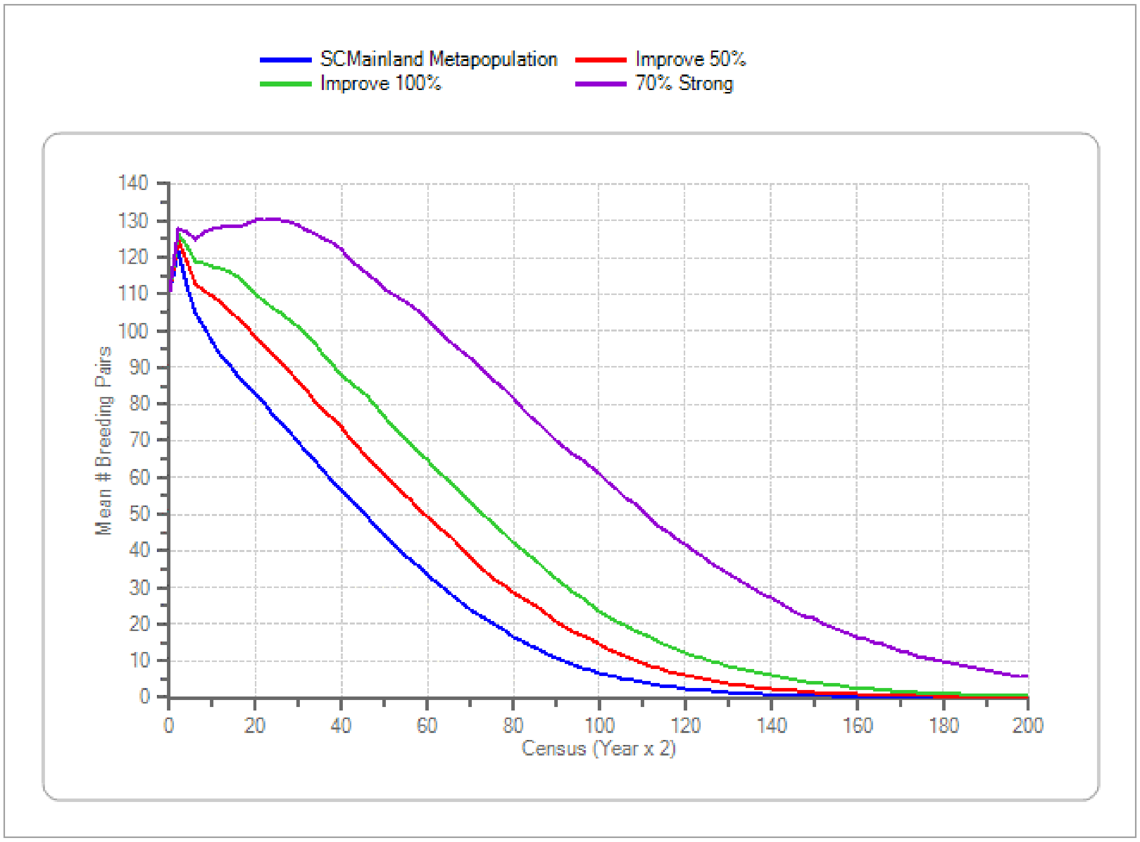

Figure 108. Projected number of breeding groups in the SC Mainland metapopulation with current habitat (blue), or 50% of Weak improved to Strong and 50% of Sink improved to Weak (red), 100% of weak improved to Strong and Sink improved to Weak (green), or 70% of potential territories Strong (purple). In these scenarios, dispersal is as estimated from distances between local populations.

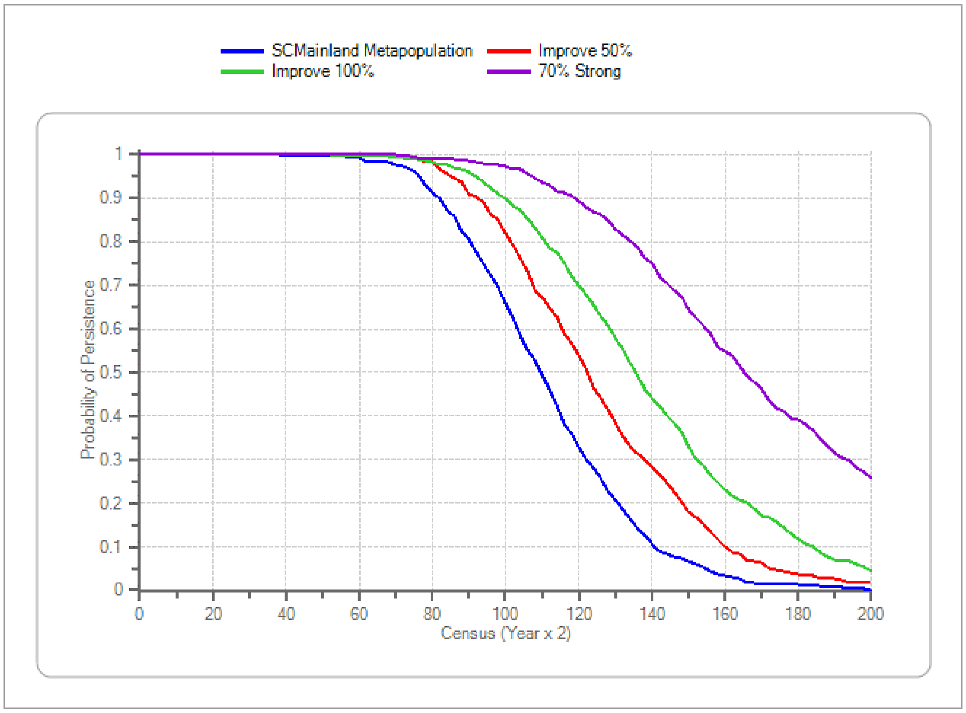

Figure 109. Probability of metapopulation persistence with current habitat, or 50% of Weak improved to Strong and 50% of Sink improved to Weak, 100% of weak improved to Strong and Sink improved to Weak, or 70% of potential territories Strong.

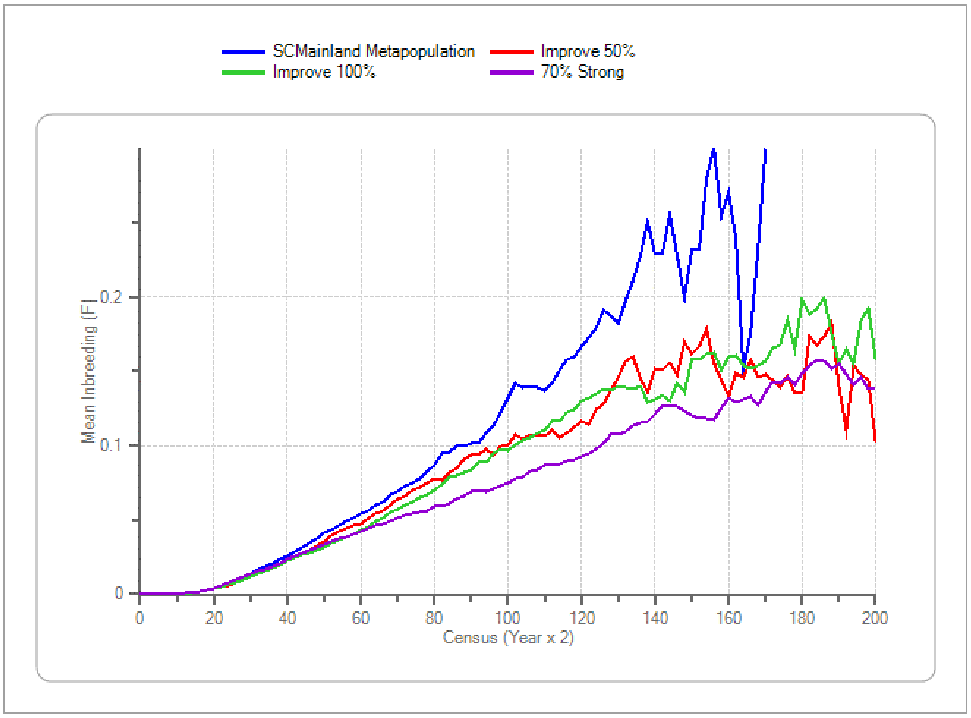

Figure 110. Accumulation of inbreeding with current habitat, or 50% of Weak improved to Strong and 50% of Sink improved to Weak, 100% of weak improved to Strong and Sink improved to Weak, or 70% of potential territories Strong.

Can a combination of habitat improvement and connectivity ensure metapopulation viability?

The next three graphs show the projections if habitat could be both improved and more connected. These scenarios used panmixia as an extreme case, but scenarios can also be run with intermediate levels of increased connectivity. In the best case (70% Strong and panmixia), the metapopulation is projected grow and then stay above 50% occupied (Fig. 111), not be at risk of extinction (Fig. 112) and keep inbreeding below 0.05 (Fig. 113). With the lesser amounts of habitat improvement, the populations decline slowly, have some probability of extinction after 80 to 90 years, and accumulate inbreeding coefficients to between 0.05 and 0.10.

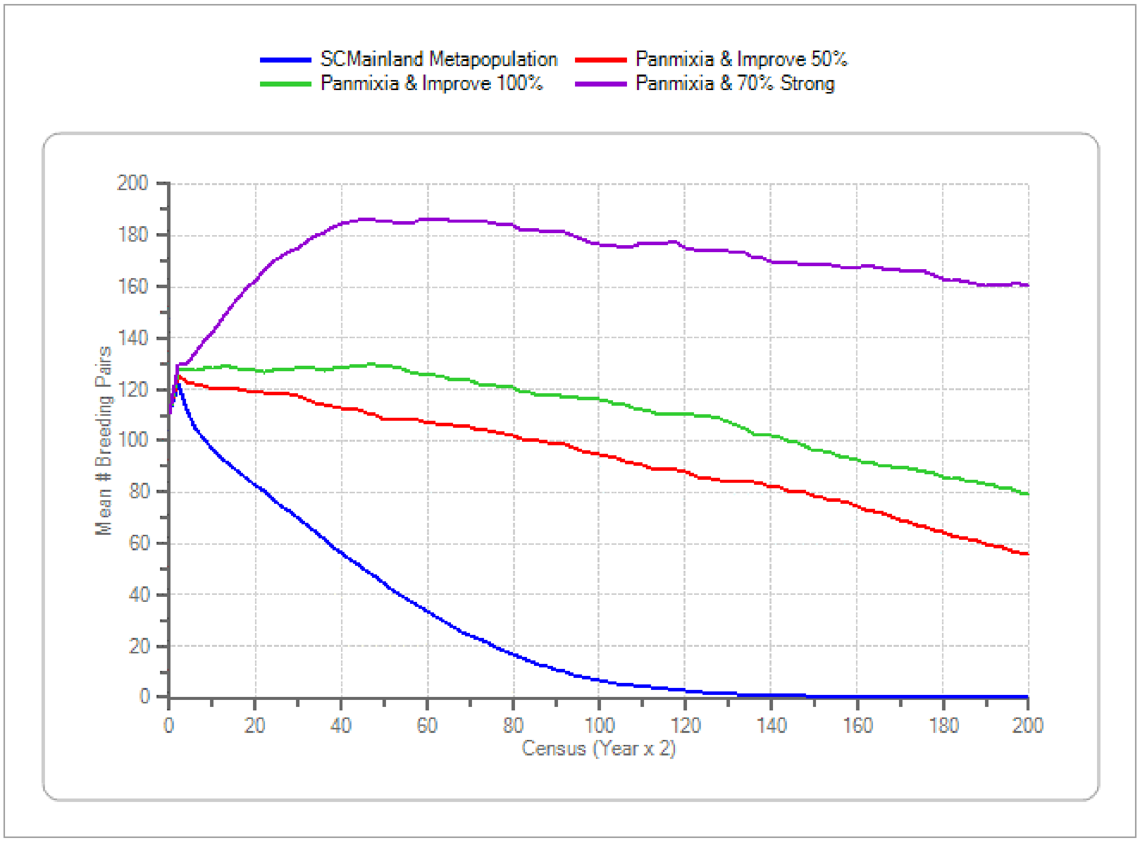

Figure 111. Projected number of breeding groups in the SC Mainland metapopulation with current habitat (blue), or 50% of Weak improved to Strong and 50% of Sink improved to Weak, combined with panmixia (red), 100% of weak improved to Strong and Sink improved to Weak, combined with panmixia (green), or 70% of potential territories Strong, combined with panmixia (purple).

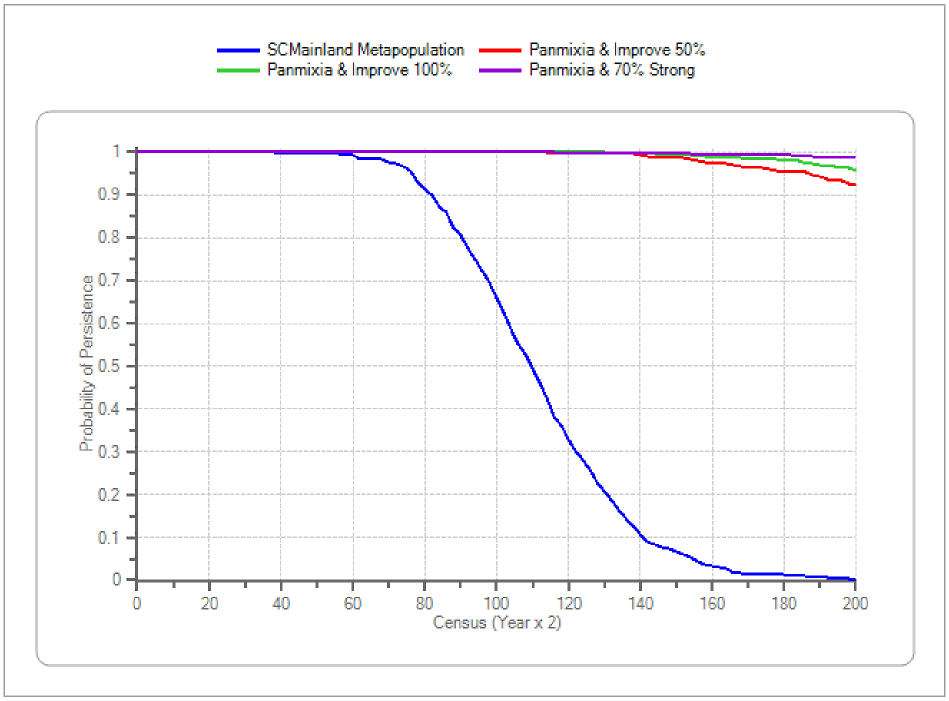

Figure 112. Probability of metapopulation persistence with current habitat, or 50% of Weak improved to Strong and 50% of Sink improved to Weak, combined with panmixia, 100% of weak improved to Strong and Sink improved to Weak, with panmixia, or 70% of potential territories Strong, with panmixia.

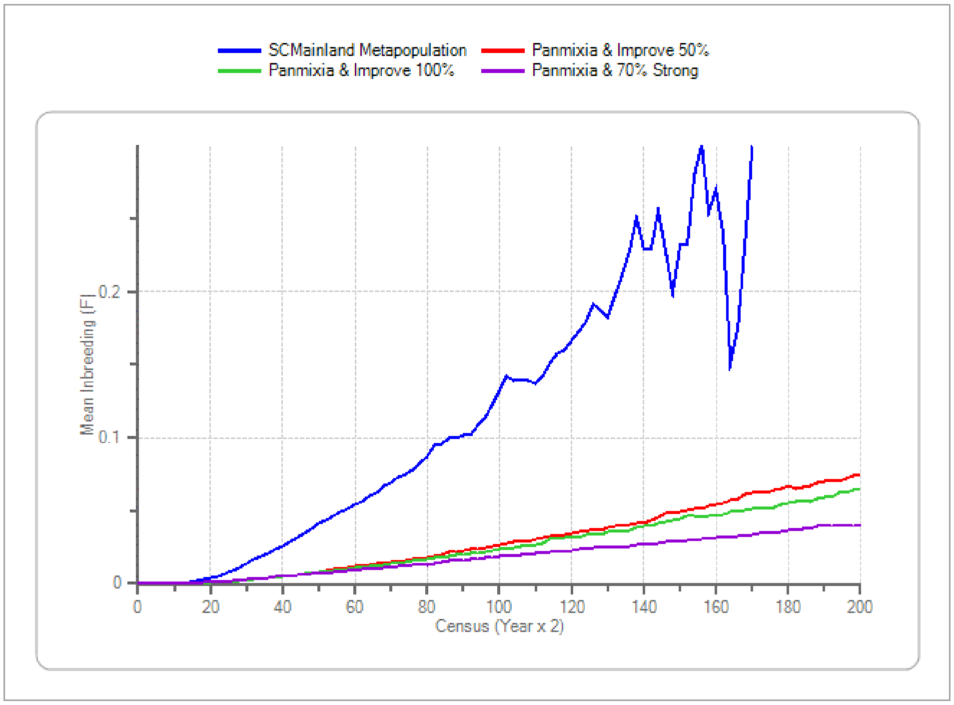

Figure 113. Accumulation of inbreeding with current habitat, or 50% of Weak improved to Strong and 50% of Sink improved to Weak, combined with panmixia, 100% of weak improved to Strong and Sink improved to Weak, with panmixia, or 70% of potential territories Strong, with panmixia.

Could metapopulation viability be achieved by regular supplementation?

To model the effect of possible supplementation with jays obtained from elsewhere, scenarios were run in which 2, 4, 8, or 12 jays were added to the metapopulation each year. The jays were added to one or two of the local populations each year, rotating among the populations so that each received the same number of immigrants over time (2 / 14 y, 4 / 14 y, 4 / 7 y, or 6 / 7 y). With such supplementation, the population size initially decreases and then plateaus at progressively higher numbers of breeding pairs with more immigration (Fig. 114). With the highest rate of supplementation tested (12 / y), the equilibrium population size closely approximates the number of Strong potential territories (80). However, this is less than the viability criterion of 50% of habitat occupied (121 breeding pairs). With any rate of ongoing supplementation, the metapopulation never goes extinct (graph not shown), and inbreeding is kept to low levels (Fig. 115).

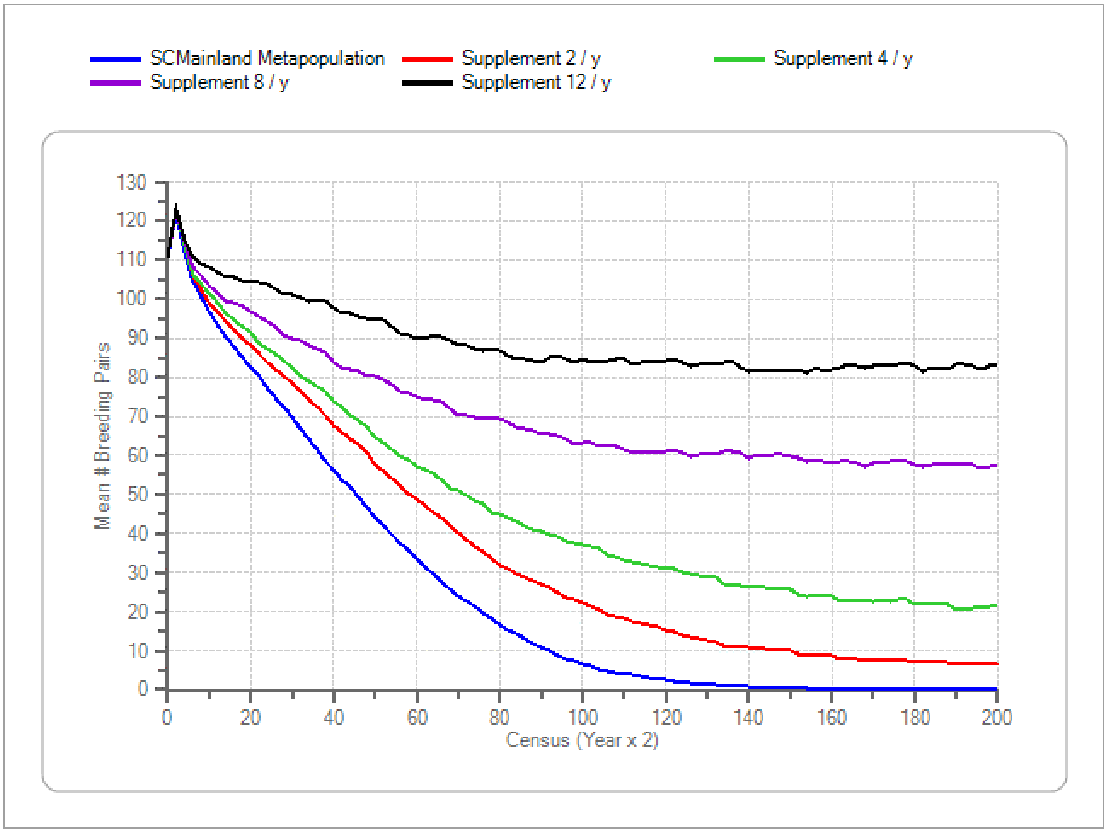

Figure 114. Projected number of breeding groups with current habitat and no supplementation (blue), or with 2, 4, 8, or 12 jays added to the SC Mainland metapopulation each year.

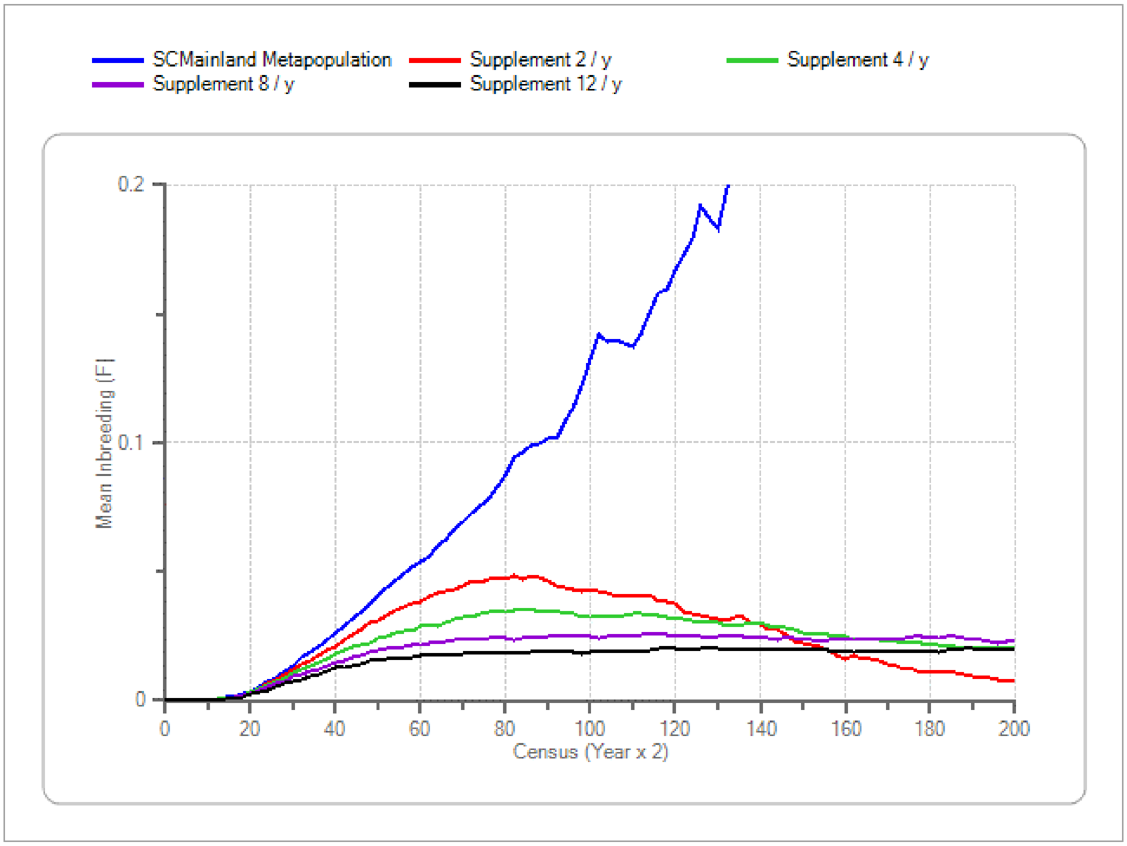

Figure 115. Accumulation of inbreeding with current habitat and no supplementation (blue), or with 2, 4, 8, or 12 jays added to the metapopulation each year.

Could metapopulation viability be achieved by a combination of habitat improvement and supplementation?

The above supplementation scenarios were run with the additional management action of improving the habitat to be 70% Strong. As above, with the highest rate of supplementation (12 jays added per year to the metapopulation), the SC Mainland metapopulation grows and then stabilizes at about the number of Strong potential territories (169, in these scenarios). With 8 or 12 jays added per year, the population remains stable above 50% occupancy (Fig. 116). With any of the rates of regular supplementation, there is no likelihood of extinction (not shown) and inbreeding stays below 0.05.

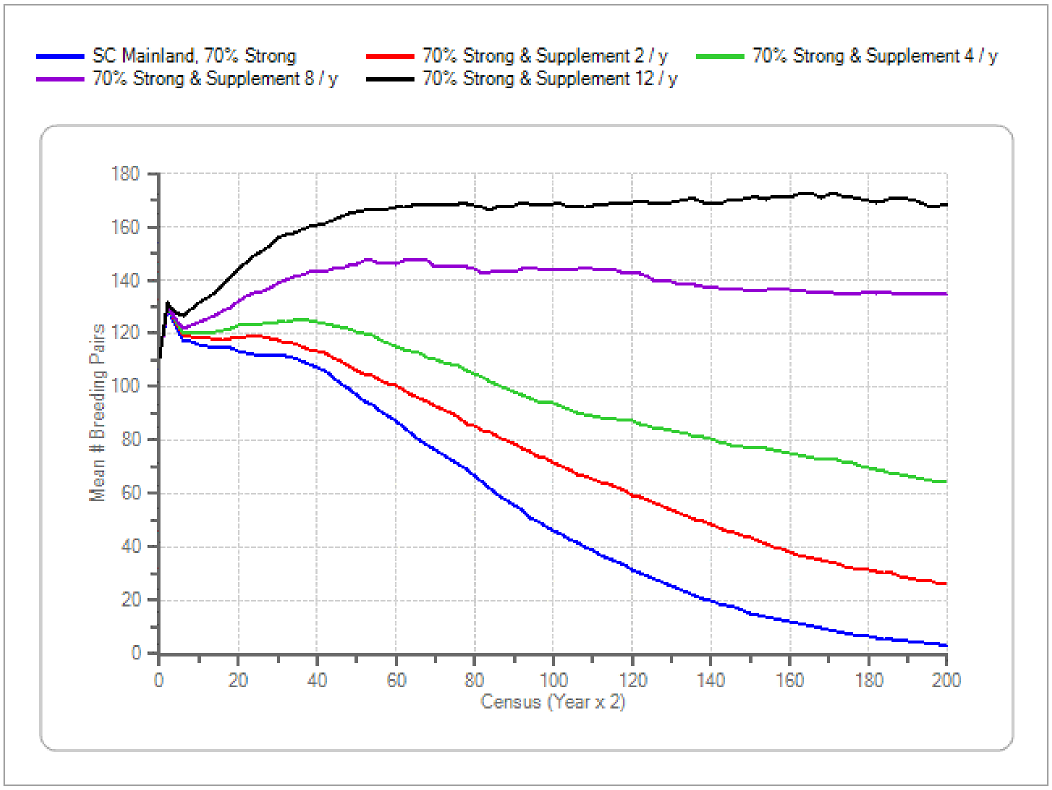

Figure 116. Projected number of breeding groups with habitat improved to be 70% Strong and no supplementation (blue), or with 2, 4, 8, or 12 jays added to the metapopulation each year.

If jays were removed from Sink territories for transfer elsewhere, how many would be removed?

If all the jays currently in Sink habitat were removed at the outset, that would provide about 126 jays (from 42 breeding groups) for release elsewhere. If all jays in Sink were removed every year, for a few decades about an additional 2 jays would be removed in each subsequent year, but that number would drop as the population declined. Very few jays would be available to remove from Sink after the initial removals, because the population is well below saturation and declining, so few jays would establish breeding groups in Sink habitat. The effect of such removals on the metapopulation trajectory would be an initial decline in numbers (the loss of the 42 breeding groups currently in Sink habitat), but much less impact on the long-term population size because the Sink habitat is expected to be largely emptied of jays over time as the metapopulation shrinks in size (Fig. 117). The impact of metapopulation persistence would also be small, with the S&C Mainland population projected to go extinct in about 30 and 70 years (Fig. 118).

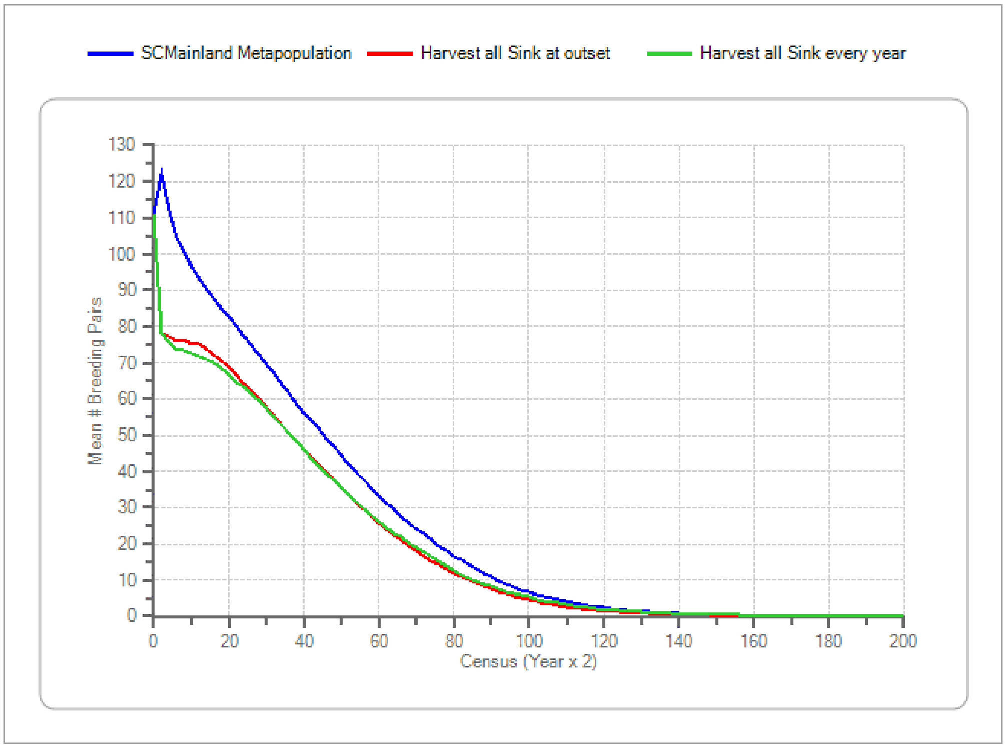

Figure 117. Projected number of breeding groups if all jays in Sink habitat are removed (red) or if in addition all jays in Sink habitat each subsequent year were removed (green).

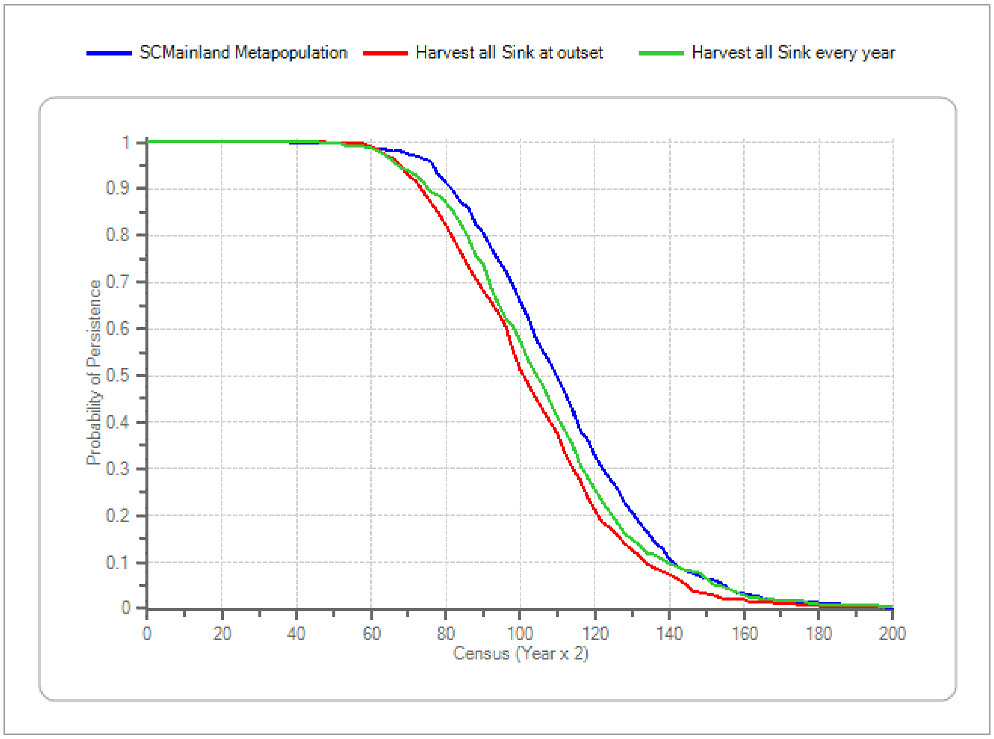

Figure 118. Probability of S&C Mainland metapopulation persistence if all jays in Sink habitat are removed or if in addition all jays in Sink habitat each subsequent year were removed.

If the habitat is improved to be 70% Strong, what is the excess that can be sustainably removed each year?

We tested scenarios that had 70% Strong territories (15% Weak and 15% Sink) and removed jays from Weak and Sink territories at rates ranging from 1 pair / 4 years / local population up to 4 pairs / year / population. As noted above (Figs. 108, 109, & 110), improvement of habitat alone does not ensure viability of the SC Mainland metapopulation, because the local populations are too small and isolated to avoid accumulation of damaging inbreeding. However, it is still informative to ask if removal of jays from Weak and Sink habitat will further threaten the metapopulation, and what levels of removal might be possible. Removing even a small number of jays from Weak and Sink habitats each year depresses population size (Fig. 119) and accelerates extinction (Fig. 120), but these reductions in population projections are not large. The impacts are not greater if attempts are made to remove more than 2 pairs of jays per population per year. This is because after the initial few years of removals, few jays remain in Weak and Sink habitat, and with the declining metapopulation few jays move into Weak and Sink habitat each year, so the realized rate of removal across the entire metapopulation stays below about 3 jays per year (Fig. 121).

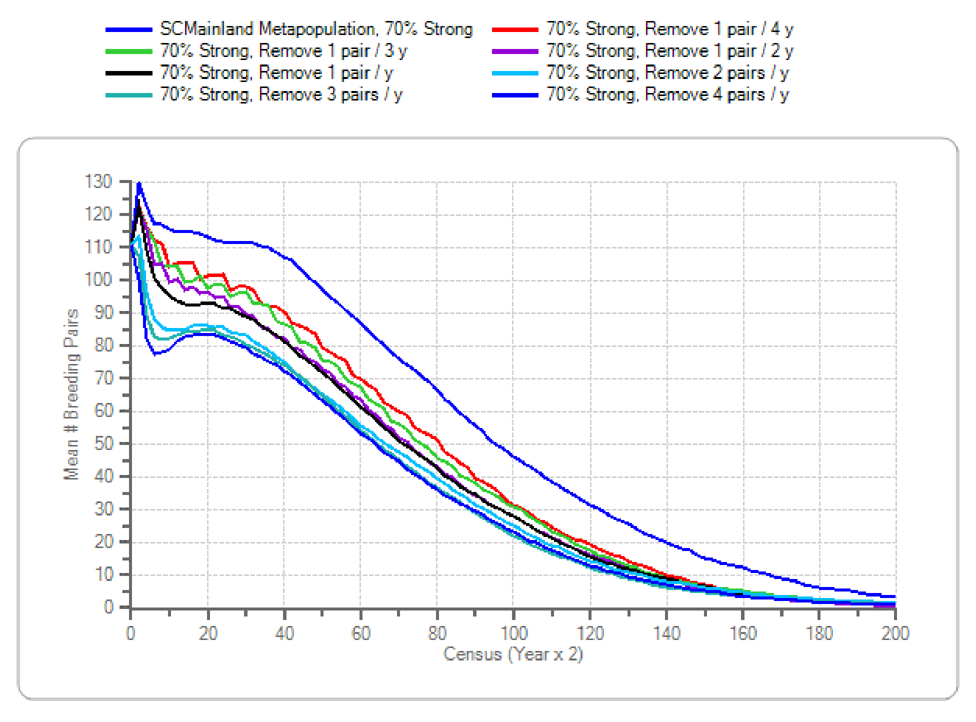

Figure 119. Project number of breeding groups in the SC Mainland metapopulation if 70% of habitat is Strong, and jays are taken from Weak and Sink habitat in each local population at rates from 1 pair / 4 y up to 4 pairs / y.

These scenarios model aggressive removal schedules and result after a few years in the nearly complete depletion of jays in all Weak and Sink habitat. Scenarios testing options for removal for only a few years or only specific local populations can be examined as such management options are identified.

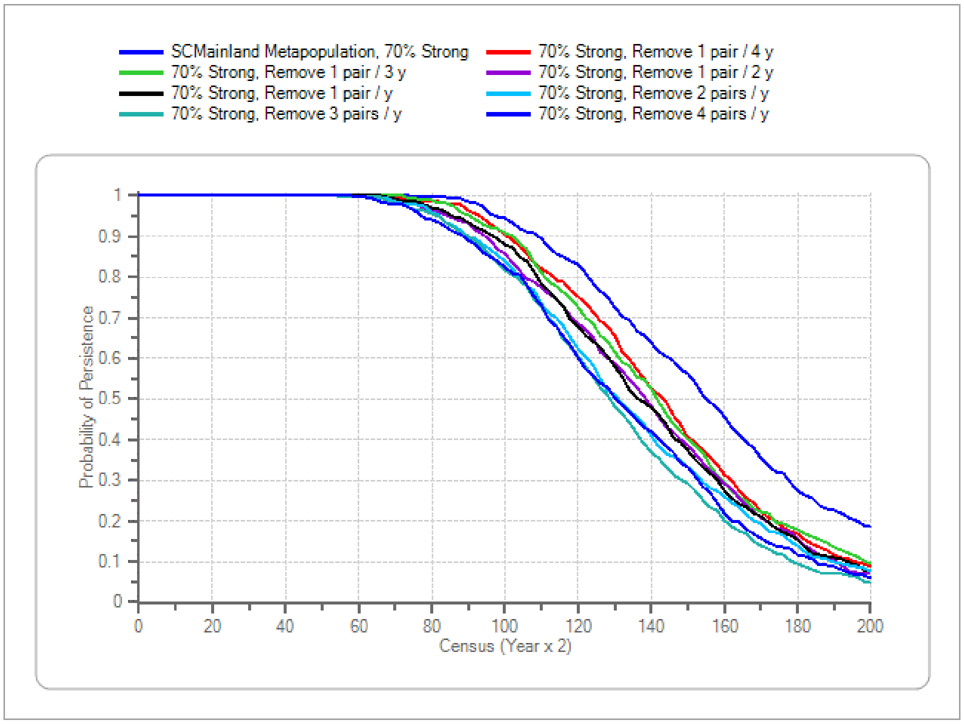

Figure 120. Probability of persistence of the SC Mainland metapopulation if 70% of habitat is Strong, and jays are taken from Weak and Sink habitat in each local population at rates from 1 pair / 4 y up to 4 pairs / y.

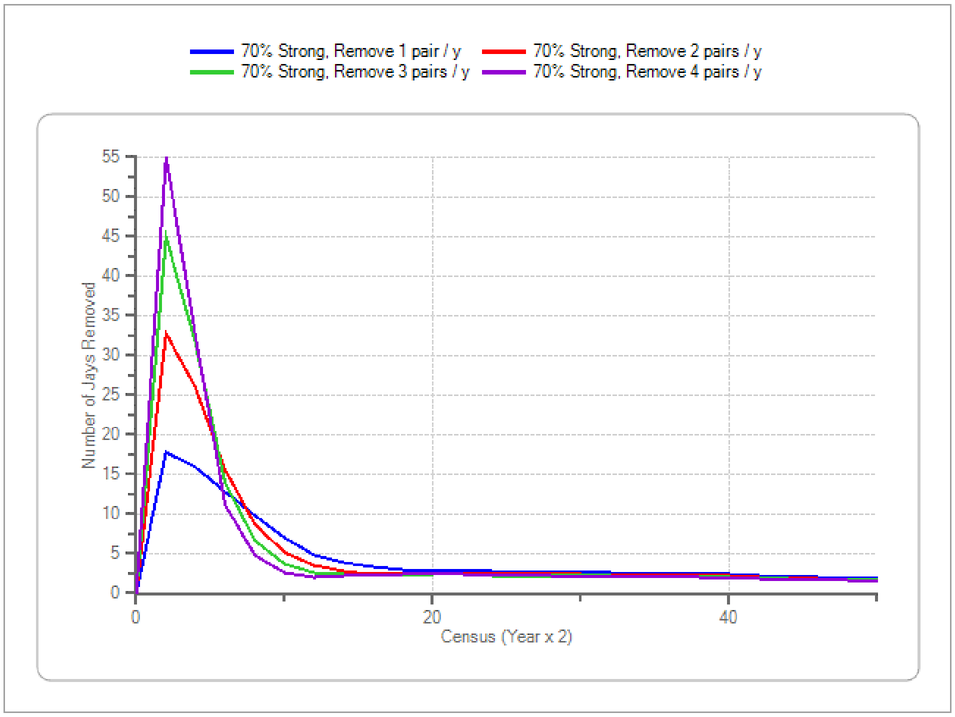

Figure 121. Number of jays removed each year (shown only for the first 25 years) if 70% of habitat is Strong, and up to 1 pair, 2 pairs, 3 pairs, or 4 pairs are taken from Weak and Sink habitat in each local population.

Specific management option tested: Acquisition of potential habitat

What if Jordan and Valkaria could be connected, and acquisitions added to BABC (+12 potential territories), CORA (+9), CORR (+5), CP (+12), JORD+VALK (+10), and FELS (new population, +5)?

We have not yet specified and then tested very many scenarios that would describe possible management actions that might be applied to specific populations – e.g., possible acquisitions to add to managed habitat, connection of nearby populations via corridors, or removal of populations in habitat that cannot be managed. Such specific management scenarios can be tested now that we have a population model that has been reasonably well validated. One scenario for the SC Mainland metapopulation has been run to test the impact of a set of possible acquisitions.

If these acquisitions, which increase potential territories by 24% (albeit mostly in currently Sink habitat), are made, the metapopulation still declines but would typically have about 10 more breeding groups at any time during the decline (Fig. 122, bottom two lines). The accumulation of inbreeding is slowed but still results in levels (F > 0.10 within 50 years, Fig. 123, top two lines) that accelerate the decline and cause extinction typically sometime between about 40 years and 80 years (Fig. 124, bottom 2 lines). If these acquisitions are made and habitat improvements result in 70% of territories being Strong, then the boost in population size is larger (Fig. 122), but inbreeding still accumulates to levels (Fig. 123) that cause high probability of extinction (Fig. 124). Thus, the acquisitions help, but do not achieve metapopulation viability because the continued isolation of the small local populations results in damaging inbreeding.

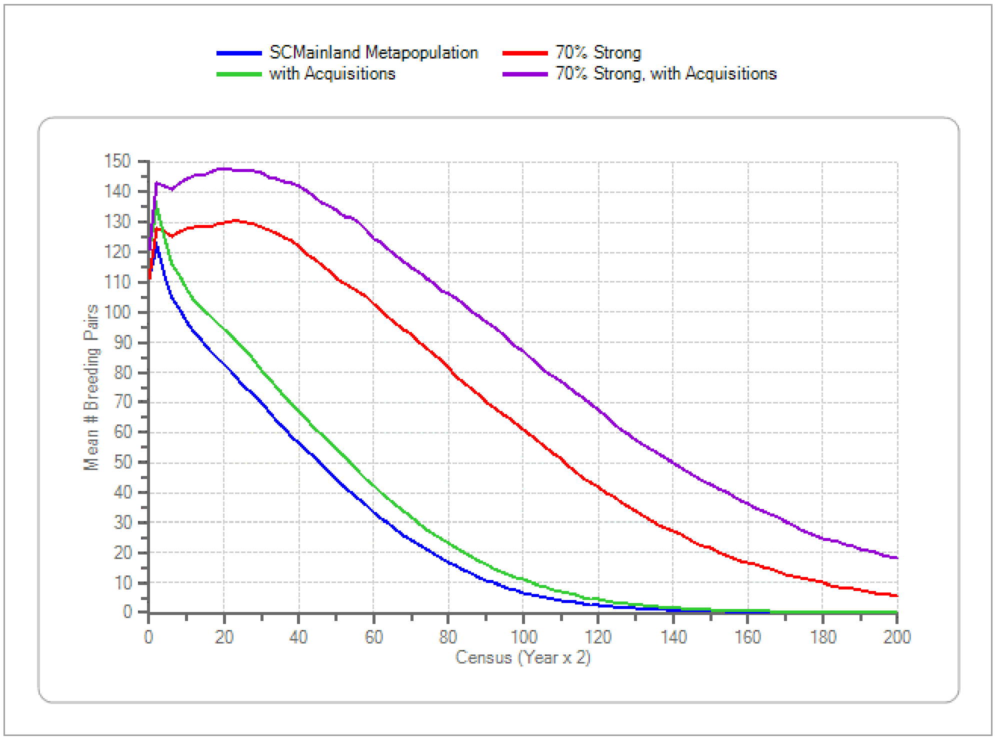

Figure 122. Projected number of breeding groups in the SC Mainland metapopulation with no change in management (blue), with some possible acquisitions (green, see text for explanation of acquisitions), if habitat is improved to be 70% Strong (red), or if habitat is improved to 70% Strong and acquisitions are made (purple).

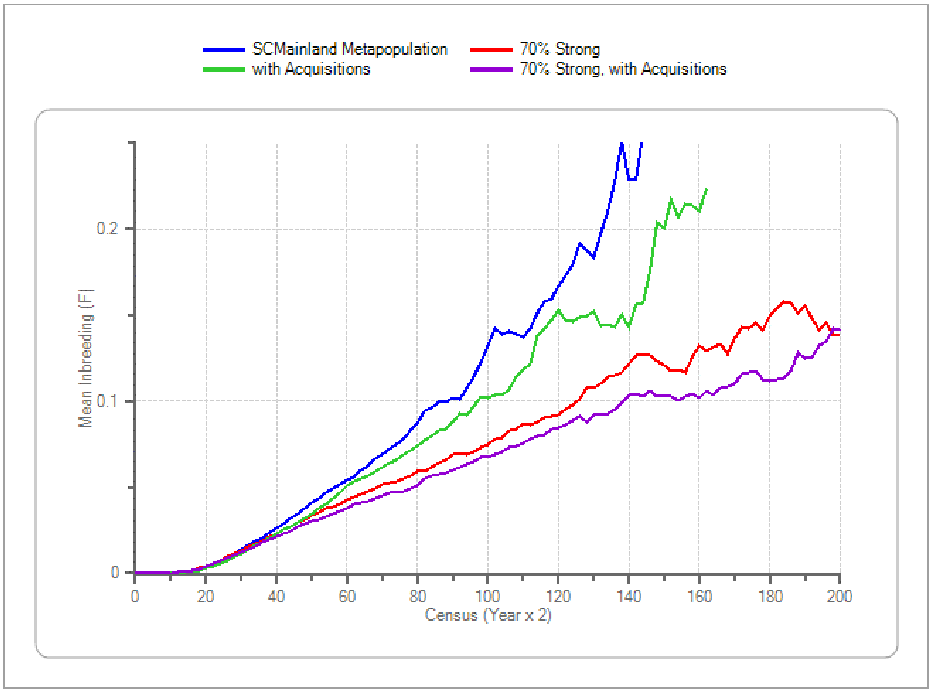

Figure 123. Accumulation of inbreeding with no change in management (blue), with some possible acquisitions (green, see text for explanation of acquisitions), if habitat is improved to be 70% Strong (red), or if habitat is improved to 70% Strong and acquisitions are made (purple).

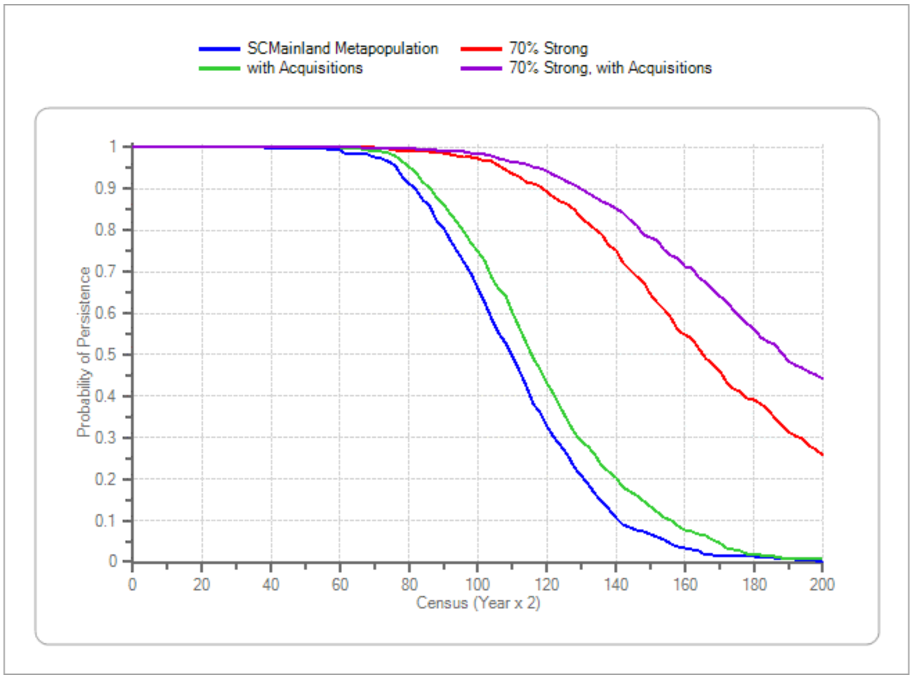

Figure 124. Probability of persistence of the SC Mainland metapopulation with no change in management, with some possible acquisitions, if habitat is improved to be 70% Strong, or if habitat is improved to 70% Strong and acquisitions are made.

What if the proposed acquisitions are made and connectivity is increased among all populations?

The damaging levels of inbreeding can be reduced or avoided by increased connectivity among all local populations – achieved either by the identified acquisitions or other management actions. If dispersal is increased 5-fold, there still is not dramatic benefit from the acquisitions if habitat is not improved throughout SC Mainland (Fig. 125, bottom two lines; Fig. 126, top two lines; Fig. 127, bottom two lines). If increased dispersal and acquisitions are combined with improving habitat to 70% Strong, then for 60 or more years the metapopulation remains at more than 50% occupancy (Fig. 125, red line), inbreeding stays at low levels (Fig. 126), and extinction is avoided (Fig. 127), and the benefit of acquisitions on boosting population size is more notable (Fig. 125, purple line). However, this combination of management actions is not projected to be enough to ensure metapopulation viability beyond about 60 years.

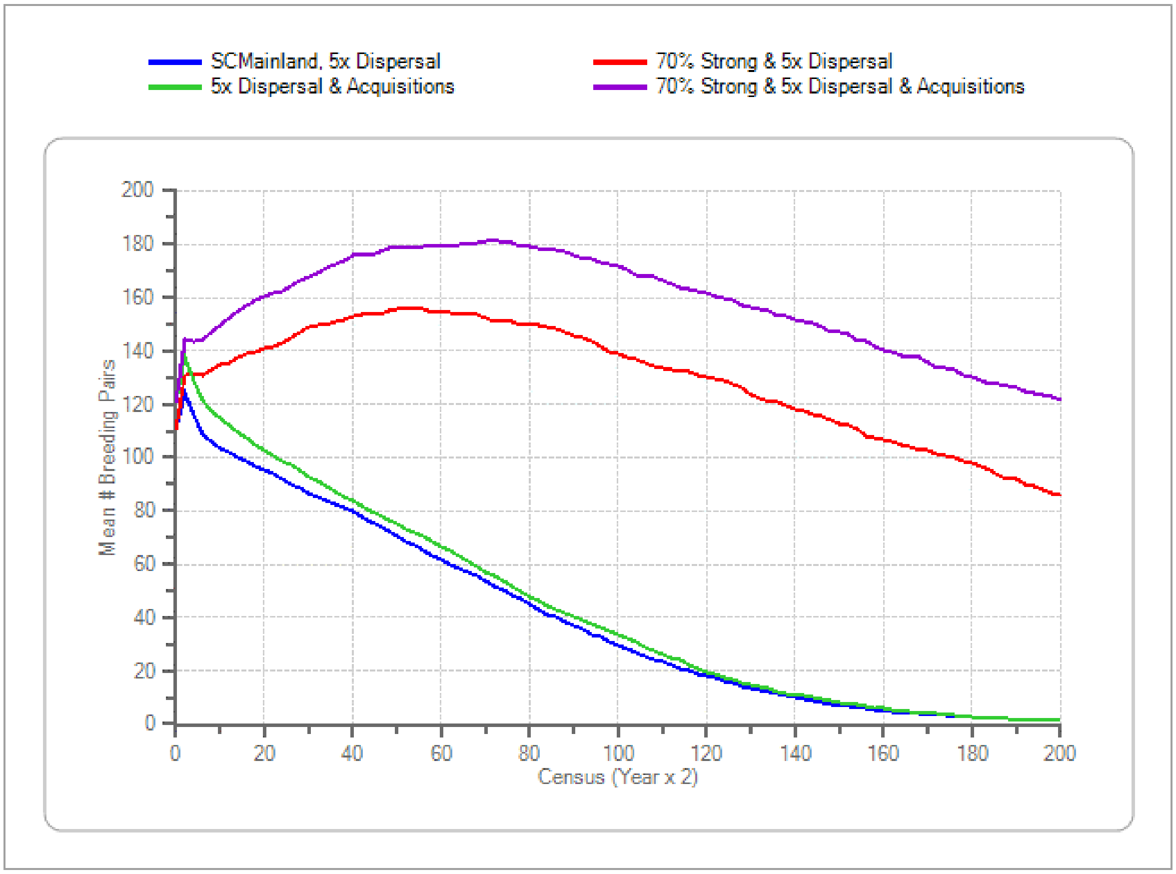

Figure 125. Projected number of breeding groups in the SC Mainland metapopulation with 5-fold increase in inter-population dispersal, with some possible acquisitions, if habitat is improved to be 70% Strong, or if habitat is improved to 70% Strong and acquisitions are made.

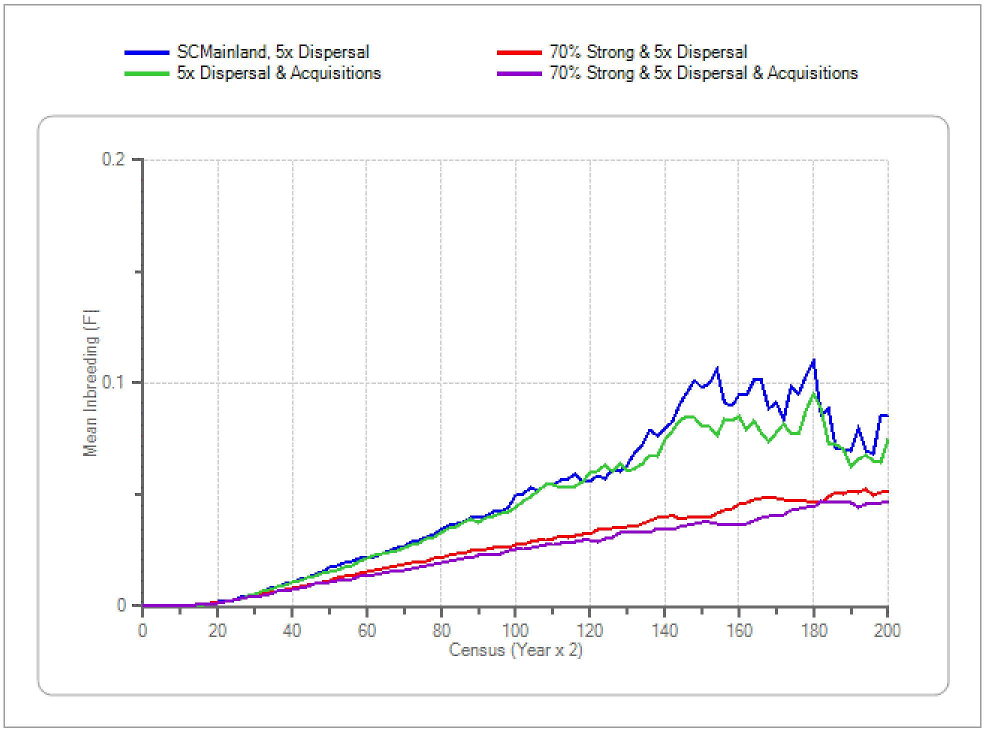

Figure 126. Accumulation of inbreeding with 5-fold increase in dispersal, with possible acquisitions, if habitat is improved to 70% Strong, or if habitat is improved to 70% Strong and acquisitions are made.

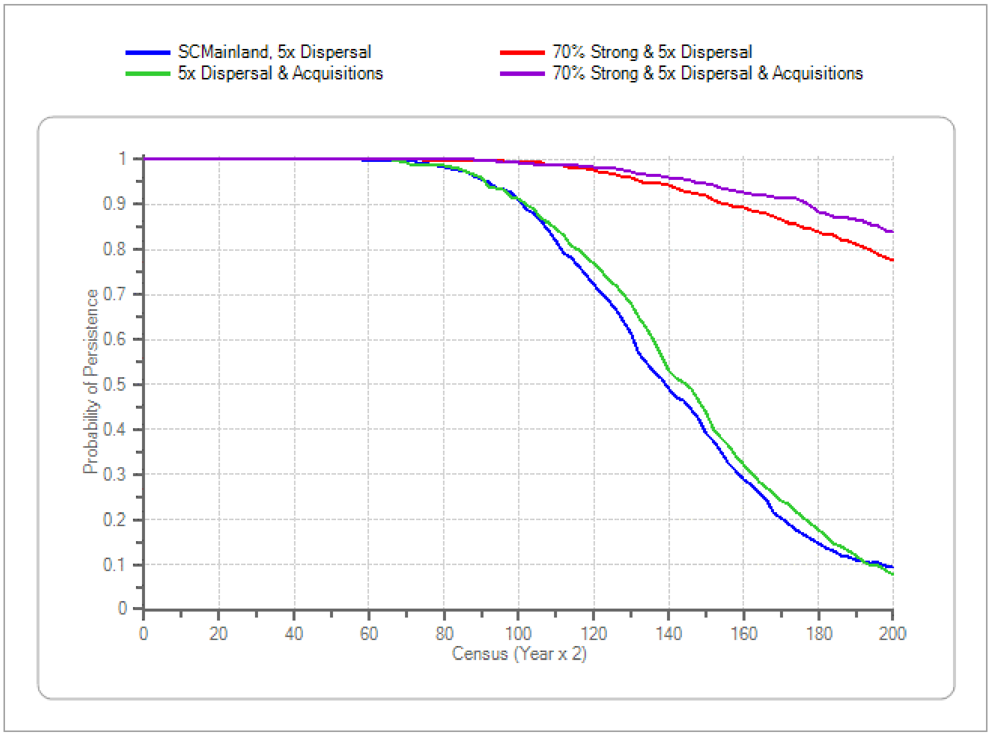

Figure 127. Probability of persistence of the SC Mainland metapopulation with 5-fold increase in inter-population dispersal, with some possible acquisitions, if habitat is improved to be 70% Strong, or if habitat is improved to 70% Strong and acquisitions are made.

North Mainland metapopulation management scenarios

The results from exploration of management scenarios for the North Mainland Brevard metapopulation are summarized below.

What would be required to keep the metapopulation persisting (probability of extinction < 5%), stable (N > Kmax), and genetically health (inbreeding < 0.10)?

As described earlier, the N Mainland metapopulation has too few breeding groups, too little optimal habitat, and is scattered among too many very small fragments to allow it to persist as a functional metapopulation. The following scenarios were examined to determine if the N Mainland metapopulation could be made viable as an isolated metapopulation, by habitat improvement, connectivity, and supplementing initial numbers of jays; or by habitat improvement and ongoing supplementation.

Would habitat improvement be enough?

As shown in the next graph, improvements in the existing potential habitat would not be sufficient to prevent the rapid decline of the North Mainland populations. The local populations are too small and isolated to sustain a viable metapopulation.

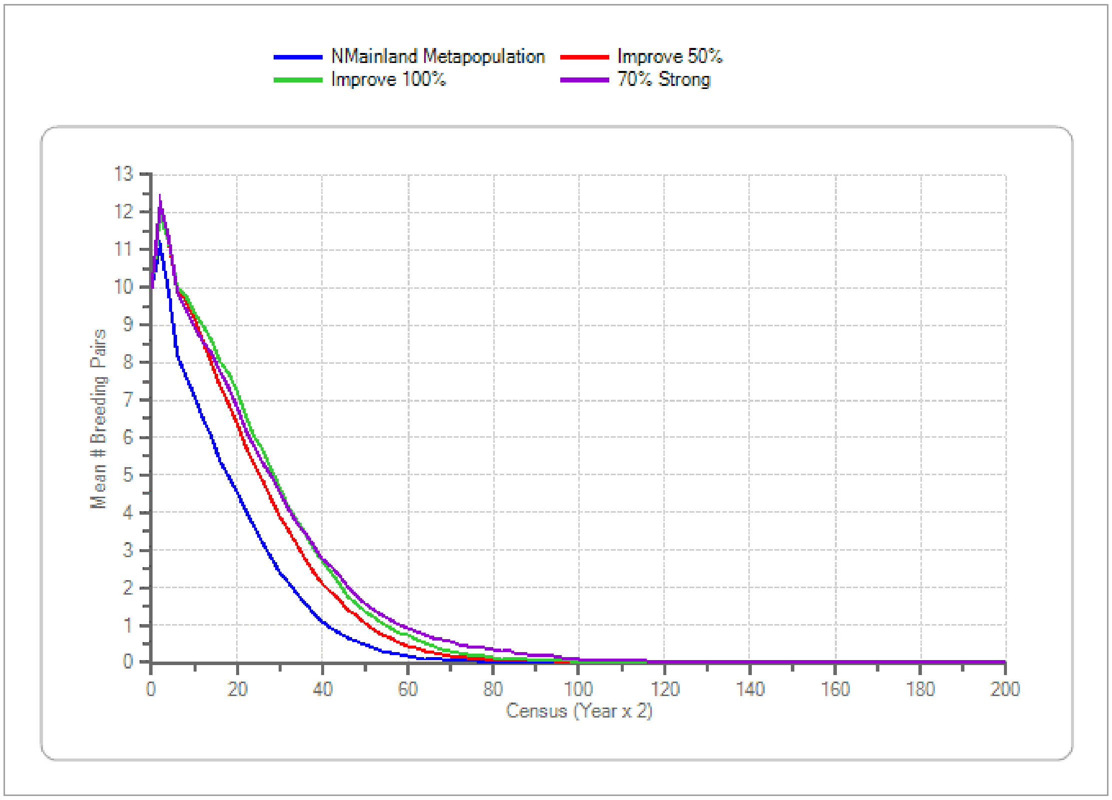

Figure 128. Projected number of breeding groups without any improvement to habitat (blue line), with 50% of Sink improved to Weak and 50% of Weak improved to Strong, with all Sink improved to Weak and all Weak improved to Strong, or with 70% maintained as Strong, 20% Weak, and 10% Sink.

Would improved connectivity be enough?

Projections in Figure 129 show that the increasing connectivity among N Mainland populations also would not be sufficient to stop the decline. The total metapopulation is too small and habitat inadequate to support a viable population, even if there was complete mixing of the local populations.

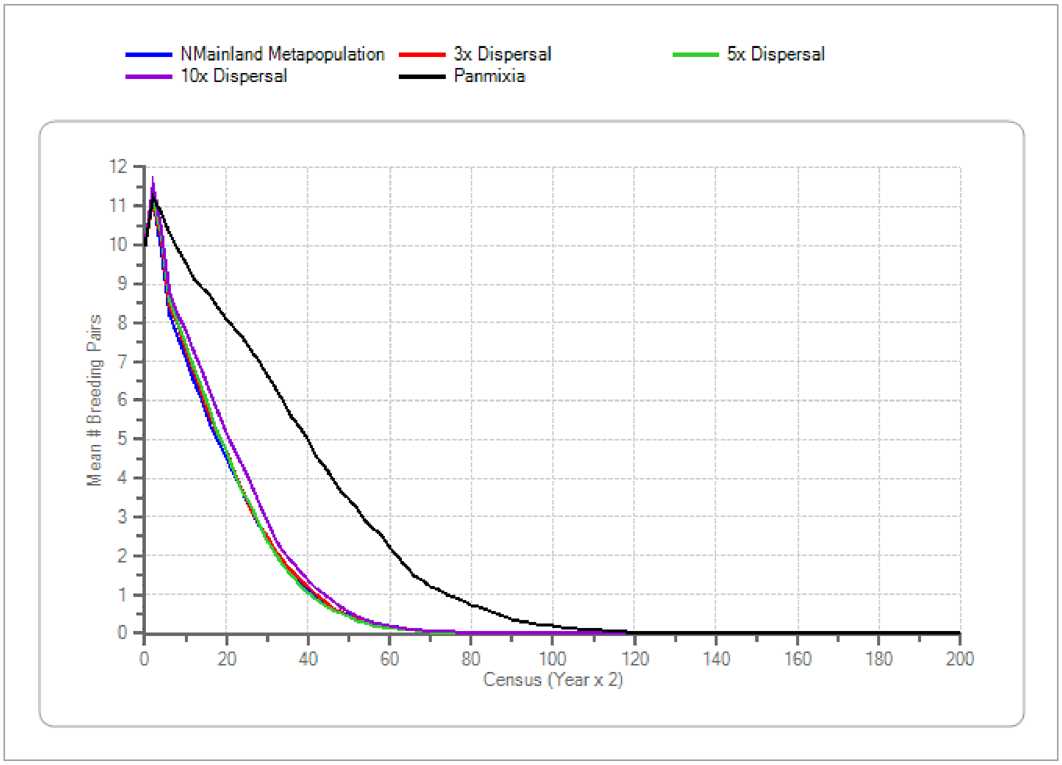

Figure 129. Projected number of breeding groups with estimated current dispersal between local populations (blue), with 3x, 5x, 10x dispersal, or panmixia among North Mainland populations.

Would a combination of habitat improvement plus increased connectivity achieve long-term population viability?

As shown in the next set of graphs, habitat improvement combined with connectivity could result in the North Mainland metapopulation persisting for 50 or even 100 years. However, even with complete connectivity (panmixia), the metapopulation would eventually go into decline (starting in about 20 years; Fig. 130) because the population is too small to avoid damage from accumulating inbreeding (Fig. 131), and extinction is likely (but not inevitable) after about 50 years (Fig. 132).

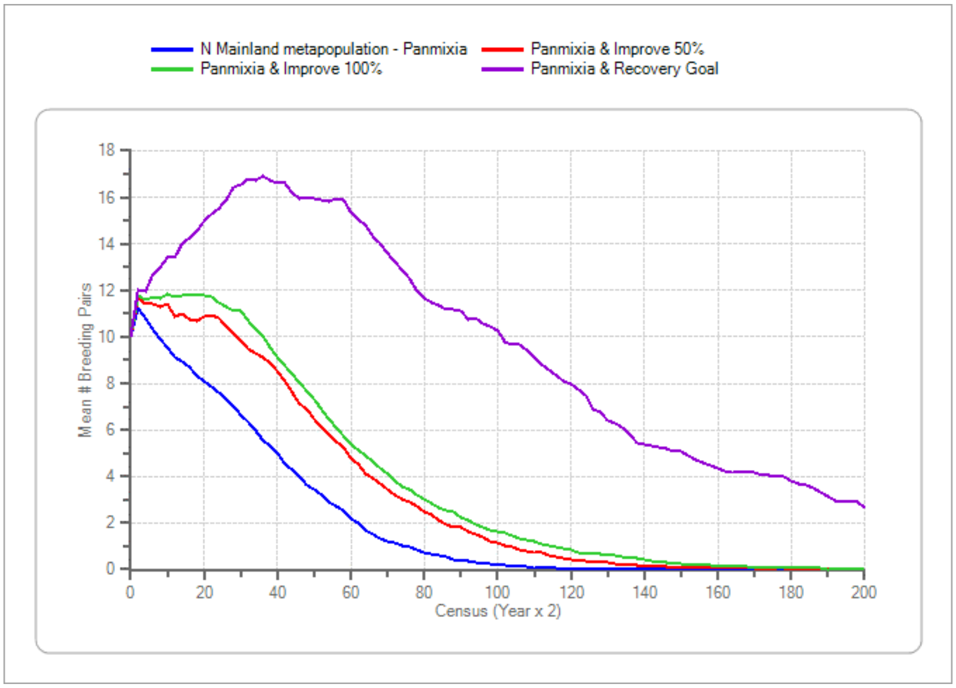

Figure 130. Projected number of breeding groups without any improvement to habitat (blue line), with 50% of Sink improved to Weak and 50% of Weak improved to Strong, with all Sink improved to Weak and all Weak improved to Strong, or with 70% maintained as Strong if there is also complete connectivity (panmixia) among the local populations.

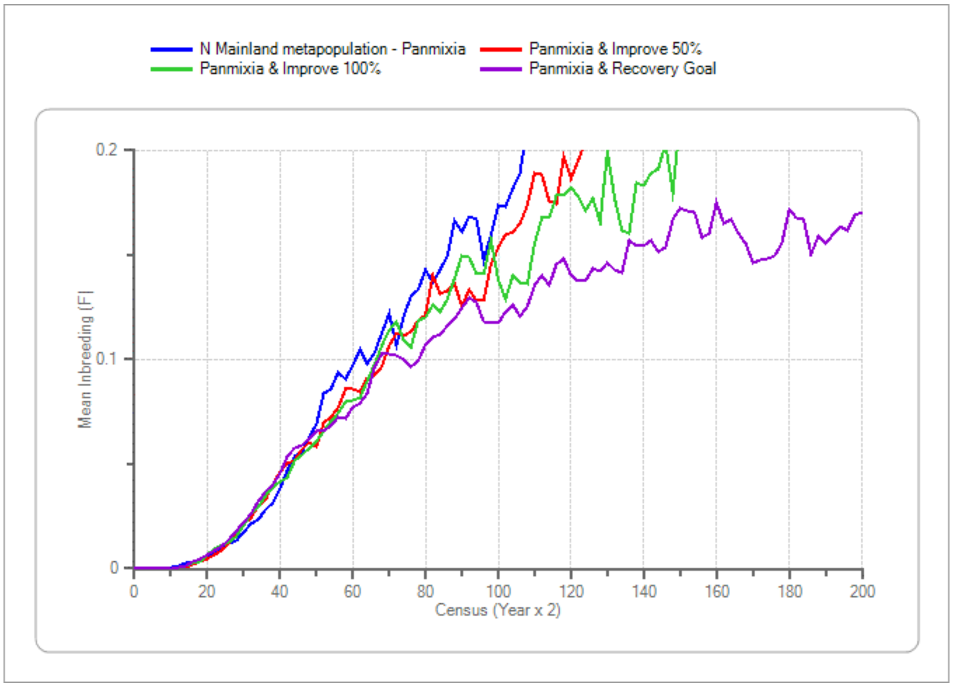

Figure 131. Accumulation of inbreeding without any improvement to habitat (blue line), with 50% of Sink improved to Weak and 50% of Weak improved to Strong, with all Sink improved to Weak and all Weak improved to Strong, or with 70% maintained as Strong if there is also complete connectivity (panmixia) among the local populations.

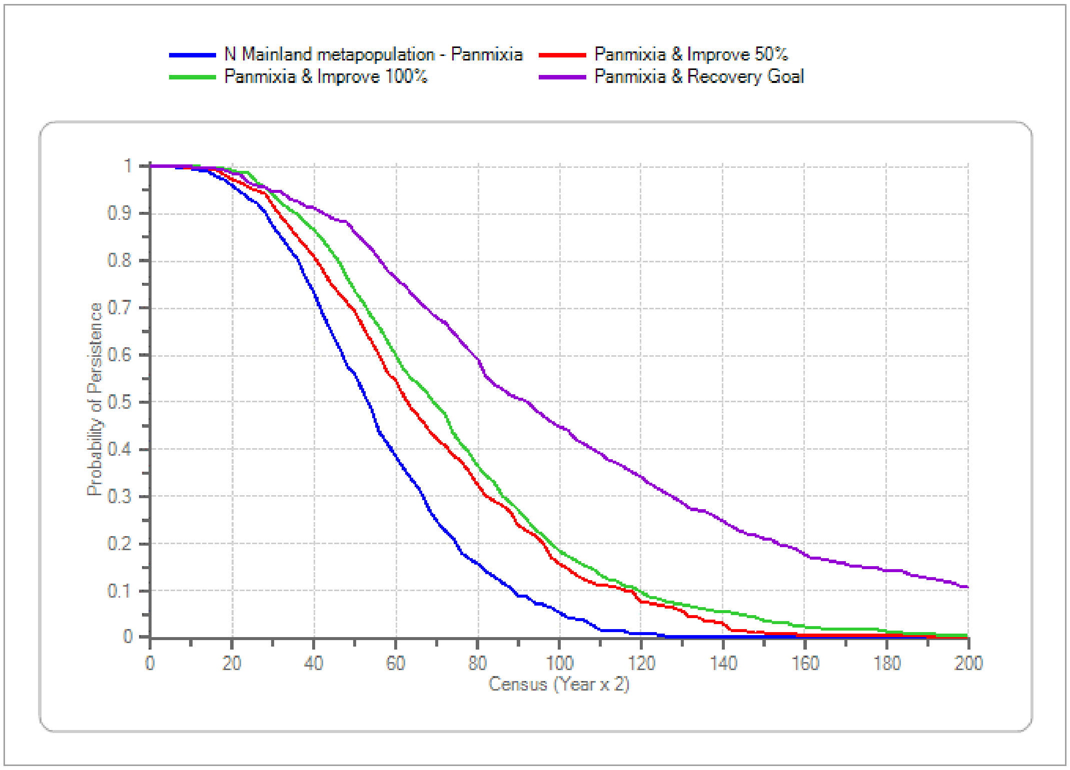

Figure 132. Probability of metapopulation persistence without any improvement to habitat (blue line), with 50% of Sink improved to Weak and 50% of Weak improved to Strong, with all Sink improved to Weak and all Weak improved to Strong, or with 70% maintained as Strong if there is also complete connectivity (panmixia) among the local populations.

Could long-term viability be achieved by a combination of habitat improvement and an initial boost in the number of jays?

Figure 133 shows projections if habitat is improved to be 70% Strong, with an initial translocation of about 100 breeding groups to fully occupy all potential habitat. Although a large release of jays to fill all habitat delays the complete loss of North Mainland metapopulation by more than 50 years (Fig. 134), the total amount of potential habitat is not sufficient to sustain a metapopulation over the long-term.

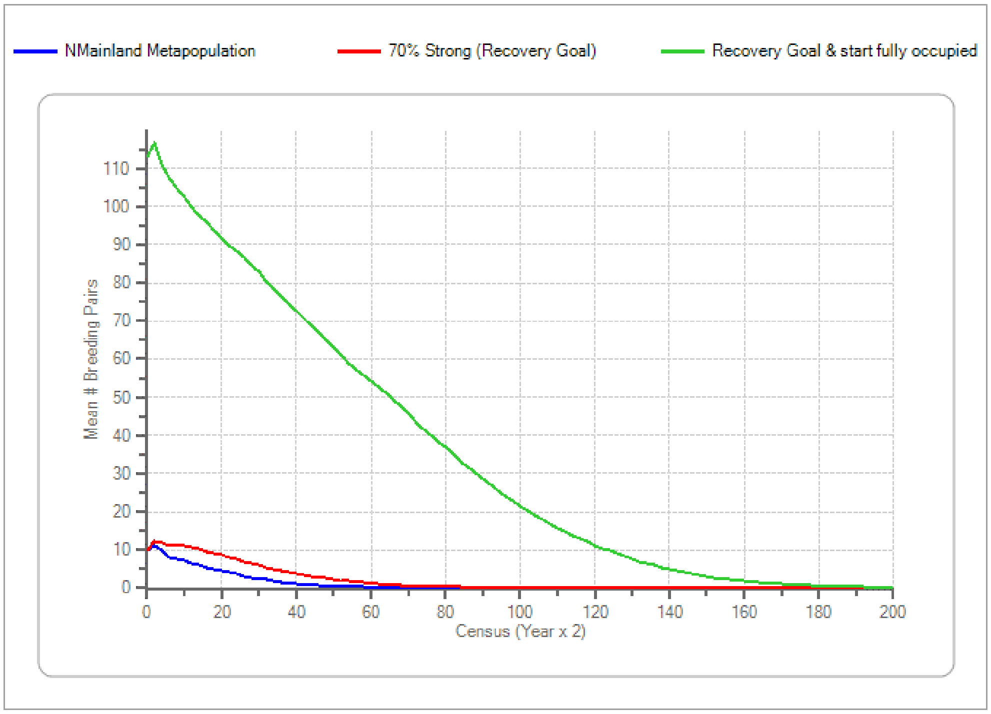

Figure 133. Projected number of breeding groups under current conditions, if habitat is improved to be 70% Strong, and if habitat improvement is accompanied by an initial translocation of jays to fully occupy all potential habitat.

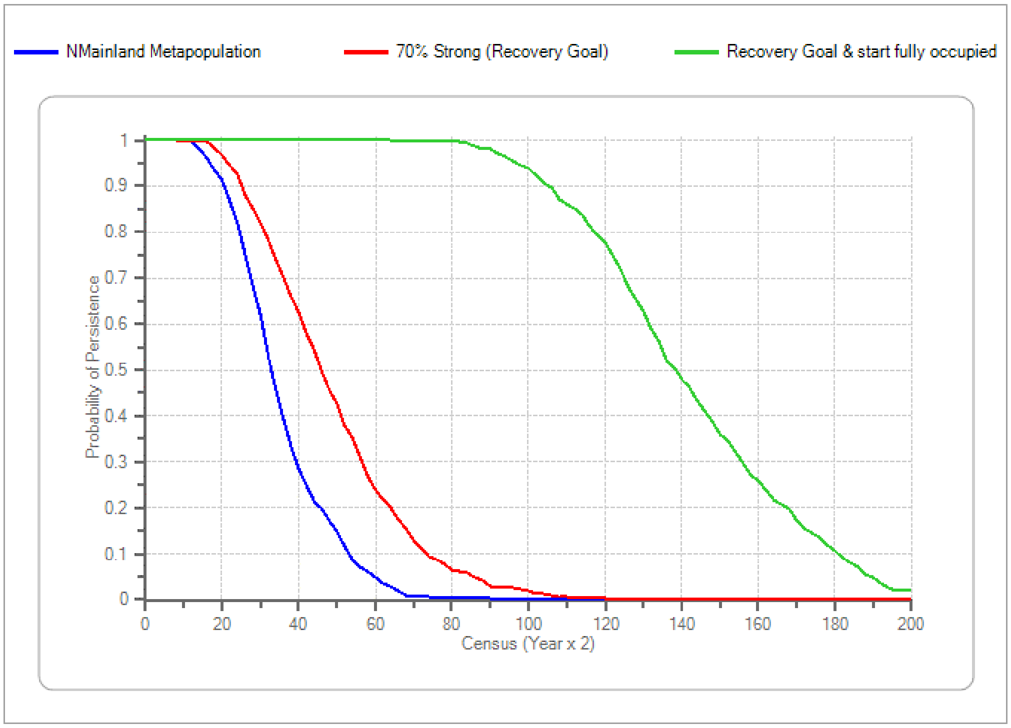

Figure 134. Probability of metapopulation persistence under current conditions (blue), if habitat is improved to be 70% Strong (red), and if habitat improvement is accompanied by an initial translocation of jays to fully occupy all potential habitat (green).

Could an aggressive program of ongoing supplementation sustain the metapopulation?

As seen in the above graphs, the North Mainland metapopulation is too small to be expected to avoid damaging effects of inbreeding and consequent population collapse, even if the existing habitat is improved to be mostly (70%) Strong, and jays could move (either naturally or by translocation) between the local populations, and the initial numbers could be boosted. Regular additions of jays, however, would prevent genetic problems, reinforce the populations after any declines, and could allow for population growth to fill available habitat. Figure 135 shows that habitat improvement followed by supplementation of each of the populations each year can achieve a growing and then stable metapopulation. (Note that there are 113 potential breeding territories, so the top line quickly saturates all available habitat.) However, these rates of supplementation require release of 9, 18, or 36 jays per year across the local populations, and sustaining this rate of release might not be possible. Scenarios with releases for a shorter number of years can be tested, although as indicated in the previous graph, the population would decline steadily even from a fully occupied condition if supplementation stopped.

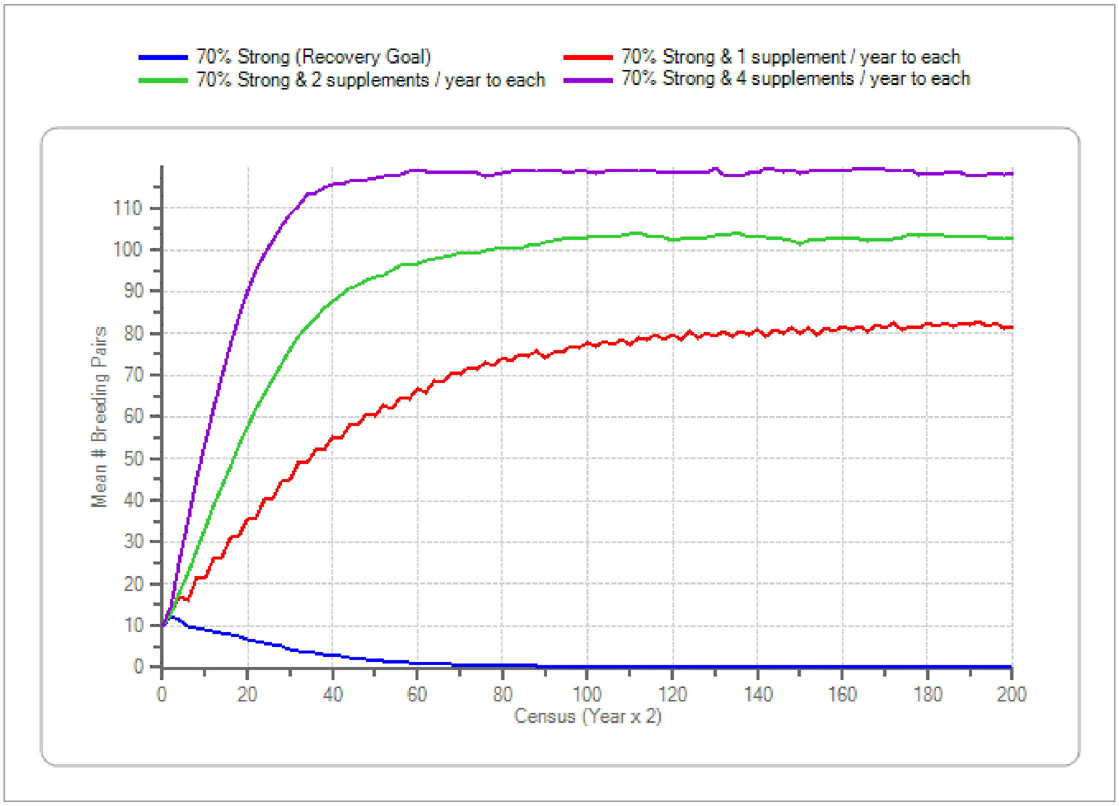

Figure 135. Projected number of breeding groups in N Mainland metapopulation if habitat is improved, or habitat improvement is followed by the addition of an average of 1, 2, or 4 jays to each local population each year.

How many releases would be necessary to achieve metapopulation viability?

If viability is defined as sustaining a population with at least half of potential territories occupied, then the projections shown in Figure 136, below, suggest that a supplementation program of releasing about 8 jays each decade to each local population could sustain a viable N Mainland metapopulation if habitat is improved to be 70% Strong. Releasing fewer jays would support a smaller size metapopulation, but as shown in Figure 137, release of 2 or fewer jays per decade to each local population leaves them vulnerable to extinction during each decade before the subsequent release. In all these release scenarios, inbreeding is kept to minimal levels (not shown) because of the regular addition of unrelated jays.

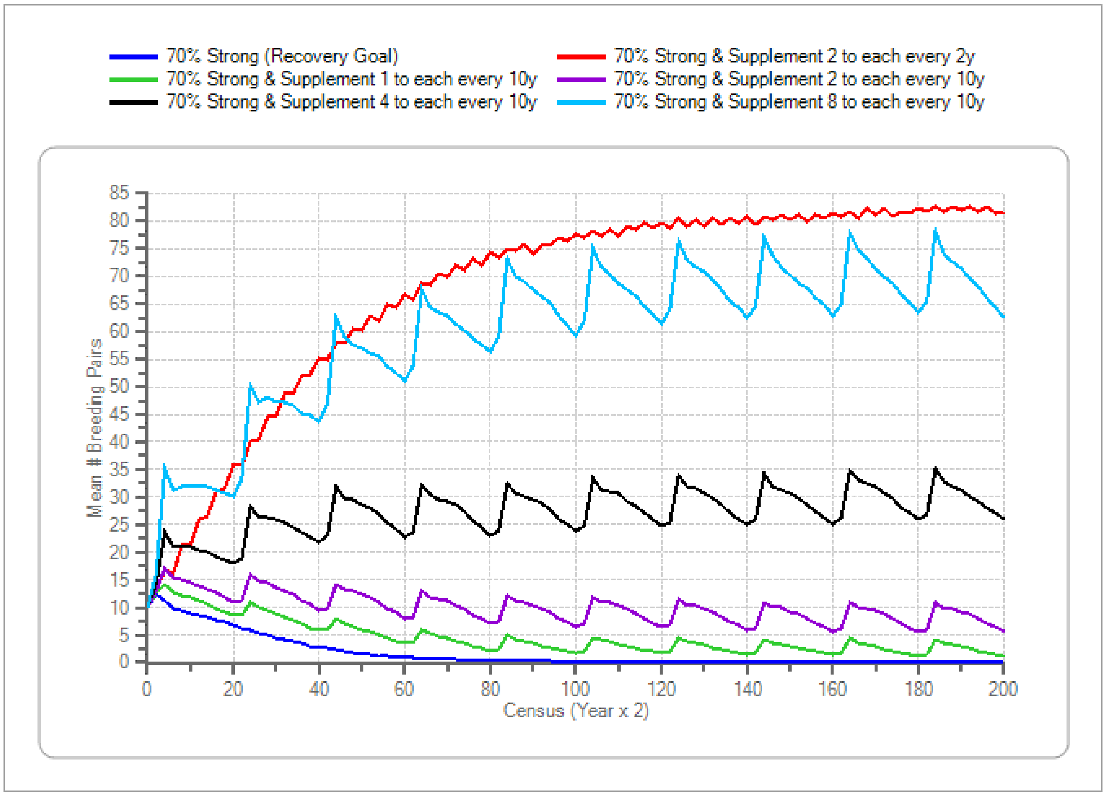

Figure 136. Projected number of breeding groups if habitat is improved to be 70% Strong, or habitat improvement is followed by the addition of 1, 2, 4, or 8 jays to each local population every decade, or 2 jays every other year.

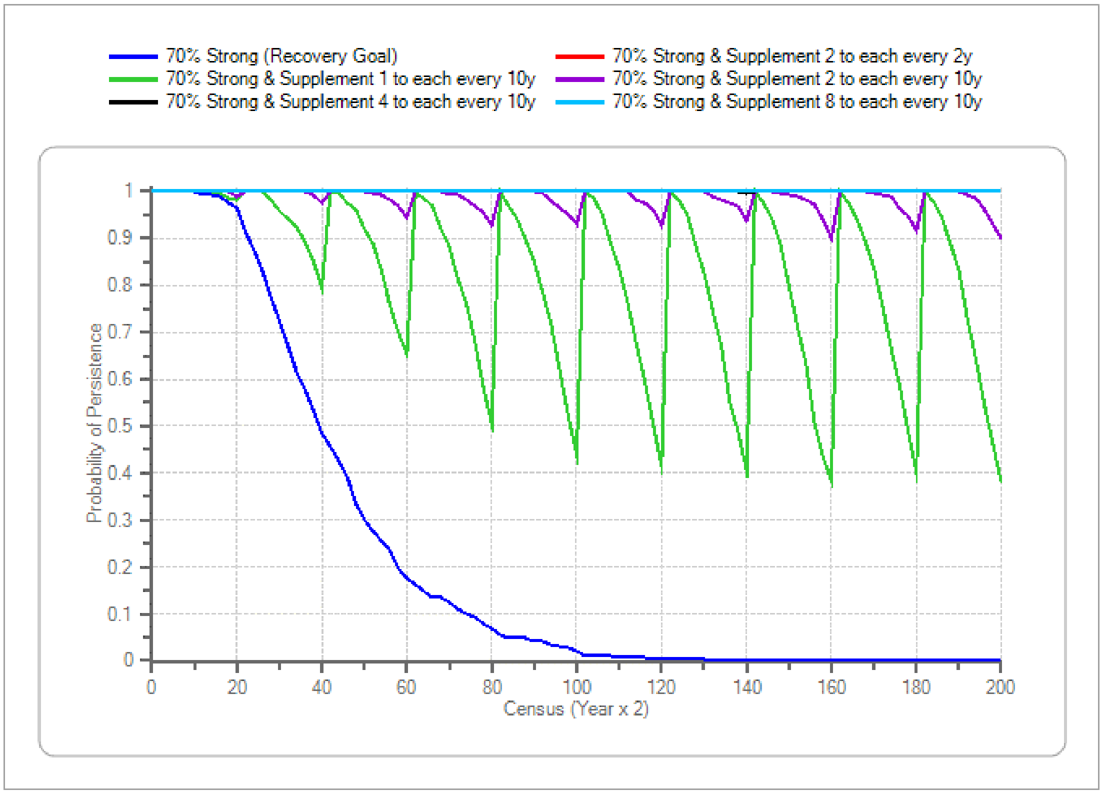

Figure 137. Probability of metapopulation persistence if habitat is improved, or habitat improvement is followed by the addition of 1, 2, 4, or 8 jays to each local population every decade, or 2 jays every other year.

What amount of supplementation is needed to sustain a viable metapopulation if it is coupled with both habitat improvement and increased connectivity?

As shown in the next two graphs, increasing connectivity between local populations via either improved corridors of habitat or translocations would further enhance the effectiveness of supplementation, because local populations that sometimes otherwise go extinct between releases would be reinforced by dispersal from nearby populations. In such a scenario, releasing 4 jays per decade to each local population would sustain a viable metapopulation and avoid extinctions.

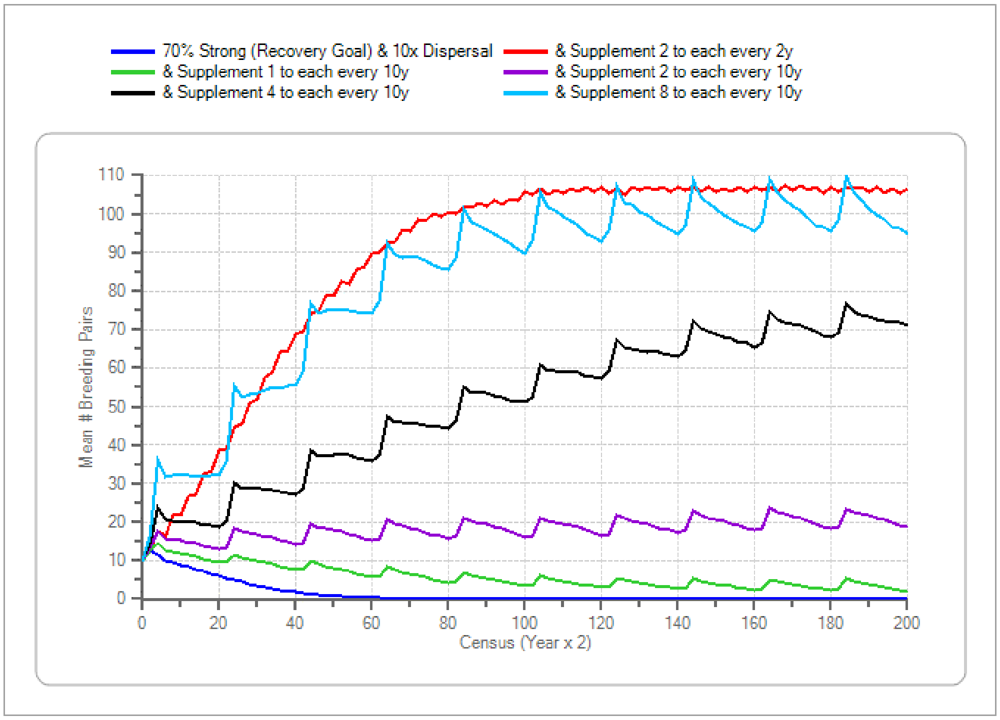

Figure 138. Projected number of breeding groups if habitat is improved and connectivity is increased 10x above current estimates, or habitat improvement and connectivity is followed by the addition of 1, 2, 4, or 8 jays to each local population every decade, or 2 jays every other year.

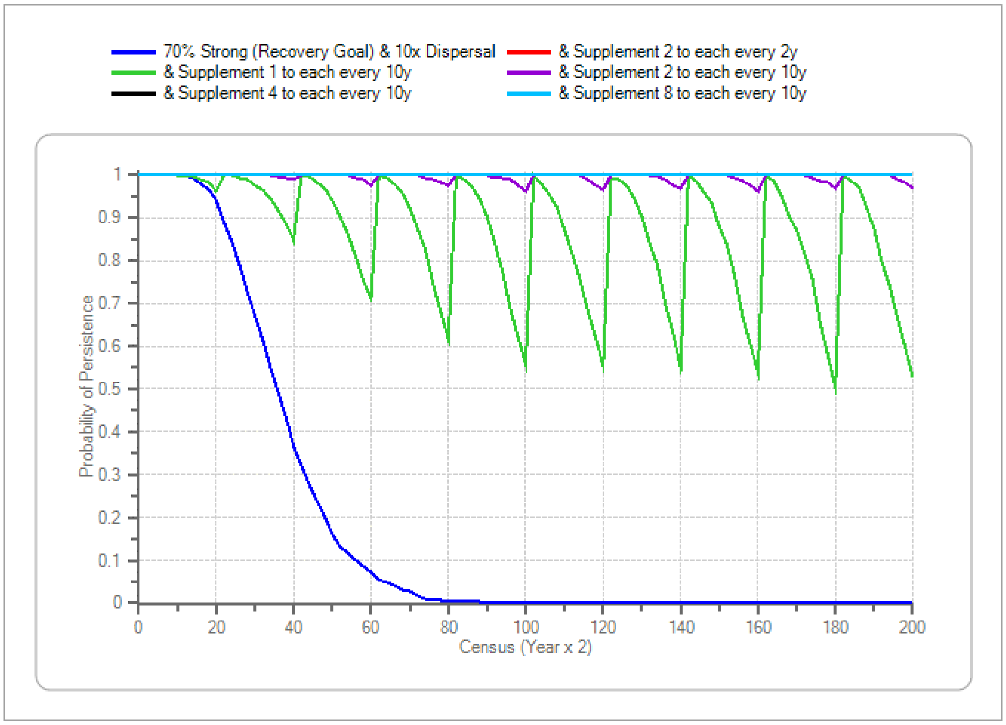

Figure 139. Probability of metapopulation extinction if habitat is improved and connectivity is increased 10x above current estimates, or habitat improvement and connectivity is followed by the addition of 1, 2, 4, or 8 jays to each local population every decade, or 2 jays every other year.

Linking the PVA to projections of habitat state

Integrating population models with habitat models

PVA models project species population trends from detailed simulations of the mechanisms and drivers of demography, but generally rely on very simplistic characterizations of trends in habitat (such as documenting past rates of loss or gain of optimal habitat) rather than building on an understanding of the mechanisms and drivers of habitat change that would allow predictions of consequences of possible future land management actions. In contrast, habitat-based conservation planning and land management now increasingly is based on detailed models of the processes that drive habitat change, but generally rely on simple characterizations of population responses (such as observed presence/absence). There have been a few notable examples of integration of habitat and population models in the assessment of vulnerability of species to climate change (Aiello-Lammens et al. 2011; Keith et al. 2008). One of the long-term goals of this project is to integrate these two approaches, so that highly detailed understanding of the drivers of both habitat change and species responses can be used to guide management decisions.

The team of researchers and managers that are working on Adaptive Resource Management (ARM) with models for predicting and refining estimates of transitions among habitat states, and working further with more fine-grained state-transition models, have been developing methods for detailed projections of scrub habitat change under various land management regimes.

In this PVA project, we have now built into the PVA model the ability to use these projections of habitat change at each of several levels of specificity.

a) At the least fine-grained level, within Vortex we can set initial conditions to match the equilibrium habitat configurations projected from the ARM transition models for each of various possible management regimes (such as a 5-year rotation of burning on reserves). We can further specify in the Vortex model that the predicted equilibrium conditions are approached gradually, due either to the time that is required to implement the management actions or the time it takes for the habitat to respond to management actions.
b) Tighter modeling of changing habitat quality can be achieved by feeding into Vortex a timeseries of the changing distribution of habitat states. Such a timeseries could be generated by an R script that would project forward a year at a time with the transition probabilities estimated in the ARM process.
c) The most precise modeling of coupled habitat-population change would involve modeling each FSJ territory and its projected fate. In this approach, the habitat transition modelers would produce a vector of the state of all territories for each year into the future. Vortex would then assign any new breeders in the simulation to specific territories. As the habitat model projected changing quality of the individual territories, Vortex can read those projections and modify the habitat quality of occupied territories as well as unoccupied ones.

Generating the habitat projections for either (a) or (b) above will likely require 3-6 months or longer by the habitat modelers. The methods have been largely demonstrated with the ARM modeling done for the mainland reserves and for a few sample management regimes but generating results for all metapopulations and for multiple management scenarios will not be a quick process. The much more precise modeling with ST-Sim that could generate territory-by-territory projections for (c) above might be a few years away.

Given those timeframes for further work on the habitat models, within this PVA project our goal was to develop and provide template Vortex scenarios that can read in sample data on habitat transitions at each of the above levels of precision. These models are now ready for use as habitat projections become available. The Vortex models to accommodate approaches at all three levels above have been completed.

Integrating projections of habitat change into the Vortex model for FSJ

Scenarios have been developed for integrating projected changes in habitat state (Strong, Weak, Sink) into the Vortex population model at three levels of specificity:

1) At the simplest, the number of potential territories of each habitat can be specified to be a function of year. For example, in the “KSC-Dx-Growth70b” scenario in the FSJ-KSCmgtX project, the change to 70% Strong Potential Territories (POTSTRONG) over time is specified as a simple linear increase of 20 years with the set functions for annual transitions of population state variables:

NYEARS=20

INCR=MIN(Y/NYEARS;1)

POTSTRONG=(1-INCR)*(LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC+CCASTerr.txt";1)))
+INCR*(PROUND(0.7*LOOKUP(P;FILECOL("C:\Vortex10Projects\FSJ\KSC+CCASTerr.txt";7))))

(P is the population index; column 1 of the specified data file is the number of Strong potential territories at present; and column 7 is the total number of potential territories.)

Other functions could similarly be used to specify other rates of change, if the change can be specified with a simple expression.

Methods for integrating more detailed and complex projections of Habitat change are illustrated in scenarios in the FSJ-KSC-Habitat Vortex project, as described briefly below.

2) If the number of potential territories in each habitat state is generated by another model (e.g., a matrix projection from habitat state transition probabilities), then the annual number of potential territories in each state can be provided to Vortex by timeseries given in a data file. For example, in the KSC-Dx-HabChange scenario, the change in numbers of habitats in each state is specified in transitions of population state variables:

POTSTRONG=TIMESERIES(FILEROW("C:\Vortex10Projects\FSJ\HCHab.txt";1))
POTWEAK =TIMESERIES(FILEROW("C:\Vortex10Projects\FSJ\HCHab.txt";2))
POTSINK =TIMESERIES(FILEROW("C:\Vortex10Projects\FSJ\HCHab.txt";3))

In which the 1st, 2nd, and 3rd rows of the HCHab.txt data file provide the numbers in Strong, Weak, and Sink states over the first 20 years (with fake data that I made up just to test the methodology):

```
48;50;52;54;56;58;60;62;64;66;68;70;72;74;76;78;80;82;84;86;88;90
35;36;37;38;39;40;41;42;43;44;45;46;47;48;49;50;51;52;53;54;55;56
179;176;173;170;167;164;161;158;155;152;149;146;143;140;137;134;131;128;125;122;119;116
```

Note that in data files provided to Vortex, values should be separated by semi-colons, spaces, or tabs (never commas, which Vortex does not allow, because that would fail on computers using European numeric formats). Also, if the simulation projects beyond the number of years listed in the file (20, in the above example), then Vortex will use the last value in each row for all subsequent years.

3) Integration of the most precise projections of habitat states can make use of projected change for each potential territory in the population. Such a specific projection of habitat states – territory by territory – might be generated from a state-transition model of habitat response to a management strategy (e.g., a burn regime). Examples of the use of such habitat state model projections are given for the KSC Tel4 population in a series of scenarios in the FSJ-KSC-Habitat project file. Note that the habitat state data files used in these sample scenarios are artificial data created simply for illustration purposes. These example scenarios could be extended to include the multiple populations within each metapopulation, but for now the KSC Tel4 population was used as a simpler, single-population test case. The PVA models that include detailed projections of habitat states for each potential territory run much more slowly than the models without such detailed habitat projection, so the test cases for now simulate only 10 years.

   In this approach, a data file would be created (by the habitat model) that lists the habitat state for each potential territory each year. An example of such a data file, used in the TEL4-Dx-TerrTransition3 scenario, would be (with a total of 262 lines of data for the 262 potential territories):

```
1;1;1;1;1;1;1;1;1;1
1;1;1;1;1;1;1;1;1;1
1;1;2;1;2;1;1;1;1;1
...
2;2;1;2;2;2;2;2;2;2
2;2;2;2;2;2;2;2;2;2
2;2;2;2;2;2;2;2;2;2
...
3;3;3;2;2;2;1;1;1;1
3;1;3;3;2;1;1;1;1;1
3;1;2;1;1;1;2;3;4;4
```

   State ‘1’ is Strong; ‘2’ is Weak; ‘3’ is Sink; and ‘4’ indicates a territory that has become unsuitable for a breeding group. The model prevents any new breeding pairs from establishing a territory in state ‘4’ habitat; while any existing group in a territory that becomes ‘4’ will remain there but be subject to the demographic rates specified either for state ‘3’ (if no state ‘4’ is given in the demographic rate file) or to rates that can be given in the Rates.txt file for the unsuitable ‘4’ territories.

The total number of potential territories in each state, each year, is needed to determine the accessibility (or preference) of new breeding pairs for each habitat state. These tallies can be specified in a file (as in the sample TEL4-Dx-TerrTransition scenario), or via a macro that sums down the columns of the above file of habitat states. For example, the POTSTRONG3.vmac macro file is:

```
# VMacro for counting number of POTSTRONG, for a given year
# Shared statement not needed, but shown for clarity
# SharedPopVars=NYR,NTERR
CT=MIN(Y;NYR)
CTHAB=0
NROW=0
DO
IF(LOOKUP(CT;FILE("C:\Vortex10Projects\FSJ\TEL4TERRSTATESCHANGE3.TXT"))=1)
CTHAB=CTHAB+1
ENDIF
CT=CT+NYR
NROW=NROW+1
WHILE(NROW<NTERR)
RETURN CTHAB
```

Further macros would be used to specify the territory and the habitat state of that territory occupied by each breeding group. A macro for an individual state variable is used to identify the habitat state and then select an unoccupied territory of that habitat state for each newly designated breeding female. The macro Tel4TerrAssign3.vmac is shown here:

```
# VMacro for assigning a Territory to new breeder females for Territory Transition modeling
# Uses TerrStatesChange3.txt
SharedIndVars=HABITAT,TERR
# New breeders only occur after odd numbered census counts
IF ((CENSUS%2)=0)
RETURN TERR
ENDIF
# Don't re-set Terr if already set
IF (TERR>0)
RETURN TERR
ENDIF
# Assign Terr only to FBREEDERs
IF (FBREEDER=0)
RETURN 0
```

```
ENDIF
# Determine Habitat
HABRAND=RAND
HABITAT=1+(HABRAND>PREFSTRONG)+(HABRAND>(PREFSTRONG+PREFWEAK))
# Find first unoccupied territory of the right Habitat
TERR=1
DO
IF ((FIND(TERR;ILIST10)=0)AND(LOOKUP[((TERR-
1)*NYR+MIN(Y;NYR));FILE("C:\Vortex10Projects\FSJ\TEL4TerrStatesChange3.txt")]=HABITAT))
RETURN TERR
ENDIF
TERR=TERR+1
# Note NTERR can be different from POTTERR if there are some Territories with Habitat>3
WHILE (TERR<(NTERR+1))
RETURN 0
```

The VMacro (Tel4InitAssign3.vmac) for making initial assignments of Habitat state and Territory for each individual at the start of the simulation is similar, but assigns Territories from among those of the designated Habitat state in sequential order (rather than needing to use the FIND function to find an unoccupied territory), because at the outset all territories are unoccupied.

Finally, a VMacro (e.g., HabTrans3.vmac) is used to specify the possibly changing Habitat state of each existing breeding group’s territory each year, such as:

```
# VMacro for determining current Habitat state based on Territory
# SharedIndVars=HABITAT
# Transition Terr state only after odd-numbered censuses
IF (CENSUS%2=0)
RETURN HABITAT
ENDIF
IF ((HELPER>0)AND(DAM11>0))
# Helpers get assigned Breeding Female's Habitat
HABITAT=DAM11
ENDIF
# Founder helpers won't have a dam, nor a Terr, so need to keep their original Habitat designation
IF (HELPER>0)
RETURN HABITAT
ENDIF
IF ((MBREEDER)AND(OID>0))
# Male breeder with a mate get the mate's Habitat
HABITAT=OIS11
ENDIF
```

```
IF ((MBREEDER)OR(UNHELPER>0))
# Initial male breeders won't have a mate, nor a Terr, so need to keep original Habitat
# HABITAT for new female breeders will have been set when Terr was assigned
RETURN HABITAT
ENDIF
# Lookup Habitat, based on Terr, in case it has changed
HABITAT=LOOKUP[(TERR-1)*NYR+Y;FILE("C:/Vortex10Projects/FSJ/TEL4TerrStatesChange3.txt")]
RETURN HABITAT
```

Note that all of the work of the above macro (and probably for each of the others too) can be packed into one very long and complex single-line function. For example, the following function should provide the same result as the above macro. However, it is much harder to interpret the nesting of IF statements in the function, and the more explicit macro is probably a better approach (although it will likely run more slowly).

```
HABITAT=IF{(CENSUS%2=0);HABITAT;
(IF[(HELPER>0);IF(DAM11>0;DAM11;HABITAT);
(IF[(MBREEDER)AND(OID>0);OIS11;
IF((UNHELPER>0)OR(MBREEDER);HABITAT;
LOOKUP[(TERR-1)*NYR+Y;FILE("C:/Vortex10Projects/FSJ/TEL4TerrStatesChange3.txt")]
)])])}
```

There would be other ways to configure Vortex scenarios to allow input from projections of habitat change. The details of the examples given above could be modified in various ways – some to make the model easier to understand and explain, and some to make the scenarios run more efficiently. There would also be other approaches that might be tested. In particular, instead of using macros within Vortex to read and process data on habitat states and territories, MetaModel Manager could be used as a higher-level integrating program to manage the flow of data from habitat models to Vortex. However, given that the FSJ population dynamics do not likely impact the habitat changes, there is likely no need to dynamically pass simulation data from Vortex to the habitat state transition model (in addition to the data flow in the reverse direction). Therefore, the extra overhead (and slowness of the simulations) of using MetaModel Manager is probably not needed. This could change, however, if habitat management were conditioned on the status of the FSJ populations each year, such that the FSJ population status influenced habitats as well as the reverse.

Vortex input files

Data and software archiving

The source code for the Vortex PVA simulation software, including all incremental changes to the code, has been archived by the Species Conservation Toolkit Initiative (SCTI) in a GitHub repository. For now, access is restricted to the SCTI development team that maintains and supports the software. A decision will be made later by SCTI as to whether to make the code open access so that any user can examine the code. In any case, access will be provided to TNC and collaborators in the Florida scrub-jay PVA work.

The input files for the Vortex projects used in the PVA are available to TNC and other collaborators, so that they can repeat and extend analyses. These files have been archived on a Zenodo.org repository and can be accessed (with permission) from http://doi.org/10.5281/zenodo.4469885.

TNC can make the decision (probably with FWS and NASA input) as to whether the Vortex input files for this project will be made openly accessible, or instead restricted to only those to whom we grant access.

Some useful suggestions for running FSJ scenarios

Some options used in the FSJ scenarios require the use of Vortex version 10.5.3 or a newer version. The installation file for version 10.5.5 is currently being distributed on the scti.tools website.

Some of the project files include a template scenario that is based on one of the scenarios, omits the detailed Section Notes, and is useful for creating additional scenarios.

All scenarios use file *Rates.txt* or *RatesSE.txt* to provide the mean and EV for breeding success in Strong, Weak, and Sink habitat, with and without helpers, and mean and EV for survival rates in Strong, Weak, and Sink habitat. *RatesSE.txt* includes also the SE for each mean rate.

Recommend using just 10 iterations for quick check to see that a scenario is working; using 100 iterations for approximate results; using 500 iterations for more precise results.

The Multi-Vortex Run option allows the computer to run multiple scenarios at once. It is recommended that you use up to about ½ of the CPUs on the computer for good performance of Vortex. Do not try to do a lot of other work on the computer while such CPU and RAM intensive batches of scenarios are running. Very occasionally, Windows has trouble managing the multiple Vortex runs that are going simultaneously. Sometimes it runs into a conflict while trying to write to multiple files simultaneously, and sometimes Windows fails to free up memory after the program closes. In either case, it might be necessary to use Task Manager to terminate the Vortex process, and then it is wise to re-boot the computer to be certain that all memory has been freed.

When running large batches of scenarios, the Special Option (under Project Settings) to “Do not show graphs during iterations” will allow the simulations to run faster.

In some projects, the ST module was used to generate the scenarios for Sensitivity Analyses. In other cases, the scenarios to compare across values of input variables were added to the project as independent scenarios.

Generic population models

A series of models were run to test the population dynamics in a hypothetical single population.

FSJ-Terr100ST.xml – Sensitivity analyses on a population with 100 potential territories, in most scenarios allocated as 40 Strong, 30 Weak, and 30 Sink. Tests run to compare across levels of Preference (or accessibility) for Strong habitat, probability of helpers becoming breeders in response to available Strong habitat, and global sensitivity analyses that varied all key demographic parameters.

FSJ-NInbreeding.xml – Scenarios to test impact of inbreeding depression on populations of varying size and all Strong habitat.

FSJ-NInbreeding2.xml – Scenarios to test impact of inbreeding depression on populations of varying size and 40% Strong habitat.

FSJ-InbreedingImm.xml – Sensitivity analyses for testing effects of inbreeding and immigration with or without counter-balancing emigration.

FSJ-Buffers.xml – General scrub-jay model with 40 Strong potential territories, with scenarios for testing effect of a range of numbers of Sink or Weak habitat as buffers that improve population performance. Tests also vary the Preference for (accessibility of) Strong habitat.

FSJ-AddW&S.xml – Scenarios testing benefit of adding variable numbers of Weak or Sink territories to a population with 100 Strong potential territories, with several levels of parameters for Preference for Strong habitat and H to B transition in response to habitat availability.

FSJ-Catastrophes.xml – Scenarios to explore resilience to catastrophes, with various population sizes, and various values for Preference parameter.

FSJ-EV.xml – Scenarios for testing alternative values for EV.

KSC/MINWR/CCSFS metapopulation models

These scenarios all use *KSC+CCASTerr.txt* to provide the number of potential territories and occupied territories of each habitat quality in each of the populations.

Distances between populations are read from file *KSCDist.txt* or *KSCCCASDist.txt.*

FSJ-KSC.xml -- Scenarios for testing different dispersal rates and impacts of inbreeding for KSC metapopulation.

FSJ-KSCmgtX.xml – Scenarios for testing management strategies for KSC metapopulation.
Uses dispersal rates determined from distance matrix. Tests:
Removal of Sink habitat;
Improvements to habitat, with and without increasing connectivity;
Attaining recovery goal of 70% Strong;
Removal of jays from Sink and Weak habitat (for translocation elsewhere);
Removal of excess jays at carrying capacity;
Connection of Happy Creek and Shiloh, with and without habitat improvement;

Loss of Schwartz Rd habitat

FSJ-KSCmgtD.xml – Same scenarios as *FSJ-KSCmgtX.xml*, except uses fixed percent dispersal rates.

FSJ-KSC+CCAS-X.xml – Models of the CCSFS populations, either in isolation or as part of a larger metapopulation linked to the KSC/MINWR populations.
Uses dispersal rates based on distance matrix derived from SC Mainland, although some scenarios tested that specify other levels of connectivity between CCSFS and KSC.
Includes also Supplementation scenarios for testing how many jays would need to be moving into CCSFS (from KSC or elsewhere) to stabilize CCSFS.

SC Mainland metapopulation models

The scenarios use *SCNMainlandTerr.txt* file to provide the number of potential territories and occupied territories of each habitat quality in each of the populations. For some management scenarios, new numbers of territories are read from file *SCMainlandTerrAdds.txt.*

Distances between populations are read from file *SCMainlandDist.txt.*

FSJ-SCMainland.xml -- Scenarios for testing different dispersal rates and impacts of inbreeding for South & Central Mainland metapopulation.

FSJ-SCMainlandMgtX.xml – Scenarios for testing management strategies for SCMainland metapopulation.
Uses dispersal rates determined from distance matrix. Tests:
Increased connectivity;
Improvements to habitat, with and without increasing connectivity;
Attaining recovery goal of 70% Strong;
Possible additions of habitat to some local populations, with and without increased connectivity, and with and without overall habitat improvement;
Removal of jays from Sink habitat (for translocation elsewhere), at the outset or over time;
Improvement of habitat, with and without full connectivity among populations

FSJ-SCMainlandMgtX3.xml – Additional scenarios for testing management strategies for SCMainland metapopulation. Uses dispersal rates determined from distance matrix. Tests:
Additional levels of habitat improvement;
Supplementation with and without habitat improvement;
Removal of various numbers of jays from Weak and Sink territories, after achieving 70% Strong

FSJ-SCMainlandMgtD.xml – A subset of the scenarios in *FSJ-SCMainlandMgtX.xml*, except uses fixed percent dispersal rates.

N Mainland metapopulation models

The scenarios use *SCNMainlandTerr.txt* file to provide the number of potential territories and occupied territories of each habitat quality in each of the populations.

Distances between populations are read from file *NMainlandDist.txt.*

FSJ-NMainland.xml -- Scenarios for testing different dispersal rates and impacts of inbreeding for North Mainland metapopulation. Includes also basic scenarios for other metapopulations, for comparison across metapopulations.

FSJ-NMainlandMgtX.xml – Scenarios for testing management strategies for NMainland metapopulation. Uses dispersal rates determined from distance matrix. Tests:
Increased connectivity;
Improvements to habitat, with and without increasing connectivity;
Attaining recovery goal of 70% Strong;
Addition of various numbers of immigrants per year, after attaining 70% Strong habitat, with several level of increased connectivity.

FSJ-NMainlandMgtD.xml – Scenarios for testing management strategies for NMainland metapopulation. Uses fixed percent dispersal rates. Tests:
Various levels of habitat improvement, with different rates of attaining habitat goals, and with several levels of connectivity.

Models for validating that population structures generated by FSJ metapopulation scenarios match reasonably well with field census data

FSJ-Validations.xml – Includes scenarios for all 3 metapopulations for validating model results against field data on Helper:Breeder:Juvenile ratios, and Strong:Weak:Sink occupancy. Validation scenarios for each metapopulation, starting with current population, starting saturated (N = K), tests with no dispersal, and tests with weaker preference for Strong habitat. Also includes tests of equilibrium K for different % of potential territories being Strong. Various state variables added to tally values that can be compared against field survey data.

Models for testing methods to read habitat state transitions (in files produced by a habitat model)

FSJ-KSC-Habitat.xml – Scenarios of the KSC metapopulation for testing models that include links to projections of changing habitat. Most tests use only Tel4 population as a test case.

Scenarios in the project use files:

KSC4Terr.txt – Listing of number of potential territories, and occupied territories of each habitat level, in each population
HCHab.txt, SchwHab.txt, ShilohHab.txt, Tel4Hab.txt – timeseries (artificial data, for testing methods) of number of Strong, Weak, and Sink potential territories for Happy Creek, Schwartz, Shiloh, and Tel4 populations
Tel4TerrStatesCount.txt – Timeseries of # potential territories of each habitat each year.

POTSTRONG.vmac, POTWEAK.vmac, POTSINK.vmac
POTSTRONG2.vmac, POTWEAK2.vmac, POTSINK2.vmac
POTSTRONG3.vmac, POTWEAK3.vmac, POTSINK3.vmac
Macros for counting up number of POTSTRONG, POTWEAK, and POTSINK for a given year.

Tel4InitAssign.vmac, Tel4InitAssign2.vmac, Tel4InitAssign3.vmac

Tel4TerrAssign.vmac, Tel4TerrAssign2.vmac, Tel4TerrAssign3.vmac, Tel4TerrConstantAssign.vmac
Macros for assigning a Territory to new breeder females for Territory Transition modeling. "InitAssign" macros assign territories at the outset of the simulation. "TerrAssign" macros are used for new breeders during the simulation.

HabTrans.vmac, HabTrans2.vmac, HabTrans3.vmac, HabNoTrans.vmac
Macros for determining current Habitat state based on Territory

All of above macros read territory states from *Tel4TerrStatesChange.txt, Tel4TerrStatesChange2.txt, or Tel4TerrStatesChange3.txt* to provide the state of each potential territory each year. The three versions of each file provide different timeseries of habitat states (all of which are artificial data, for testing methodologies).

Future needs and opportunities

Information needs

The detailed information on the Florida scrub-jay social structure, demography, habitat, and population structure that has been collected over the last few decades allowed us to develop a PVA model that we believe represents well the population dynamics and therefore can be used to help guide management. However, there remain uncertainties about aspects of the biology and imprecise estimates of important population parameters. Consequently, the projected trajectories have large variation across iterations of the simulation, due both to the uncertainties in data and to the inherent unpredictability of many demographic, genetic, and environmental processes. An important goal of this project was to create the modeling framework for exploring scenarios and options for the FSJ, so that understanding and confidence in projections can be increased as new data become available for updating the model. Among the data needs that should be addressed, if possible, are:

- Ongoing monitoring of the local populations: The decline in FSJ populations observed over the recent decades is projected to continue, with loss of some or all of the mainland Brevard populations, due to too little optimal (Strong) habitat and too much fragmentation of the habitat that remains. It will be important to continue monitoring the populations to determine if the projected declines do occur. If so, actions will need to be taken to reverse the declines. If the population declines do not continue as projected, it will be important to determine what aspects of the population model are not characterizing the actual population dynamics.
- Measuring population responses to management actions: More optimistically, the PVA modeling suggests actions that might slow or even halt the declines (such as improving habitat quality and connectivity). If such actions are taken, it will be important to monitor whether the expected benefits to the populations occur over the projected time spans.
- Assessment of the genetic structure of the populations, and more precise measurement of the fitness effects of inbreeding: The PVA models predict that the small and isolated populations of FSJs in the Brevard region will become inbred to the extent that inbreeding significantly depresses fitness, will diverge due to random drift, and will lose genetic diversity that is necessary for continued adaptation to changing environments. Molecular genetic surveys could confirm the rate of genetic loss and divergence among populations. In addition, the estimates of the impacts of inbreeding have large standard errors. More precise estimates would confirm or allow refinement of this important parameter in the population projections.
- Additional information on dispersal rates between populations: Rates of movement within each of the four metapopulations and between metapopulations appear to be too low to provide healthy genetic mixing. The rates and the factors influencing dispersal can have major effects on metapopulation stability, the ability to recover from local declines, and the prospects for population expansion into newly suitable habitat. However, because dispersal between populations is infrequent, amassing enough data to estimate dispersal rates is a slow process. Measurement of genetic divergence among populations can provide an additional means to estimate connectivity.
- Patterns of movement within local populations and likelihood that new breeding groups will establish territories in the best available habitat: Survival and breeding rates are much better in

optimal scrub habitat, and population performance was found to depend on the ability of new breeding pairs to establish territories in the best habitat that is available in the population. Patterns of occupancy of Strong, Weak, and Sink habitat indicate that jays are likely to select better habitat when it is available, but perhaps do not always move into the best vacant territories. It will be useful to know how far they will disperse from natal territories in the search for the best available sites and to document how the dispersal patterns depend on the configuration of the matrix of habitat quality.

- Further measurement of the determinants of helper to breeder transition probabilities: Helper scrub-jays can help buffer the populations from decline, by providing a pool of jays that can establish new breeding groups when good habitat becomes available. In the PVA simulation, we included functions to describe the response of helpers becoming breeders to fill vacancies, but we lack direct measurement of the function parameters and had instead rely on trial-and-error testing to see what values generated ratios of helpers to breeders that were consistent with field data.
- Management scenarios and habitat responses: As described above (*Linking PVA to projections of habitat state*), the PVA model structure is currently in place to allow the population model to make use of projections of habitat under various regimes of management. Habitat projections can be read by Vortex at three levels of increasing specificity: changed amounts of each habitat type, time series of changing states, or projections for each potential breeding territory. Models of habitat transitions in response to management regimes are being developed. For use in coupled habitat-population models, it will likely be necessary to translate or aggregate these habitat projections into patch dynamics at the scale of FSJ territories.
- Climate change, management, and habitat responses: Modeling scenarios for long-term species viability required the use of long-time spans to account for genetic considerations. The ability to improve habitat quality varies depending on topography, management history, and the locations that constrain the use of controlled fires. Sea level rise is expected to further affect the availability of habitat and considerable work has gone into spatial predictions of saltwater inundation in these landscapes. Models of these predictions should be combined with the PVA model to more realistically explore how combinations of management scenarios could be used to maintain population viability.

Developing capacity among local land and resource managers

This project depended completely on the involvement and collaboration by a number of people who brought diverse knowledge and expertise to the discussions and analyses. This included research biologists, some of whom have spent decades studying Florida scrub-jays, land managers, data analysts, mapping and imagery experts, agency administrators, modelers, and others. As with any technical tool, using the Vortex PVA software requires detailed knowledge of the model that it implements, the mechanics of using the software, and the interpretation of the results generated by the simulations. To date, application of Vortex to wildlife population assessment and management has therefore usually involved species experts working with one or more experts in the use of Vortex. However, it would be much more efficient, would allow for ongoing refinement of the PVA, and would generate more understanding of the PVA results and support for their application to management if the expertise to use Vortex was put into the hands of people with expertise on the species and the management options. Some natural resource management agencies, such as Canada Department of Fisheries and Oceans, has been developing expertise in their scientific staff so that they could apply Vortex to multiple scenarios and species for which they have responsibility. Other agencies have continued to rely on external experts in population modeling, but this often limits their ability to advance models as new data, issues, or options arise.

As a follow-up to the considerable amount of work that has gone into this PVA project, we (meaning the project principles, with support from FWS and TNC) will convene workshops to train a core team of biologists from KSC and likely partner organizations (e.g., FWS, Archbold, NWR) in the mechanics of using the Vortex modeling software. To be useful, the training will need to be extensive enough so that the participants understand not just how to run PVAs for non-complex situations, but also understand the details of all of the very complex functions and model parameterizations that were necessary to represent the complexities of the social system and habitat dependencies of the FSJ. This will likely require several intensive in-person workshops, interspersed with practice on sample scenarios and exploration of the scenarios used in this project, and followed up by ongoing consultation and collaborations.

Modeling other FSJ metapopulations

The Florida scrub-jay populations in other parts of Florida (especially the large metapopulations in Ocala National Forest and in the Lake Wales Ridge scrub in and around Archbold Biological Station) are also critical components of the distribution of this Florida endemic. Moreover, the viability of regional metapopulations and possibly the species as a whole might depend on the available of immigrants from other metapopulations (whether by natural dispersal or, more likely now, by managed translocations) for reinforcing or reestablishing populations that have declined. The habitat characteristics and distribution differ among the metapopulations of FSJs, and consequently it is likely that demographic rates and possibly even the social system differ to some extent as well. Fortunately, there have been detailed and long-term studies of other populations, especially at Archbold. Therefore, the Vortex model structure that has been developed for the Brevard County scrub-jay populations could now be applied to other metapopulations, with adjustments for any known regional differences. This could provide greater understanding of the nature of regional differences and provide guidance on the management options that might be most useful for each metapopulation. Extending the FSJ modeling to other populations would depend on the same kind of close collaboration with the experts on those populations and management of those systems as has been the case for this project.

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