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A SYSTEM DYNAMICS INVESTIGATION OF GENETIC DRIFT AND TRANSLOCATION IN THE RED-COCKADED WOODPECKER METAPOPULATION

THESIS

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AFIT/GEE/ENV/03-22

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THESIS

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Jason E. Yates

Table of Contents

Page

List of Figures

Figure Page

List of Tables

Table Page

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Abstract

The red-cockaded woodpecker (*Picoides borealis*) is classified under the Endangered Species Act of 1973 as an endangered species. As such, the red-cockaded woodpecker (RCW) is afforded strict protection in an effort to return the RCW population to a self-sustainable level. Endemic to southeastern United States mature pine forests, the presence of the RCW impacts the operations of many Department of Defense (DoD) installations. A particular challenge in sustaining what are often small populations of RCW at these locations is the loss of genetic variation due to genetic drift. The optimal method for mitigating such loss is through the artificial immigration, termed translocation, of individual RCWs from other populations. The research objective of this effort was to quantify the translocation rate that would counter genetic drift in small populations though the modeling of RCW populations using a system dynamics approach. Both source and target populations utilizing various magnitudes and frequencies of translocations were modeled over a time period of 50 generations. While the optimal translocation rate is dependent on the initial population size, the results of this research indicate that it is possible to counter the effects of genetic drift in RCW populations as small as 10 mating pairs with the translocation of two pairs of red-cockaded woodpeckers twice per generation.

A SYSTEM DYNAMICS INVESTIGATION OF GENETIC DRIFT AND TRANSLOCATION IN THE RED-COCKADED WOODPECKER METAPOPULATION

1. Introduction

Background

The red-cockaded woodpecker (Picoides borealis) is classified under the Endangered Species Act of 1973 as an endangered species. As such, the red-cockaded woodpecker (RCW) is afforded strict protection in an effort to return the RCW population to a self-sustainable level. Endemic to southeastern United States mature pine forests (Jackson, 1977:448), the presence of the RCW impacts the operations of many Department of Defense (DoD) installations. In accordance with the Endangered Species Act (ESA) and through cooperation with the U.S. Fish and Wildlife Service (USFWS), each DoD installation possessing the RCW has undertaken the task of managing its population to optimize RCW habitat and maximize population growth. The natural resource managers at these locations are faced with the delicate balance of ensuring that the provisions of the ESA are met while hindering the installation's mission as little as possible.

DoD installations or, more specifically, testing and training ranges are particularly likely to harbor endangered species. Military lands preserve ecosystem types that are often unique and not preserved on other federal or state lands. This is because military training ranges were established nation-wide to provide representative environments of possible battlefield terrain (Ripley & Leslie, 1997:95). Further, DoD lands are ecologically important in that, in many locations throughout the nation, urban growth has destroyed vital habitat for many endangered and vulnerable species. Only the military lands in these regions provide the habitat for such species to survive. "DoD lands are increasingly becoming 'islands' of habitat protection within 'seas' of development" (Ripley & Leslie, 1997:95).

Ripley and Leslie's description certainly holds true for the RCW populations found throughout the Southeast. The populations are largely fragmented and isolated from one another (Conner and Rudolph, 1991:446). The size of RCW populations range from 1 to 486 active clusters (USFWS, 2000:117-119) with the majority having less than 50 (Lennartz and Heckel, 1987:48). A cluster describes the area of trees in which RCWs have created cavities to house their social unit, the group (USFWS, 2000:35). A group can consist of a breeding pair with one or more helpers, a breeding pair without helpers, or a solitary male (Walters et al., 1992a:91). Helpers are non-breeding adults that are typically previous male offspring of the breeding pair and are involved in activities that increase the productivity of the group (Walters et al., 1992a:91). These topics are discussed in greater detail below and in Chapter 2.

Problem

Given that most of RCW populations are quite small, occupy fragmented habitat, and are often isolated from one another, such RCW populations are particularly vulnerable to local extinction (extirpation) due to random demographic, environmental, catastrophic, and genetic events (Shaffer, 1981:131). Of these concerns, much less research has been performed regarding the effects of genetic events on small RCW populations (USFWS, 2002). One such event of specific concern to this study is genetic drift, which is the loss of genetic variation because of the failure of an individual who possesses a rare gene to breed (Stiling, 2002:26).

A proven way of bolstering small, vulnerable populations is through immigration, both natural and artificial. Artificial immigration through a capture and release program is known as translocation. Immigration of either type has the benefit of countering the loss of genetic variation through genetic drift (Lacey, 1987:148). While general estimates exist for the number of migrants recommended to infuse into a small population to decrease their genetic vulnerabilities, no guidance on immigration rates is available that is specific to the RCW and its eccentricities.

The challenge is to develop a model that illustrates the effect of genetic drift on the RCW over time. The purpose of this research is to provide natural resource managers a reference for determining how many red-cockaded woodpeckers should be translocated from a large population to a small population to counter the detrimental effects of genetic drift. Additionally, the research explores the degree of genetic drift present in various population sizes and the relationship of genetic drift to other model parameters affecting RCW populations.

Summary of Current Knowledge

The red-cockaded woodpecker has been shown to be an essential keystone species of the southern pine forest ecosystem (Conner et al., 1997b:140). A keystone species is one that has an effect on its ecosystem out of proportion to its abundance (Stiling, 2002:344). RCWs are the primary species that excavate their cavities in live southeastern U.S. pine trees (Conner et al., 1997a:11). In other regions of the country where fire is not as prevalent, standing dead trees (snags) provide the location for many types of wildlife to make their homes. In southeastern pine forests, snags were historically uncommon because they were consumed in the frequent fires typical to the region (Frost, 1993:34-35). With no means to construct cavities in live pine themselves, 24 species of vertebrate are dependent on the RCW for its long-lasting tree cavities and compete with the RCW for such homes (Conner et al., 1997a:12). Because of this dependence, southern pine forest biodiversity would certainly suffer significantly without the continued existence of the RCW (Conner et al., 1997b:141).

The RCW works cooperatively with others of its species to occupy and defend its territory from its competitors. The species is not migratory, occupying the same territories year-round (Lignon, 1970:258). Breeding pairs of the RCW are highly monogamous during the breeding season and only 10 percent of females switch breeding groups between breeding seasons (USFWS, 2000:11-12).

The formation of a group is best illustrated by the options exercised by young RCWs. During its first year, a young bird may either disperse to seek a breeding vacancy or may remain as a helper to its parents or close kin (Walters et al., 1992b:625). As many as four helpers have been observed in a group, but one or no helper is the most typical (USFWS, 2000:10). While helpers do not breed (Walters et al., 1992b:625), they are active in almost every activity associated with raising new young and maintaining the group to include: feeding, incubation, territory and nest defense, and cavity excavation (USFWS, 2000:10).

For those young RCWs that disperse in their first year, the mean distance traveled is less than that of other avian species (USFWS, 2000:11). Dispersing fledglings typically travel between three and five kilometers, with males generally traveling farther

(Walters et al., 1988:290,292-293). While movements over 100 km have been observed, such long distance travels are rare (USFWS, 2000:11). Females are more likely to disperse, while males commonly stay behind as helpers, eventually inheriting their natal territory or an adjacent one (Walters et al., 1992b:625).

The relatively short dispersal distances and field observations indicate that the preference of dispersing birds is towards existing RCW clusters rather than unoccupied territory (Walters et al., 1988:301). The conclusion of researchers is that pioneering, the acquisition of habitat through the construction of new cavities, is a rare occurrence in RCW populations (USFWS, 2000:19; Walters et al., 1988:301).

Certainly a substantial reason for this tendency is the length of time required for the construction of new cavities (Walters et al., 1988:301). Unlike other woodpeckers that typically select dead trees for cavity construction, red-cockaded woodpeckers construct their cavities in live southern pine (Hooper et al., 1980:2). Because of the resiliency of live pine, it often takes many years for an RCW group to construct a new cavity (USFWS, 2000:32). Therefore, the RCW as a species is particularly vulnerable since the rate of pioneering is typically much less than the rate at which habitat has been and may continue to be lost (Walters et al., 1988:301).

Like all endangered species, the red-cockaded woodpecker is also vulnerable to a loss of genetic variation (Stiling, 2002:24). This potential loss comes in two forms: inbreeding and genetic drift (USFWS, 2000:26; Stiling, 2002:24-27). While inbreeding, the breeding of closely related individuals, is common amongst social animals (Stiling, 2002:24), its detrimental effects threaten only small populations (Lande, 1988:1456). The effects seen in RCW populations affected by inbreeding are reduced hatching rates of eggs and greater mortality of fledglings less than one year in age (USFWS, 2000:26). It is the commonly held view that a population of at least 50 individuals is enough to negate the effects of inbreeding (Stiling, 2002:25). Current research regarding inbreeding in the RCW indicates that greater numbers may be necessary; a stable population of 50 to 100 or more breeding groups is recommended (USFWS, 2000:27). For those populations of RCW that are smaller than the recommended size, the immigration of 2 or more individuals from outside the local population are required to protect against genetic loss due to inbreeding (USFWS, 2000:27).

Genetic drift is the loss of genetic variation over time. More specifically, it is the loss of unique alleles through a lack of breeding of those individuals possessing such alleles (Stiling, 2002:26). Again, smaller populations are more vulnerable to the effects of genetic drift. However, the magnitude is relative; whereas 50 individuals are the rule of thumb for countering the effects of inbreeding, 500 is the number commonly recommended to counter genetic drift (Stiling, 2002:27). Some recent research, however, indicates that in actuality at least 1000 individuals are required because of the effect of deleterious mutations (USFWS, 2000:28). The accumulation of such mutations can lead to extinction, especially in small, fragmented populations (Higgins & Lynch, 2001:2928). Because the current constraints on RCW populations are unlikely to ever permit populations of such magnitudes, the only solution is immigration (USFWS, 2000:28).

As has already been noted, natural immigration (dispersal) from one population to another is relatively rare. When it does occur, the direction of immigration is most often from a small population to a large one because of the preference of the RCW to compete for existing cavities rather than excavate new ones (Walters et al., 1988:301). This immigration takes the opposite direction of the desired movement to counter the loss of genetic variation. Thus artificial immigration, or translocation, is the sole practice that is applicable for the management of RCW genetic resources (Lennartz et al., 1983:11).

Translocations have been shown to maintain genetic variability in isolated populations (Storfer, 1999:174). Through this artificial gene flow, the genetic variability of a smaller population can be restored to that of a larger population (Hudson et al., 2000:105). Unfortunately, the number of individuals recommended for translocation to achieve such goals is unclear (Storfer, 1999:174). Lacy constructed a model that indicated that a single migrant each generation could counter genetic drift in a non-specific population of 120 individuals (1987:148). Mills and Allendorf (1996:1516-1517) assert that between one and ten migrants per generation are sufficient to maintain genetic variation. While such guidance is vague, this is the standard currently supported by the U.S. Fish & Wildlife Service (2000:28).

Scope

It is the purpose of this effort to quantify the immigration rate that will counter genetic drift in small populations by modeling of RCW populations using a system dynamics approach. The emphasis is on the theoretical behavior of the model and on the relationship between model parameters such as birth and death rates, population size, and the presence of one or more helpers. These parameters are defined and related through the efforts of past research. Experimentation and field analysis were not conducted due to the time constraints involved.

The investigation of these objectives is achieved through the construction of a system dynamics model. The systems dynamics approach initially involves the creation of one or more behavioral reference modes and influence diagrams that serve as the dynamic hypothesis. The behavior of each version of the model is compared iteratively with the predicted behavior of the reference mode and adjustments are made to the model. With this iterative process, and through other verification and validation techniques, confidence in the model is established. It is then that the real work begins with the design and execution of the experiment. The system dynamics model provides insights into the system in question that other notional methods cannot.

Research Approach

The system dynamics approach dictates the methodology that is followed in this effort and is particularly suited to the problem of modeling genetic drift in the RCW. System dynamics is a method and philosophy that facilitates understanding in complex systems (Sterman, 2000:4). Like all modeling efforts, system dynamics provides a method of investigating a problem without the high costs associated with a field study or testing program. However, unlike many other modeling approaches, system dynamics focuses on the system as the cause (Shelley, 2002:32). Most variables are endogenous (Sterman, 2000:94), interactions between variables are explicitly defined in terms of cause-and-effect, and the behavioral pattern arises from the causal structure within the system (Shelley, 2002:32).

Expected Gain

The additional insight contributed by this effort will add to the growing knowledge base associated with the successful management of the RCW. The importance of genetic drift in the management of the RCW will be realized and well-supported guidelines will be established to aid U.S. Air Force natural resource managers in their endeavor to maximize and genetically optimize RCW populations. Ultimately, the contribution of this research is intended to aid in the full recovery of the species.

2. Literature Review

This research developed a model to aid natural resource managers in determining the optimum rate of translocating individual birds from a large population of red-cockaded woodpeckers to a small population to counter the effects of genetic drift. Genetic drift is the loss of genetic variation due to the randomness of the genetic transfer process. The literature review that follows discusses the functional sections of the Endangered Species Act (ESA) and the impact of that act on military lands with specific regard to the red-cockaded woodpecker, which was protected as an endangered species with the passing of the ESA in 1973. Additionally, it outlines the biology and behavior of the red-cockaded woodpecker and delves into the fragmentation of the RCW habitat and the effects of this fragmentation. The exploration of fragmentation leads to the discussion of inbreeding and genetic drift of which the latter is the primary concern of this effort. The review concludes with a discussion of system dynamics and the applicability of this method to the problem.

Endangered Species Act

The Endangered Species Act was created as an attempt to mitigate the disappearance of a growing number of species from the United States. The ESA is made up of 18 sections (US Congress, 2002:n. pag.) and has remained largely unchanged since its creation (Vaughan, 1994:11). Sections 4, 7, and 9 provide the functional backbone to the ESA (Vaughan, 1994:14). These sections outline listing criteria, the creation of recovery plans, federal compliance, and how species are to be protected.

Section 4 outlines the criteria that must be met for a species to be classified as endangered or threatened or to have such classification removed (Clark *et al.*, 1994:21). A species is not afforded any protections under the act unless it meets the qualifications to be placed on the endangered or threatened species list (Vaughan, 1994:22). In addition to outlining the listing process, section 4 also requires that a recovery plan be developed for each listed species (Clark *et al*., 1994:22). Largely due to an increased understanding of RCW habitat requirements, three recovery plans have been developed for the RCW in 1979, 1985, and in 2001 (Jackson, 1995:44-45).

Section 7 requires all agencies of the federal government to cooperate with the USFWS in accordance with the ESA and prohibits said agencies from harming or otherwise disturbing a listed species without first consulting the USFWS (Vaughan, 1994:15). Federal government agencies are singled out in section 7 because the federal government manages so much land that species protection and recovery simply could not occur without the full cooperation of federal agencies. For instance, federal lands provide habitat for about 50% of all federally listed threatened and endangered species (Stein *et al.*, 2002:n. pag.). Additionally, 12% of listed species occur almost exclusively on federal lands (Stein *et al.*, 2002:n. pag).

The final significant section of the ESA is section 9, which forbids the “takings” of listed species. “The term 'take' means to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct” (US Congress, 2002, n. pag.). Note that a taking is also considered to have occurred if a listed species’ habitat is damaged or otherwise altered (Vaughan, 1994:63-65). Another important clarification is that, unlike section 7, section 9 applies to all individuals and groups of people, not just federal organizations (Clark et al., 1994:23).

The ESA and Military Lands

The ESA's scope gives it considerable influence on the Department of Defense (DoD). First, the ESA dictates much of what can and cannot occur on military lands, of which there are approximately 25 million acres (Ripley and Leslie, 1997:94). As a point of interest, the proportion of listed species that are located on DoD lands in comparison to all federal lands is 4% (Stein *et al.*, 2002:n. pag.). This value may suggest that the DoD does not have a large stake in land on which listed species make their home. However, DoD lands actually have a significantly greater number of federally listed species per acre than do other federal agencies, such as the U.S. Forest Service, Bureau of Land Management, and U.S. Fish and Wildlife Service (Ripley & Leslie, 1997:95). Further, military lands preserve ecosystem types that are often unique and not preserved by other federal or state lands (Ripley & Leslie, 1997:95).

An additional factor that makes DoD lands important is that in many locations throughout the nation, urban growth has consumed vital habitat for many listed and candidate species. Only the military lands in these regions provide the habitat for such species to survive. "DoD lands are increasingly becoming 'islands' of habitat protection within 'seas' of development" (Ripley & Leslie, 1997:95). Given the importance of DoD lands as habitat, it is encouraging to note that the DoD has confronted its responsibilities regarding the ESA and has worked diligently towards the recovery of endangered and threatened species on its lands.

Although many examples of such successes exist, the population of red-cockaded woodpeckers on military lands throughout the southeastern U.S. is of particular interest to this study. At Eglin Air Force Base, natural resource managers have secured the future of the red-cockaded woodpecker by taking an ecosystem-based approach in applying the ESA (Ripley and Leslie, 1997:101). RCW numbers there have been stabilized and it is the fourth largest of all RCW populations with 295 active nesting sites (USFWS, 2000:122). The Army has had similar success with ecosystem management of the red-cockaded woodpecker in their endeavor to maintain training activities at Fort Bragg, North Carolina (Ripley and Leslie, 1997:101). Further, the U.S. Marine Corps has reported the highest rates of increase in RCW populations at Camp LeJeune and Fort Stewart (USFWS, 2000:122). From the U.S. Fish and Wildlife's perspective, the military is managing its RCW populations more effectively than all other federal agencies with the RCW on their lands (USFWS, 2000:122).

RCW Biology and Ecology

.Red-cockaded woodpeckers are smaller than other southeastern woodpeckers, measuring 8 to 9 inches in length and weighing 1.5 to 1.75 ounces (USFWS, 2000:9). The coloring of adults is an alternating black and white pattern, with black dominating the wings and tail and white, the belly. Large white cheek patches are the RCW's most recognizable feature (USFWS, 2000:9). The red-cockade from which their name derives is only present behind each eye of the male and is barely discernable unless the bird is excited or agitated (Bigony, 1991:13). Juvenile males can easily be recognized by a circular spot of red on the crown of the head that disappears once the bird matures (Lignon, 1970:273).

Figure 2.1 The Red-Cockaded Woodpecker (Applied Biomathematics, 2002)

The red-cockaded woodpecker is distinctive for its cooperative breeding system, in which it works with others of its species to occupy and defend its territory. The RCW occupies the same territories year-round, not migrating as many other avian species do (Lignon, 1970:258). The RCW is also monogamous, with breeding pairs mating for life (Haig *et al.*, 1993:191).

A group, the RCW social unit, is made up of a solitary male or a pair of breeders with or without one or more helpers (Walters *et al.*, 1992a:91). The formation of a group is determined by the actions taken by young RCWs. During its first year, a young bird may remain in the existing group as a helper to its parents, move to join an adjacent group as a helper, or it may disperse to seek a breeding vacancy (Walters *et al.*, 1992b:625). One or no helpers is the most typical number present in a group, but up to four helpers have been observed (USFWS, 2000:10). While helpers do not breed (Walters *et al.*, 1992b:625), their actions do improve the productivity of the group of which they are a member. It is not explicitly understood how helpers do this, but they are active in almost every activity associated with raising new young and maintaining the group to include: feeding, incubation, territory and nest defense, and cavity excavation (USFWS, 2000:10).

For those young RCWs that choose to disperse in their first year rather than become a helper, the mean distance traveled is less than that of other species of birds (USFWS, 2000:11). Dispersing fledglings typically travel between three and five kilometers, with males generally traveling further than females (Walters *et al*., 1988:290,292-293). Long distance travels of over 100 km are rare, but have been observed (USFWS, 2000:11). Females are more likely to disperse, while males commonly stay behind as helpers, eventually inheriting their natal territory or another nearby (Walters *et al.*, 1992b:625).

The relatively short dispersal distances of young RCWs and observations of field researchers indicate that dispersing birds move toward existing RCW clusters rather than unoccupied territory (Walters *et al*., 1988:301). Therefore, the acquisition of habitat through the construction of new cavities, which is termed pioneering, has been shown to occur only rarely (USFWS, 2000:19; Walters *et al*., 1988:301). Certainly a substantial reason for this tendency is the length of time required for the construction of new cavities (Walters *et al*., 1988:301).

Unlike other woodpeckers that typically select dead trees for cavity construction, red-cockaded woodpeckers construct their cavities in live southern pine (Hooper et al., 1980:2). While RCWs have been observed to construct their homes in many pine species types including loblolly and slash (USFWS, 2000:32), their preferred tree for cavity excavation is the long-leaf pine, a species that is estimated to have once inhabited 92 million acres of the southeastern U.S. (Frost, 1993:20). Depending on many factors, to include the pine type and number of helpers, cavity construction has been documented to take anywhere from 1 to 13 years (Hooper et al., 1980:2; Jackson *et al.,* 1979:102-103; USFWS, 2000:32-33). It is thought that the reason RCW evolved to select only live pines for cavity construction is due to the historical lack of dead snags (Lignon, 1970:261). These were likely consumed in fires common to the region before the modern age of fire suppression (USFWS, 2000:5).

Another important aspect of cavity construction is the RCW's preference for large, old-growth pine species. The reason for this preference is that generally only older trees (>70 years; Jackson *et al.*, 1979:103) are afflicted with red heart disease, a fungal disease that causes a tree's heartwood (core) to rot and become soft (Lignon, 1970:259). Only larger trees have a sufficient diameter of heartwood to allow adequate space for RCW cavity construction (Conner *et al.*, 1999:494). The presence of red heart disease ensures that it takes less effort and time for an RCW to excavate its cavity (Conner, 1995:335). The availability of suitable cavity trees is directly correlated with the quantity and distribution of RCW groups (Conner *et al.*, 1999:494). Unfortunately, many areas are lacking adequate cavity trees and it may be 20 to 40 years before existing trees meet cavity qualifications (Hooper, 1995:59).

The primary reasons for the lack of large old-growth pine trees is the prevalence of logging in the southeastern region since the 18th century (Frost, 1993:23-31), conversion to pine plantations on short-rotation harvests (Frost, 1993:36), and fire suppression allowing hardwoods to choke the midstory and out-compete pine seedlings (Frost, 1993:34-35). Only three percent of the estimated 92 million acres of longleaf pine existing at the time of European settlement is standing today (Frost, 1993:37). While the longleaf pine is the RCW's species of choice (Lennartz and Heckel, 1987:48), it also has been observed to successfully inhabit loblolly (Lennartz and Heckel, 1987:51) and slash pine (Bowman and Huh, 1995:415).

Management Techniques

The RCW, like all endangered species, requires active management on the part of natural resource managers if the RCW population is to recover to a self-sustainable level (USFWS, 2000: 126). The 2000 RCW recovery plan outlines ecological requirements for the RCW and specific techniques to enhance and expand both habitat and local populations (USFWS, 2000: 64-106,143-166). Such techniques include artificial cavity construction (USFWS, 2000:73), prescribed burning (USFWS, 2000:88), and translocation (USFWS, 2000:84).

Artificial Cavities. One way that natural resource managers have dealt with an area that is poor in cavities and cavity suitable trees is through the construction of artificial cavities (Krusac *et al.*, 1995:62). Two separate techniques have been developed. The first method utilizes the drilling of two holes, a near vertical one for the interior cavity and then a horizontal one for the RCW entrance; the former is then blocked, and the constructed cavity now closely resembles a natural one (Copeyon, 1990:303-311). See Figure 2.2 for a diagram of this type of cavity.

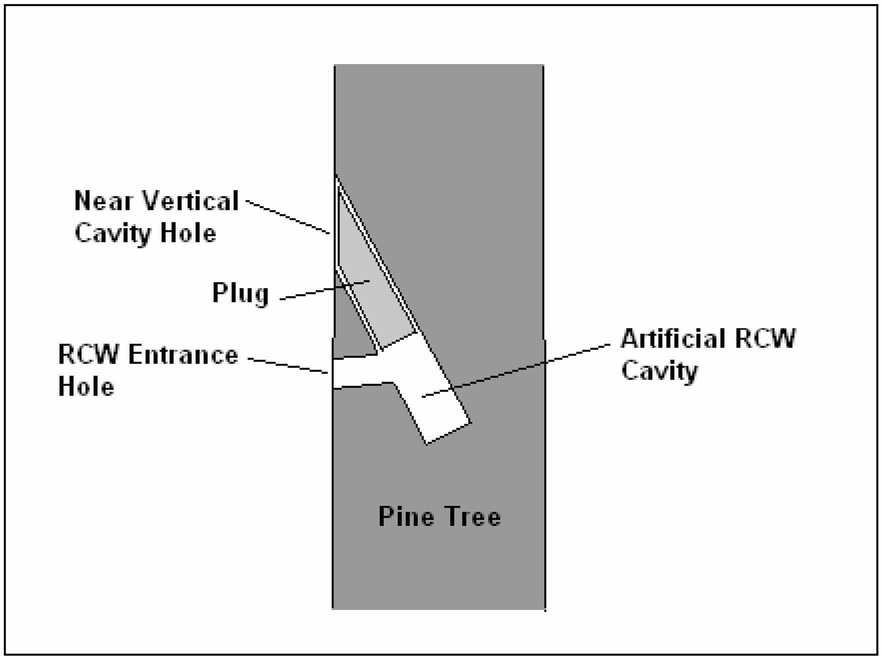


Figure 2.2 Drilled Artificial Cavity (adapted from Copeyon, 1990)

The other technique is to remove a box-shaped section from a pine and insert in its place a similarly sized wooden box with a man-made vertical cavity and entrance hole (Allen, 1991:2-3). The latter method has the advantage of being able to be placed in younger trees with very little heartwood because the cavity is located in the artificial box rather than in the tree itself (Allen, 1991:2). Both techniques have been used effectively to both rehabilitate populations in existing locations and expand RCW population into new locations (Krusac *et al.*, 1995:62; Walters *et al.*, 1995:380).

Results indicate that artificial cavity construction is a more effective means to expand RCW populations into new habitat than creating or providing suitable habitat without existing cavities (Walters *et al.*, 1995:384). As noted previously, because of the time and effort involved, RCWs prefer to compete for existing cavities as opposed to pioneering new territory through the construction of new cavities (Walters *et al.*, 1988:301). Artificial cavities are a way to compensate for this tendency and successfully expand RCW populations. (Walters *et al.*, 1995:384).

Figure 2.3 Artificial Cavity Box (Schroeder, 2001:59)

Prescribed Burning. The controlled burning of small areas of southeastern pine forest is used to simulate the regular natural fires that were prevalent in the region prior to European settlement (USFWS, 2000:94; Frost, 1993:21). The purposes of such prescribed fires are to consume the forest debris that accumulates in the forest understory, return nutrients to the soil, eliminate hardwood encroachment into the mid- and understory, and initiate growth in fire-adapted species (Hermann *et al.*, 1998:384-385). Of these, the elimination of hardwoods is a key habitat improvement for the RCW because the invasion of hardwoods into the midstory dissuades RCWs from inhabiting otherwise suitable areas (Bigony, 1991: 14). Due to the resiliency of the hardwoods, it is necessary to apply successive burns every one to five years depending on geographic area (USFWS, 2000:162).

Translocation. Translocation is the artificial immigration of individuals between or within populations (USFWS: 2000, 84). The 2000 Recovery Plan highlights three applications of translocation: (1) demographic—the addition of individuals to small populations that are particularly vulnerable to local extinction, (2) geographic—a rearrangement of a population to eliminate isolation and/or provide for more effective interactions, (3) genetic—to manage genetic resources and counter loss of diversity (USFWS: 2000:85). The latter application is of particular concern to this study and is explored further in the document.

Fragmentation

The distribution of the red-cockaded woodpecker across the southeastern U.S. can be characterized as a metapopulation. Metapopulation is a term used by ecologists to describe a population that is characterized by a discontinuous distribution; it is a population that is fragmented (McCullough, 1996:1,3). A metapopulation describes a patchwork of geographically separated smaller populations in which the movement of a species between patches (dispersal) is restricted (McCullough, 1996:1-2). According to this definition, the RCW certainly qualifies as a metapopulation given that as of 1999, there were 89 separate populations of RCWs distributed over federal and state lands across 12 states (USFWS, 2000:117-119). With the metapopulation classification comes its vulnerabilities. Primarily these include an increased chance of local extinction (extirpation) due to natural and anthropogenic causes (McCullough, 1996:7), limited dispersal (McCullough, 1996:1-2), increased predator vulnerability (McCullough, 1996:7), and loss of genetic diversity (Hedrick, 1996:46).

The current RCW distribution as a metapopulation did not happen naturally. It is estimated that approximately 420,000 RCWs occupied the pine forests of the southeastern United States prior to European settlement. Current estimates put the total RCW population at 12,500 (USFWS, 2000:vi). This dramatic decrease can be primarily attributed to loss of longleaf pine habitat through logging, plantation conversion, and fire suppression (Hardesty *et al*., 1997:1; Frost, 1993:23-31, 34-36). Due to these anthropogenic factors, most of the RCW populations are small (<50 groups; Lennartz and Heckel, 1987:48), occupy fragmented habitat, and are often isolated from one another (Conner and Rudolph, 1991:446).

Particularly small populations of the RCW metapopulation are vulnerable to environmental and demographic effects (Conner and Rudolph, 1995:141). For instance, Conner and Rudolph showed that fragmentation significantly limited an RCW group's access to foraging habitat that ultimately resulted in abandonment of an active cluster (1991:452). Further, it was shown that small populations of RCW are at a greater risk of extirpation due to forest removal than are larger, dense populations (Conner and Rudolph, 1991:454). Additionally, small, fragmented populations are more likely to become extinct (Crowder *et al*., 1998:5; Conner and Rudolph, 1995:141). Note that it has been shown that the RCW is more persistent in small populations than other avian species due to its cooperative breeding system (Crowder *et al*., 1998:1). While resistant if the proper conditions (proximity and size of nearby populations and spatial configuration) are satisfied, small populations (less than 10 groups) are unlikely to persist over a 20-year time span (Crowder *et al*., 1998:7).

Another consequence of the metapopulation distribution is that it commonly increases the loss of genetic variation (USFWS, 2000:7). This is due to the fact that the RCW's already limited dispersal (Walters *et al*., 1988:301) is further is constrained by the isolation of fragmentation (USFWS, 2000:7). Small populations are again the most vulnerable, being particularly prone to the loss of genetic variability (Storfer, 1998:174; Montgomery *et al*., 2000:42). This topic is dealt with further in the next section.

Genetic Factors

As noted, a particular concern for small populations is the loss of genetic variation. This potential loss comes in two forms: inbreeding and genetic drift (USFWS, 2000:26; Stiling, 2002:24-27; Storfer, 1998:174). While inbreeding, mating between close relatives, is common among social animals (Stiling, 2002:24), its detrimental effects only truly threaten small populations (Lande, 1988:1456). Such effects include: sterility; a decrease in population fitness through the reduction of heterozygosity and unmasking of deleterious alleles; and reduced tolerance of disease and environmental change (Lande, 1988:1456; Storfer, 1998:174).

The specific effects of inbreeding in RCW populations have been reduced hatching rates and greater mortality of fledglings less than one year in age (USFWS, 2000:26). It is the commonly held view that a population of at least 50 individuals is enough to negate the effects of inbreeding (Stiling, 2002:25). However, current research regarding inbreeding of RCWs indicates that greater numbers may be necessary; a stable population of 50 to 100 or more breeding groups is recommended (USFWS, 2000:27). For those populations of RCW that are smaller than the recommended size, the immigration of 2 or more individuals per year from outside the local population are required to protect against genetic loss due to inbreeding (USFWS, 2000:27).

Genetic drift is the loss of genetic variations over time. More specifically, it is the loss of unique alleles through a lack of breeding of those individuals possessing such alleles (Stiling, 2002:26). The primary consequences are the increase in homozygosity and the decrease in a species' ability to adapt to its environment through natural selection (Lande, 1988:1456).

Again, smaller populations are more vulnerable to the effects of genetic drift. However, the magnitude is relative; whereas 50 individuals are the rule of thumb for countering the effects of inbreeding, 500 is the number commonly recommended to combat genetic drift (Lande, 1988:1456; Lennartz *et al.*, 1983:11; Stiling, 2002:27). Some recent research indicates, however, that in actuality at least 1000 individuals are required, due to the effect of deleterious mutations (USFWS, 2000:28). Because of the metapopulation distribution of the RCW and the lack of sites large enough to permit continuous populations of such magnitudes, the only solution is immigration (USFWS, 2000:28).

As has already been noted, natural immigration (dispersal) from one population to another is relatively rare. When it does occur, the direction of immigration is most often from a small population to a large one because of the preference of the RCW to compete for existing cavities rather than excavate new ones (Walters *et al.*, 1988:301). Such natural immigration is counter to the direction of the desired movement necessary to mitigate the loss of genetic variation. Thus, translocation is the sole practice that is applicable for the management of RCW genetic resources (Lennartz *et al.*, 1983:11).

Translocations have been shown to maintain genetic variability in isolated populations (Storfer, 1999:174). Through this artificial gene flow, the genetic variability of a smaller population can be restored to that of a larger population (Hudson *et al.*, 2000:105). Unfortunately, the number of individuals recommended for translocation to achieve such goals is unclear (Storfer, 1999:174). Lacy performed a computer simulation of 120 individuals in which a single migrant each generation for 100 generations was estimated to counter genetic drift (1987:148). Mills and Allendorf (1996:1516-1517) assert that between one and ten migrants per generation exchanged between separate RCW populations are sufficient to maintain genetic variation. This is the standard currently supported by the U.S. Fish & Wildlife Service in their 2000 RCW Recovery Plan (28). Note that no guidance is provided as to what size population of RCWs this standard applies to. The objective of this effort is to develop a model specific to the RCW to better quantify the number of translocated individuals necessary to mitigate genetic drift based on population size.

A particular challenge for the modeler was to determine how to estimate genetic drift, particularly since genetic drift is a stochastic process. A number of options were considered but ultimately it was determined that a mechanistic approximation of genetic drift would be the most appropriate to incorporate into a system dynamics modeling process. A paper by Russell Lande entitled, “Breeding Plans for Small Populations Based on the Dynamics of Quantitative Genetic Variance” provided just such a set of mechanistic equations (1995:318-339). Note that these equations presented by Lande were intended to apply to a captive population, such as in a zoo or wildlife sanctuary, but their application to a wild, geographically isolated set of populations, does not invalidate their function. For an isolated population with no immigration, the simple approximation used throughout the field of population genetics is:

$$\frac{dV_g}{dt} = \frac{-V_g}{2N_e} + V_m \qquad \text{Equation 2.1}$$

where V_g is the additive genetic variance in a quantitative character, t is the time measured in generations, V_m is the additive genetic variance from mutation, and N_e is the effective population size (Lande, 1995:320-321). In this work, the effect of mutation is ignored ($V_m = 0$), as its effect on genetic variation is still a point of contention amongst researchers (USFWS, 2000:28). For simulated populations, the effective population size is the actual breeding population size (Lacy, 1987:146).

For a population with immigration or translocation, hence termed the managed population, the modeling of genetic drift requires additional variables and terms. Equation 2.2 incorporates the effect of the additive genetic variance from immigration in the managed population (Lande, 1995:325). Equation 2.3 is the expected random genetic drift in the captive population's mean phenotype of interest (Lande, 1995:325).

$$\frac{dV_g}{dt} = \frac{-V_g}{2N_e} + V_m + m\left(V_g(0) - V_g\right) + \frac{m(1-m)}{2} \cdot V_z \qquad \text{Equation 2.2}$$

$$\frac{dV_z}{dt} = -2m \cdot V_z + \frac{V_g}{N_e} \qquad \text{Equation 2.3}$$

The immigration rate m is the proportion of the managed population that is replaced by individuals from a source population; m equals the number of translocated individuals divided by the managed population's effective population size, N_e. It is assumed that the translocated individuals from the source populaiton replace individuals in the managed population, matched for sex and age (Lande, 1995:325). The other new variable introduced is the variance V_z, caused by random genetic drift, in the probability distribution of the mean phenotype in the captive population over the period in question (Lande, 1995:325). The phenotype is the physical expression of the corresponding quantitative character in question. If the source population has an additive genetic variance denoted by $V_g(0)$ in a quantitative character with mean phenotype $z(0)$, then $V_z = \mathrm{E}[(z(t) - \mathrm{z}(0))^2]$ (Lande, 1995:325). That is, the expected value of the squared difference (the definition of variance; Mclave *et al.*, 2001:179) between the managed and source population's mean phenotype is denoted by V_z. It is assumed that the phenotype is measured on a hypothetically large number of offspring (Lande, 1995:325). The difference in the distribution associated with V_g and V_z is due to the environmental variance in the quantitative character that is even present in a genetically uniform population (Lande, 1995:322).

The effect of mutation is again ignored in Equation 2.2. The second to last term of Equation 2.2 is the genetic variance carried by the translocated individuals. The last term in 2.2 is the genetic variance produced by the hybridization between populations. Regarding Equation 2.3, the variance of the mean phenotype V_z decreases with increasing immigration rate m and increasing effective population size N_e. Additionally V_z decreases with an increase in the additive genetic variance, V_g and decreasing N_e.

The above equations provide the necessary mechanistic approximations of the genetic drift for the two populations modeled; that is, the source population with translocation out of the population and the managed population with translocation into the population. Each was incorporated into the system dynamics modeling process that follows.

System Dynamics Modeling

The system dynamics approach is particularly suited to the problem of modeling genetic drift in the RCW. System dynamics is a method and philosophy that facilitates understanding in complex systems (Grant *et al.*, 1997:6; Sterman, 2000:4). Like all modeling efforts, system dynamics provides a method of investigating a problem without the high costs associated with a field study and/or lab experiments. However, unlike many other modeling approaches, system dynamics focuses on the system as the cause (Shelley, 2002:32). Most variables are endogenous (Sterman, 2000:94), interactions between variables are explicitly defined in terms of cause-and-effect, and the behavioral pattern arises from the causal structure within the system (Shelley, 2002:32).

The system dynamics approach can best be understood through the stages taken to create a model. These are: conceptualization, formulation, testing, and implementation (Shelley, 2002:36). The process is iterative, often requiring a modeler to return to a previous step, revise, and continue (Shelley, 2002:35). Revisions to an earlier step are necessary when new insights are gained in proceeding through the process (Sterman, 2000: 87). The process commonly involves the modeler working closely with a client who has a vested interest in the problem at hand (Sterman, 2000:84-85).

In the conceptualization stage, the modeler articulates the problem based initially on a vague mental notion of the influences involved in the system behavior (Shelley, 2002:36,61). This is the most important step (Sterman, 2000:89). Not only is the problem defined, but also the key variables and applicable time horizon (Sterman, 2000:86). Concurrently, the reference mode is developed. The reference mode is a graph or set of graphs showing the behavior of the variables of interest over time (Shelley, 2002:38,40). The reference mode diagrams provide an image of the long-term behavior of the problem, from which the modeler and client develop the rest of the model (Sterman, 2000:90).

With the reference mode created, the next step of the conceptualization stage is the formulation of the basic mechanism that is hypothesized to generate the reference mode (Shelley, 2002:36,42). The basic mechanism takes the form of a causal diagram termed the influence diagram (Shelley, 2002:36). The influence diagram is described by feedback loops indicating reinforcing (+) or compensating (-) behaviors between the minimum set of variables necessary to describe the problem (Shelley, 2002:42,48). Together, the reference mode and influence diagram form the dynamic hypothesis (Shelley, 2002:36,42). It is a working theory of the origin and behavior of the problem (Sterman, 2000:95). It is important that the dynamic hypothesis make sense to the client, both communicating and confirming the underlying structure of the problem (Shelley, 2002:62).

Once the dynamic hypothesis has been developed and the client concurs that it represents the problem in question, the modeler can move on to the formulation stage. In this stage, the flow diagram is developed (Shelley, 2002:61). The flow diagram is a mechanistic representation of the dynamic hypothesis (Shelley, 2002:62). It translates the influence diagram structure to an operating system incorporating stocks (accumulations) and flows (rates in/out) representing the logic of the dynamic hypothesis (Shelley, 2002:62-63). The formulization process defines equations, parameters, and initial conditions for the translated structure (Sterman, 2000:103). Often additional details not present in the influence diagram are necessary to solidify vague concepts and resolve contradictions (Shelley, 2002:63; Sterman, 2000:103). The key is to not add additional structure that goes beyond that which is conceptually shown in the influence diagram (Shelley, 2002:63). If this guidance is not followed the model will no longer properly represent the connections between the assumptions and the output; the model will be deemed to be out of control (Shelley, 2002:42).

When a formal model has been constructed, the testing stage is the next important step. Testing actually occurs throughout the entire process, again in an iterative fashion (Sterman, 2000:103). One of the most telling tests is whether the formal model accurately reproduces the behavior of the problem as outlined by the reference mode. If it does then the model is considered at least partially validated. Other tests include determining if the flow diagram matches the influence diagram (verification; Shelley, 2002:72), testing the model at extreme values to evaluate the robustness of the model (Shelley, 2002:76), and sensitivity tests to quantify the effects of parameter values in relation to model behavior (Shelley, 2002:78). No single test can provide validation; many tests must be applied and confidence in the model gained gradually with the passing of each (Shelley, 2002:74).

With confidence established through testing, the modeler and client can utilize the model for its intended purpose in the implementation phase (Shelley, 2002:36; Sterman, 2000:103). Various scenarios can be explored and the system behavior noted. Policies and management techniques can be “switched on” to test the system’s response. In short, the model can be used for simulation and perhaps an optimal solution to a complex problem can be found.

In the case of this research, the population dynamics of the RCW and its intraspecific interactions can be characterized as a complex system. There is a need to understand the specific effects of translocation on genetic drift in the RCW. The problem is too extensive and involves too many parameters such that a simple notional model will not suffice. System dynamics provides the tools and methods with which this complex system is better understood. Policies are developed to guide a natural resource manager in his or her efforts to counter genetic drift in small RCW populations.

3. Methodology

Modeling Approach

It is apparent that natural resource managers simply cannot have enough information regarding an ecosystem under their direction. When that ecosystem is occupied by one or more endangered species, the job of managing that system becomes particularly complex. The resource manager does not have the luxury of taking a "wait-and-see" approach. They need guidelines that will ensure the future of the species in question, but they often possess only a snapshot of the current situation. Modeling, and particularly dynamic modeling, allows the natural resource manager to see the behavior of system over time (Ford, 1999:6). The insight gained through such models permits the resource managers to make better-educated decisions about today's actions and how they will affect the future.

The system dynamics approach is particularly suited to developing models that are representative of complex ecological systems. System dynamics allows modeling for increased understanding and generalized predictions outside the range of historical data, rather than precise short-term prediction (Shelley, 2002:34). The advantage of such models is that heuristics, or rules of thumb, can be developed for use by the manager(s) of the complex ecological system in question (Ford, 1999:11). What a system dynamics model does not provide is for the manager to say to him or herself, "I have data point A, and data point B, that means according to the model, I need to take action C and that will result in data points A+D and B+E which will fix my problem." Instead, the manager can think more in terms of, "I am seeing this trend in metric A and this other trend in metric B. I can feel confident in taking action C because the model indicates A and B respond favorably to such an action." Given a need for such heuristics to mitigate the adverse effects of genetic drift, the system dynamics process provides a series of iterative steps that lead to the development of a model. The implementation of the model results in the heuristics for the management of the system.

System Dynamics Process

The systems dynamics methodology consists of four stages: conceptualization, formulation, testing, and implementation (Shelley, 2002:35-36). The process is iterative; that is, the modeler often must go back to a previous step, modify it, and return. The stages that characterize system dynamics were employed for the methodology of this thesis.

Conceptualization

The purpose of the conceptualization stage is to become familiar with the problem and the factors related to it. This was done through discussions with thesis committee members that led to the formulation of the research questions and objectives. These actions provided the direction of the literature review on the topics in question.

<u>Literature Review.</u> The literature review was conducted to develop background to the problem of genetic drift in the RCW and investigate the factors and relationships that define and contribute to that problem. The bulk of the information utilized was obtained through published journal articles. Through the literature review, the model structure and parameters were defined. As the modeling progressed, additional literature was needed to clarify issues that arose.

Problem Statement. In conjunction with the literature review, a formal problem statement was developed that states:

> The purpose of this research is to provide natural resource managers a reference for determining how many red-cockaded woodpeckers should be translocated from a large population to a small population to counter the detrimental effects of genetic drift. Additionally, the research explores the degree of genetic drift present in various population sizes and the relationship of genetic drift to other model parameters affecting RCW populations.

This statement was developed through coordination with the thesis committee and concisely expresses the scope of the work completed.

Reference Mode. With background of the literature review and direction from the problem statement, a reference mode was developed. The time horizon was defined as 50 generations, which equates roughly to 50 years as RCW offspring are able to reproduce at age 1 (USFWS, 2000:11). The basis for this choice was that such a time period fall within a manager's lifetime making it is easier to comprehend the results. The variable of primary interest was the magnitude of the genetic variation. The reference mode as originally conceived is shown below for the managed population of concern. The graph

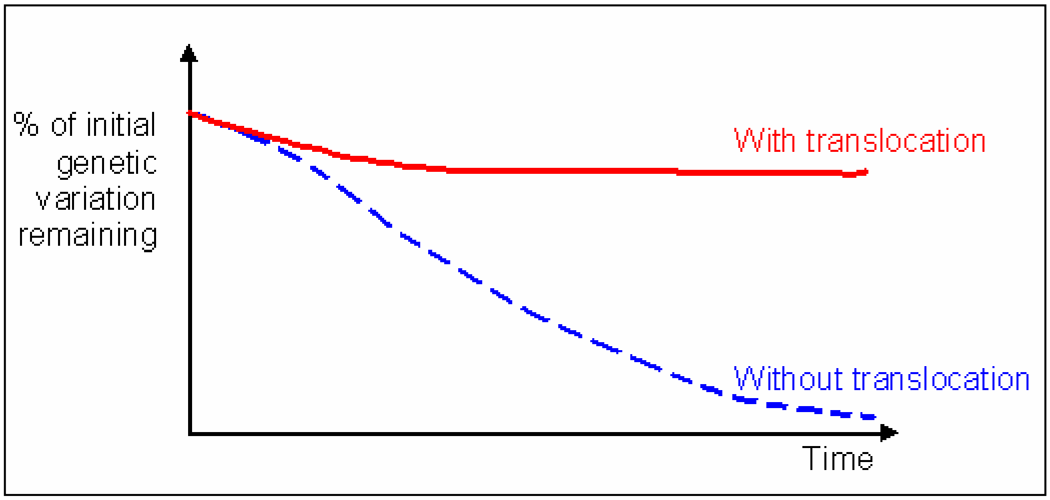


Figure 3.1 Managed Population's Genetic Variation Reference Mode

shows what is conjectured to happen to the percentage of genetic variation remaining when no birds are translocated into the population versus when birds are translocated.

A second reference mode was created to define another variable of interest, the magnitude of the managed population over the same time horizon. Note that the hypothetically small, managed population is extirpated if no translocation occurs. With translocation, the population is sustained.

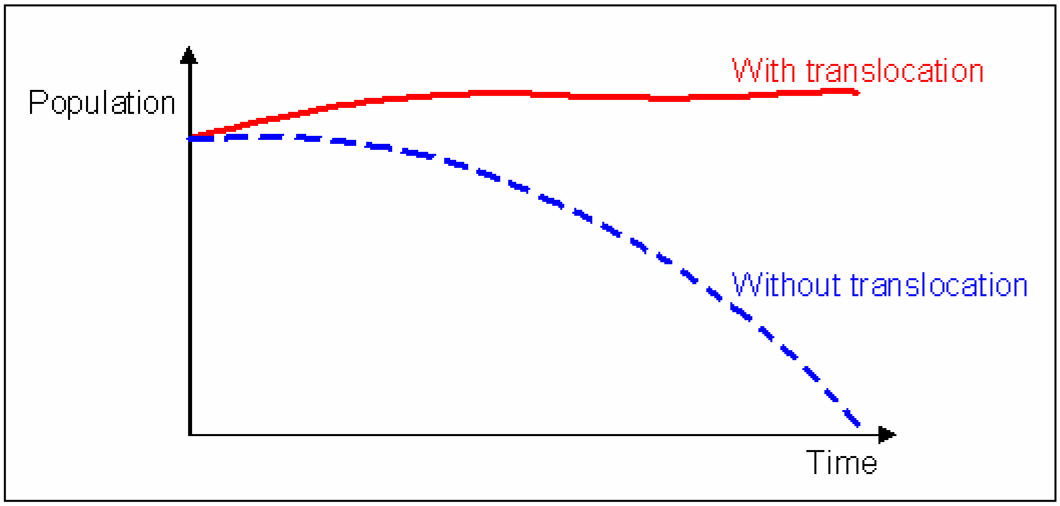


Figure 3.2 Managed Population Reference Mode

Influence Diagram. Typically in the system dynamics approach, the reference modes would provide the impetus for the next step in the conceptualization stage, the creation of the influence diagram. In this case, while the reference modes do provide a foundation for understanding the system and a means of validation, they are not directly tied to the structure represented in the influence diagram. That is, the influence diagram was not created based on the shape and behaviors of the reference modes, but on the real world relationships between the variables of concern.

The influence diagram in Figure 3.3 describes the minimum set of variables necessary to describe the problem and their causal relationships (Shelley, 2002:42).

These relationships are described by feedback loops indicating reinforcing (+) or compensating (-) behaviors (Shelley, 2002:48). Together, the reference modes and influence diagram form the dynamic hypothesis, which is a working theory of the origin and behavior of the problem (Shelley, 2002:36,42; Sterman, 2000:95).

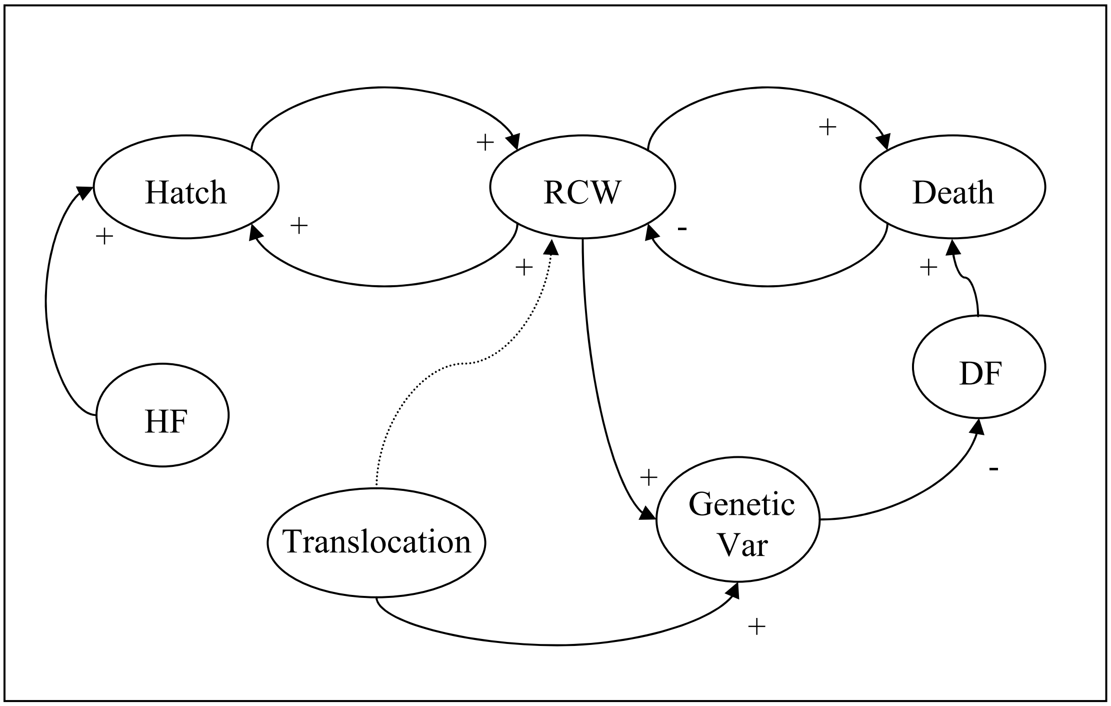


Figure 3.3 Influence Diagram

In Figure 3.3, the two basic mechanisms affecting the managed RCW population are the rate of hatching and the mortality rate, denoted by *HF*, the hatch fraction, and *DF*, the death fraction. There is a direct correlation between the magnitude of the population and the genetic variation; that is, the smaller the population, the less robust the population and the greater its loss of genetic diversity. In turn, the loss of genetic diversity decreases the resiliency of the species in its environment; the RCW loses variations that make it successful. Therefore, the death rate of the managed population increases. In order to counter that effect, individuals are translocated, adding genetic variation and reducing the mortality rate to an acceptable level. Note that the dotted line from “Translocation” to the RCW population indicates that two scenarios were explored: translocation with replacement and translocation without. The reasons for this formulation are explained in Chapter 4, but it is important to define that replacement means that for every individual translocated into a population, one is taken out from that same population. The dotted line applies to the case where replacement is not occurring and therefore, the population is bolstered demographically by the addition of translocated individuals.

Formulation

The dynamic hypothesis led to the formulation of the flow diagram. For this stage, STELLA computer modeling software was utilized. STELLA, developed by High Performance Systems, allows a modeler to create differential equations via a graphical interface. The modeler uses stocks, flows, and converters to represent the structure and relationships developed in the influence diagram. When the model is “run,” STELLA utilizes numerical integration to compute the values of the stocks and flows.

The model created in this effort consisted of five sectors. A large (400 pairs) population of RCW was modeled and labeled as the “Source Population.” A smaller (10, 25, or 50 pairs) population used the identical model structure and parameters as the large population and was labeled “Managed Population.” One genetic drift sector was created for population. Equation 2.1 was the basis for modeling the genetic drift in the source population and equations 2.2 and 2.3 for the managed population. The final sector consisted of the structure that allows for the translocation of individual birds from the source population to the managed population. This sector permits the user to adjust the number of individuals to be translocated between 0 and 4 and the amount of time between translocations between one-half and two generations. Model sectors can be seen in appendix A with model equations in appendix B.

Testing

Testing is the next stage of the system dynamics approach, but it is important to point out that it occurs throughout the process in an iterative fashion. Tests are classified as providing either validation or verification. The primary verification test is whether the flow diagram is consistent with the influence diagram. Additionally, verification consists of checking for reasonable performance under a reasonable range of input in stages throughout the modeling effort (Shelley, 2002:72).

The validation portion of the testing is somewhat more extensive, but it too is done throughout the modeling process. The purpose of validation is to establish confidence in the usefulness and robustness of a model (Shelley, 2002:74). This can be done with a variety of methods of which the comparison of the model output to the reference mode is one of the most critical. It is important to note that no single test validates a model; confidence is accumulated gradually with the passing of each test (Shelley, 2002:76).

The model output presented in this thesis compared favorably with the reference modes presented in this section. Additionally, a sensitivity analysis was performed to determine which parameters in the model were affected the most by manipulation. Detail was added and accuracy readdressed when it was found that the adjustment of a particular parameter created dramatic shifts in model output. Further, boundary adequacy tests were employed throughout the creation of the model to ensure that the model structure accurately represented the assumptions present in the model. To do this, parameters, logic, and structure were adjusted to confirm that the model output was dependent on the set assumptions.

Implementation

With confidence in the model established, the design of the experiment to be investigated can begin. The purpose of this effort was to quantify the number and frequency of RCWs necessary to counter genetic drift in various small populations. A simulation experiment was designed to investigate the effect of translocating 0, 1 (female), 2, or 4 birds every half-generation, every full generation, or every two generations. The managed populations in question had initial sizes of 10, 25, and 50 pairs and the source population was fixed at 400 pairs. Also incorporated was translocation with and without replacement. The results of the experiment were tabulated and presented in a form that can be utilized to provide the heuristics sought by natural resource managers to determine the number and frequency of RCWs to bring into a managed population.

4. Data Analysis and Results

Experiment Definition

The model incorporates two parameters that represent natural resource manager action and these are varied to create the various management scenarios. The two management parameters are the number of individual RCWs translocated and the interval between translocations. The number of RCWs translocated is assigned values of 0, 1, 2, and 4. A value of 1 indicates a single female, a value of 2 is one pair, and 4 indicates two pairs are translocated. The interval at which these translocations are performed can take on values of 0, 0.5, 1, and 2. These values indicate no translocation, translocation every half-generation, every generation, and every two generations, respectively.

The initial value of the source population was held constant at 400 pairs for all scenarios. The smaller managed population was assigned initial values of 10, 25, and 50 pairs and are labeled as such in Table 4.1 below, which shows the initial age demographics assigned for each population. Note that the pairs labeled in the second column are computed by the number of adult females plus the number of old females with the assumption that all have mates, as female helpers are rare (USFWS, 2000:10). The difference between the number of adult males and number of adult females is the number of male helpers available initially.

Table 4.1 Initial Age Demographics

	RCW	Fledglings		Adults		Old	
	Pairs	Male	Female	Male	Female	Male	Female
Managed	10	4	4	9	7	3	3
Managed	25	10	10	25	18	7	7
Managed	50	20	20	45	35	15	15
Source	400	150	150	400	300	100	100

The age demographics of a real population of red-cockaded woodpeckers were not utilized because it was deemed that a generalized set of populations would suffice for the purpose of the experiment. Initial values were based on what could be gleaned from the literature. A sensitivity analysis was then performed, adjusting the values incrementally and independently, noting model behavior. Ratios between categories (fledging, adult, old, male, and female) are nearly constant amongst the various populations so as to ensure better comparability.

As was noted in Chapter 2, the equations used for the calculation of genetic drift are based on a captive population. An inherent assumption made by Lande in developing these equations was that translocations replace captive individuals with wild ones, matched for sex and age (1995:325). Matching for sex and age was adhered to in the design of the model, with those individual birds from the managed population who are replaced leaving the system. Regarding the purpose of the replacement assumption, it would appear to have been made in order to make it easier to solve the differential equations, maintaining population as a constant and thereby eliminating a variable.

With the STELLA modeling software, such complication is easily incorporated and the populations are modeled as a variable. Additionally, it is not realistic to assume that a natural resource manager would remove an individual RCW from the local population for every RCW they brought in; this would be especially true for any population under 50 pairs due to the demographic vulnerability of smaller populations. Yet, given limited habitat for some populations, translocations with replacement may indeed be a necessary technique for mitigating genetic drift. For these reasons, the management scenarios are performed for translocations both with and without replacement.

With both versions of the experiment, one important inherent assumption is that natural resource managers are performing additional habitat and population management techniques in conjunction with the translocations for both the managed and source populations. Such techniques include those mentioned in Chapter 2: prescribed burning, artificial cavity construction, and relocations of individuals within the population for better geographic arrangement. Additionally, it is assumed that the modeled populations are not constrained by habitat availability. While not an entirely realistic assumption, the additional structure necessary to incorporate a habitat constraint into the model was beyond the scope of this effort.

The design of the experiment is summarized in Table 4.2. The management scenarios are nearly self-explanatory. For instance, one such scenario is a managed population with an initial value of 10 pairs having translocations of two RCWs (one pair) every generation with replacement. Note that neither the number of RCWs to be translocated or the interval is equal to zero when the other is non-zero; that is, translocating a pair of RCWs at an interval of zero generations is not a valid scenario. To reiterate, the figures shown in Table 4.2 for both the source and managed populations are

Table 4.2 Experiment Design

Source Pop. RCW Pairs	Managed Pop. RCW Pairs	Translocations		
		Replacement	From Source Pop	Interval (generations)
400	10	Y	0, 1, 2, 4	0, 0.5, 1, 2
400	25	Y	0, 1, 2, 4	0, 0.5, 1, 2
400	50	Y	0, 1, 2, 4	0, 0.5, 1, 2
400	10	N	0, 1, 2, 4	0, 0.5, 1, 2
400	25	N	0, 1, 2, 4	0, 0.5, 1, 2
400	50	N	0, 1, 2, 4	0, 0.5, 1, 2

values that describe and correspond to the actual initial values inputted into the model as per Table 4.1.

Simulation Results

Final Values. Simulations were run for a duration of 50 generations for each of the combinations described in Table 4.2. The final population value and percentage of genetic variation remaining (V_g/V_{g0} x 100%) were recorded for both the source and managed populations. Table 4.3 presents the results of the simulations incorporating

Table 4.3 Results With Replacement

Variables			Managed Population		Source Population	
Initial Pair #	RCW per Trans	Trans Interval	Final Pair #	% V_g/V_{g0}	Final Pair #	% V_g/V_{g0}
10	0	0	0	0.0	480	96.6
	1	2	2	45.5	470	96.5
	1	1	3	65.6	459	96.5
	1	0.5	5	79.9	437	96.4
	2	2	3	64.3	460	96.5
	2	1	5	79.5	438	96.4
	2	0.5	7	88.8	396	96.2
	4	2	5	79.1	439	96.4
	4	1	8	88.7	397	96.2
	4	0.5	10	94.1	312	95.8
25	0	0	6	35.7	480	96.6
	1	2	11	66.4	470	96.5
	1	1	15	78.2	459	96.5
	1	0.5	20	87.1	437	96.4
	2	2	13	73.2	460	96.5
	2	1	18	84.2	438	96.4
	2	0.5	23	91.6	396	96.2
	4	2	15	80.0	439	96.4
	4	1	20	88.8	397	96.2
	4	0.5	25	94.4	312	95.8
50	0	0	26	68.6	480	96.6
	1	2	34	79.5	470	96.5
	1	1	39	85.4	459	96.5
	1	0.5	47	90.8	437	96.4
	2	2	38	84.2	460	96.5
	2	1	45	89.8	438	96.4
	2	0.5	52	93.8	396	96.2
	4	2	42	87.4	439	96.4
	4	1	48	92.3	397	96.2
	4	0.5	54	95.8	312	95.8

replacement and Table 4.4 is the results without replacement.

Immediately evident when comparing the tables, the final managed population figure is less in Table 4.3 than the managed population in Table 4.4 for a given scenario. The same holds true for the percent of genetic diversity remaining. This was expected as translocation with replacement does not include the demographic benefit of additional individuals. Therefore, the genetic benefit of translocation is effectively isolated for the results presented Table 4.3. Such a comparison provides valuable insight into the impact of genetic drift.

With Replacement. The managed populations are clearly hampered. From Table 4.3, the final number of pairs is equal or better than the initial value of the three managed populations only if 2 pairs are translocated every half-generation. The primary focus of the experiment is the percentage of genetic variation remaining. A population is judged as being genetically healthy if it maintains 90% of its genetic variation over the substantially long time span of 200 years (Lande, 1995:319). Since the duration of this experiment is 50 generations, management scenarios resulting in percentages of genetic variation higher than 90% are desired.

In the replacement version of the experiment, translocating 2 pairs every half-generation is the only management scenario that achieves such a genetic variation goal for an initial population of 10 pairs. With such a scenario, the source population declines significantly from 400 to 312 pairs. This is an outcome that managers of the source population would likely not find acceptable. A positive outcome is that the level of genetic variation in the source population maintains a healthy percentage even with two pairs translocated every half-generation. Again, the version of the experiment incorporating replacement is not realistic from a natural resource manager's point of view; however, it does isolate the decisive impact genetic drift has on small, isolated populations.

Without Replacement. Table 4.4 displays the results of the experiment when replacement is ignored. The reader will no doubt note that the final values for the source population for each scenario are the same as those from Table 4.3. This is simply because it makes no difference to the source population what happens to the individuals

Table 4.4 Results Without Replacement

Variables			Managed Population		Source Population	
Initial Pair #	RCW per Trans	Trans Interval	Final Pair #	% V_g/V_{g0}	Final Pair #	% V_g/V_{g0}
10	0	0	0	0.0	480	96.6
	1	2	7	56.3	470	96.5
	1	1	17	77.1	459	96.5
	1	0.5	41	88.5	437	96.4
	2	2	13	69.1	460	96.5
	2	1	34	85.2	438	96.4
	2	0.5	79	92.9	396	96.2
	4	2	31	82.0	439	96.4
	4	1	75	91.7	397	96.2
	4	0.5	165	96.2	312	95.8
25	0	0	6	35.7	480	96.6
	1	2	20	73.6	470	96.5
	1	1	35	84.7	459	96.5
	1	0.5	63	92.2	437	96.4
	2	2	30	81.2	460	96.5
	2	1	57	90.0	438	96.4
	2	0.5	105	95.0	396	96.2
	4	2	48	86.1	439	96.4
	4	1	96	93.1	397	96.2
	4	0.5	188	96.7	312	95.8
50	0	0	26	68.6	480	96.6
	1	2	45	83.3	470	96.5
	1	1	63	89.9	459	96.5
	1	0.5	96	95.4	437	96.4
	2	2	60	88.6	460	96.5
	2	1	91	94.5	438	96.4
	2	0.5	146	97.7	396	96.2
	4	2	84	92.2	439	96.4
	4	1	137	96.3	397	96.2
	4	0.5	235	98.6	312	95.8

taken from that population. Only the amount of individuals removed and the rate at which that removal occurs has influence on the final population and genetic value for the source population. This is also evidenced from the fact that the final source population values are the same for the ten scenarios for each of the three managed population sizes.

The lack of replacement incorporates the demographic benefit of translocation. The initial population is relatively easily maintained and in fact, growth of the managed populations can be achieved with as little effort as translocating of a pair of RCWs every other generation. However, ensuring that the percentage of genetic variation remaining is at a healthy level requires more individuals to be translocated and/or more frequent translocations. With an initial managed population of 10 pairs, translocating one pair every half-generation is the minimum rate and magnitude of translocation that maintains genetic health; the percentage of genetic variation remaining is 92.9%. The resulting managed population is a significantly more robust 79 pairs and the source population is maintained at nearly 400 pairs with a healthy genetic variation of 96.2%.

The importance of initial population size is clearly evident. With an initial population of 25, translocating a single female twice per generation becomes a viable management option for maintaining genetic health. Furthermore, with 50 initial RCW pairs, the translocation of a pair of RCWs every generation is sufficient to maintain the remaining genetic variation at nearly 95%. Those natural resource managers working to maintain genetic health in populations that were initially at the low end of the scale certainly face a greater challenge. Translocations must be frequent, occurring at least every generation and consist of a pair or more in order to negate the effects of genetic drift.

Behavior Over Time. While the results displayed in Tables 4.3 and 4.4 convey a significant amount of information, of additional interest are the trends of the variables of concern over time. A particular advantage of utilizing the STELLA modeling software is that it is easy to create graphs displaying model behavior over time. The graphs from a few of the representative management scenarios from Tables 4.3 and 4.4 are presented and discussed below.

Figure 4.1 shows the behavior over time of a population initially having 25 pairs with no translocation. The corresponding genetic variation is shown in Figure 4.2. In Figure 4.1, the initial drop in the first few generations is due to the model coming into equilibrium. After the equilibrium drop, the population stabilizes and then begins to decline near the 10th generation. The decline is due to the ever decreasing genetic variation shown in Figure 4.2. While the genetic variation appears initially to be declining linearly, the decline accelerates beyond the 40th generation. The management

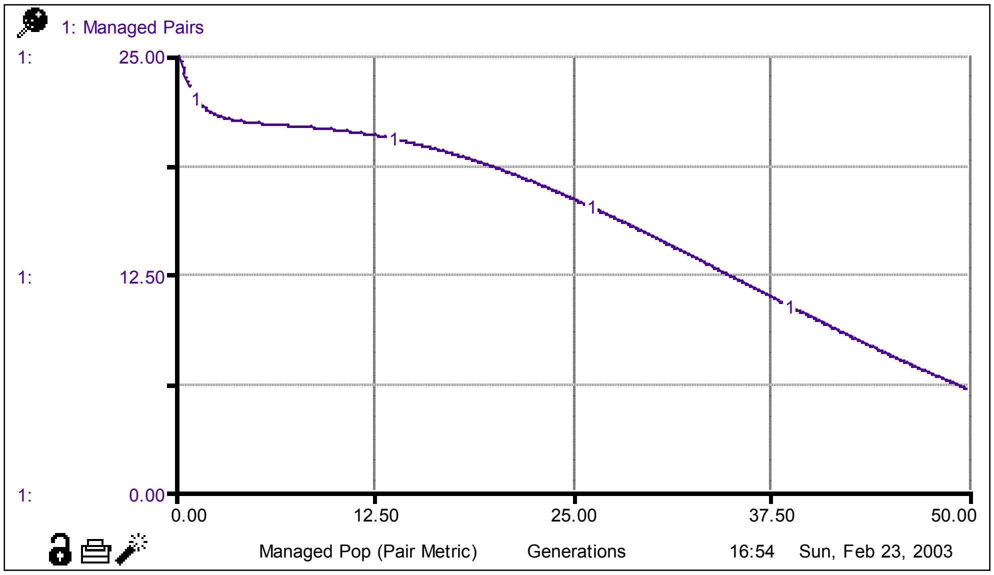


Figure 4.1 Population, 25 Pairs, No Translocation

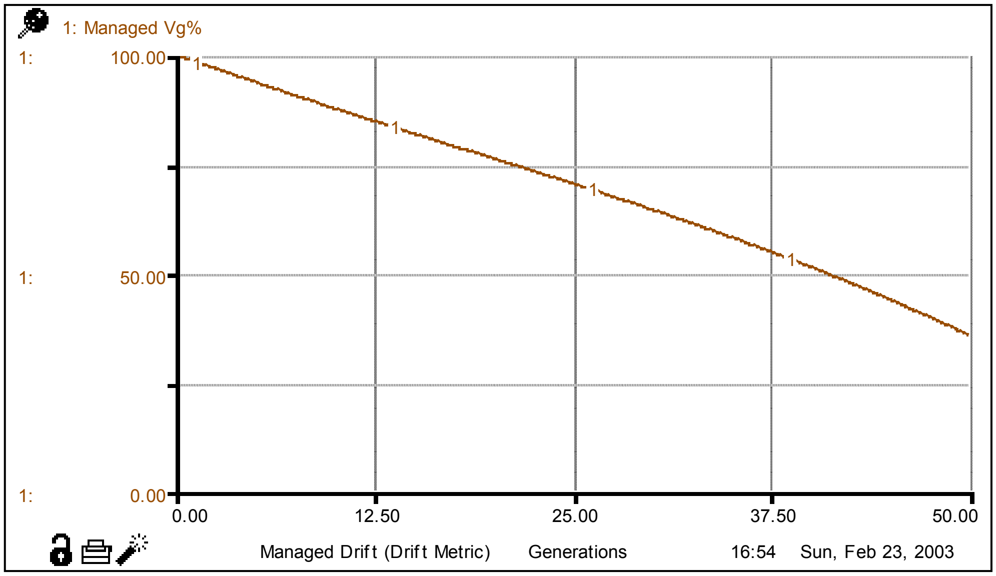


Figure 4.2 Genetic Variation, 25 Pairs, No Translocation

implication is that the longer a small population is isolated, the greater the danger that it will be extirpated due to a loss of genetic variation.

Figures 4.3 and 4.4 show the results for the same scenario, no translocation, for the source population. Clearly, the greater initial size makes the population less vulnerable to the effects of genetic drift. Growth is linear after the initial equilibrium

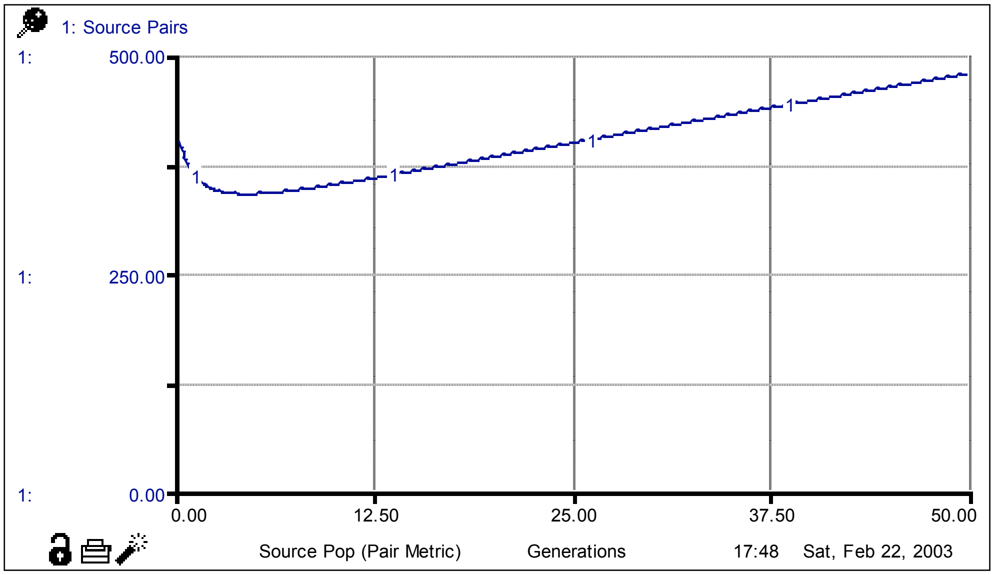


Figure 4.3 Source Population, No Translocation

drop to nearly 500 pairs. The decline in genetic variation is nearly negligible and indicates the population is genetically healthy as an isolated population after 50 generations.

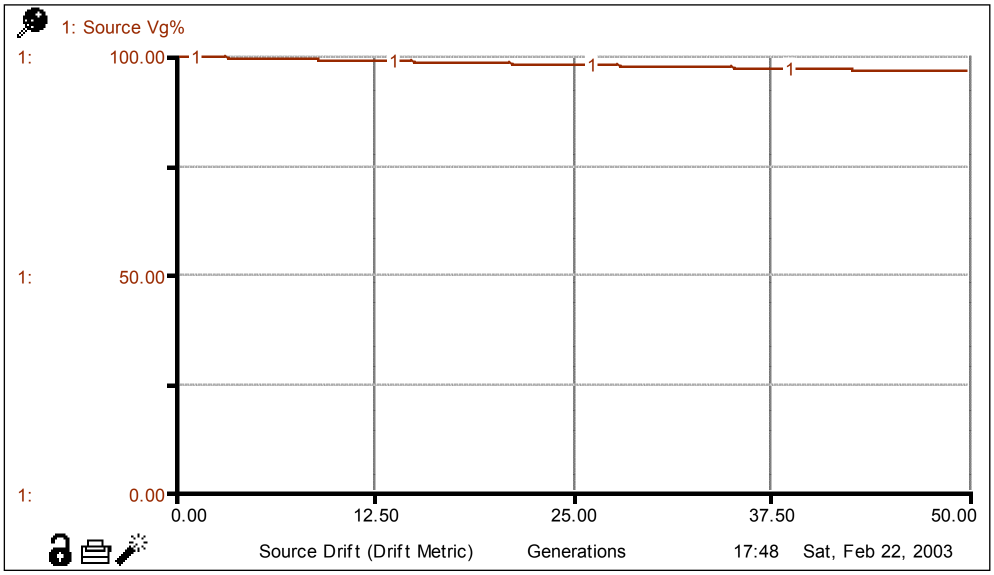


Figure 4.4 Genetic Variation, Source Population, No Translocation

With replacement, the only management scenario demonstrated to keep genetic variability at a healthy level was translocating two pairs every half-generation. Figures

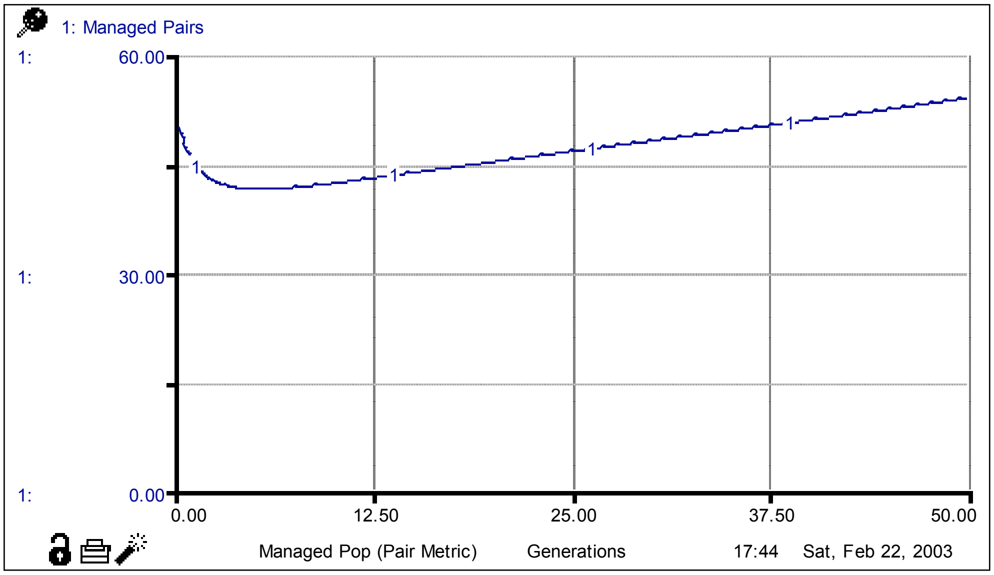


Figure 4.5 Population, 50 pairs, Replacement, 2 Pairs @ 0.5

4.5 and 4.6 show such a scenario for an initial population of 50 pairs. Steady growth in the population and the level of genetic variation are established early and maintained. Through translocation, the behavior over time of both the population and drift metrics in the managed population closely resembles that of the source population in Figures 4.3 and 4.4. The size of the managed population is effectively increased.

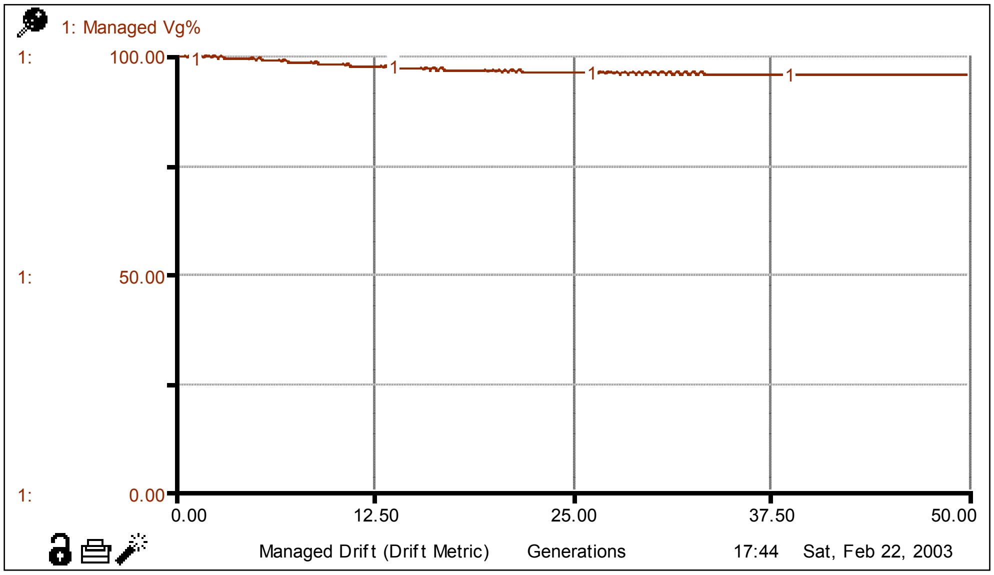


Figure 4.6 Genetic Variation, 50 pairs, Replacement, 2 Pairs @ 0.5

The behavior over time in the source population for the same management scenario is also of interest. Figure 4.7 shows that while the source population does decrease rather than grow, it does so early and maintains a constant level. This indicates that while such a management scenario is likely not the first choice of the natural resource manager in charge of the source population, removing two pairs every half-generation is sustainable over 50 generations.

Figure 4.8 confirms the sustainability of removing two pairs of RCWs twice per generation. The shape and level of the genetic variation is nearly identical to that of the "no translocation" graph of Figure 4.4. Note that both pairs removed would not

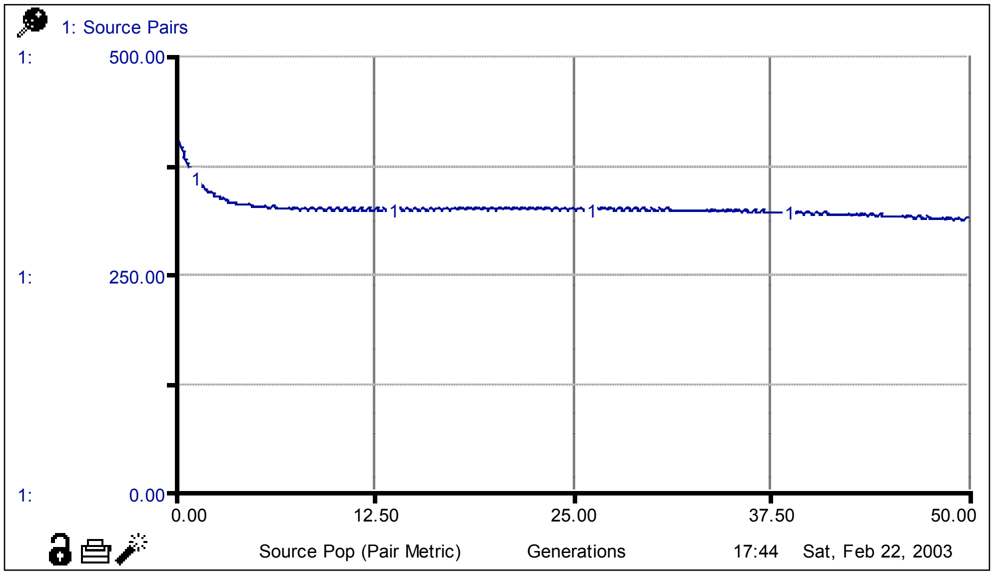


Figure 4.7 Source Population, Translocation, 2 Pairs @ 0.5

necessarily have to go to the same smaller, managed population. This scenario indicates that a single large population could be used to help maintain the genetic health of at least two smaller populations. Note that Figures 4.7 and 4.8 document source population behavior for both replacement and no replacement versions of the experiment for the management scenarios in which two pairs are translocated every half-generation.

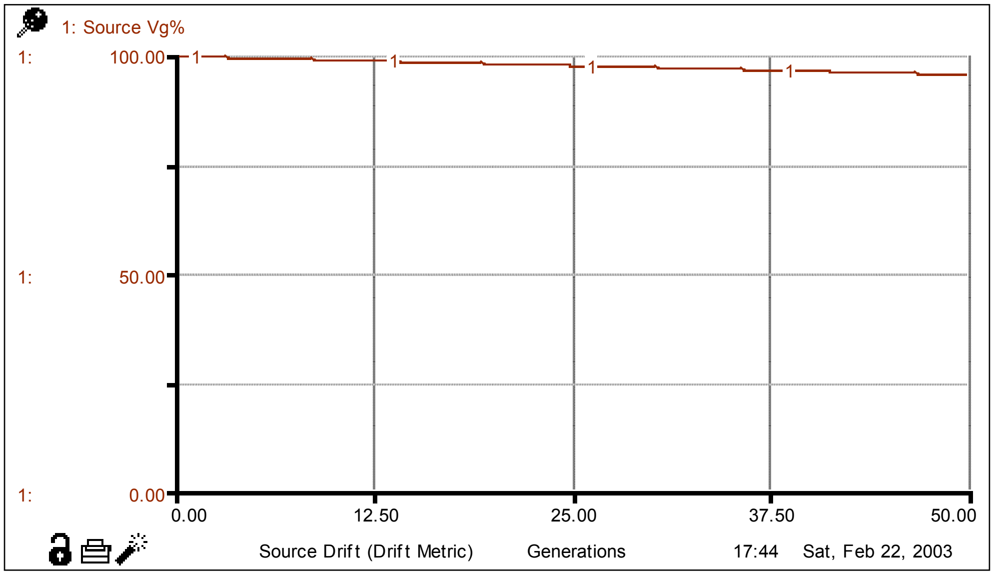


Figure 4.8 Genetic Variation, Source, Translocation, 2 Pairs @ 0.5

As Tables 4.3 and 4.4 have already shown, translocation without replacement is the more effective version of the experiment. Figures 4.9 and 4.10 detail the scenario of bringing one pair of RCWs every half-generation into a population beginning with 10 pairs. Growth in the population is established immediately and continues linearly to 79 pairs at the 50th generation. Since such a small population is particularly vulnerable to genetic drift, the more significant graph is that of Figure 4.10 that shows that after a

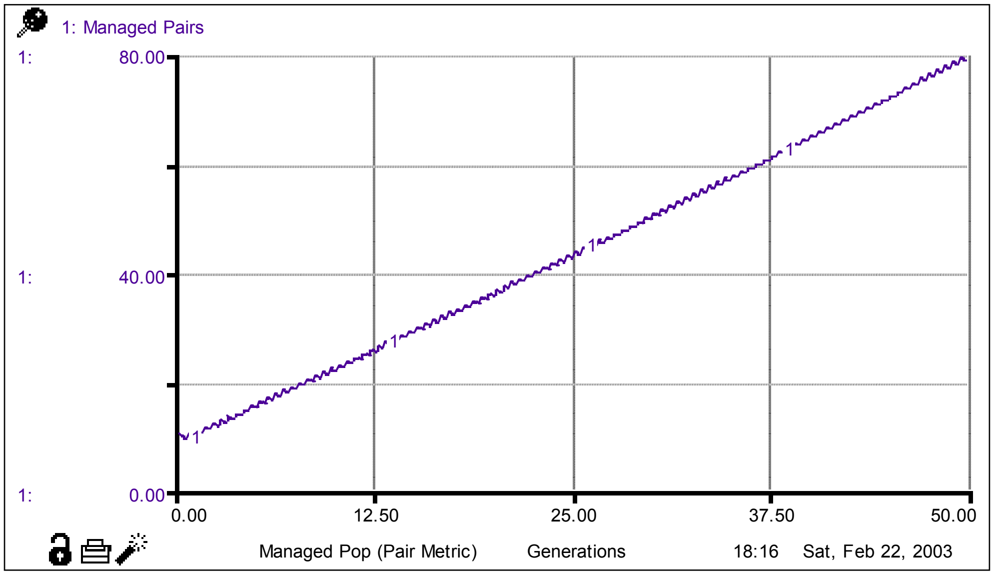


Figure 4.9 Population, 10 pairs, No Replacement, 2 Pairs @ 0.5

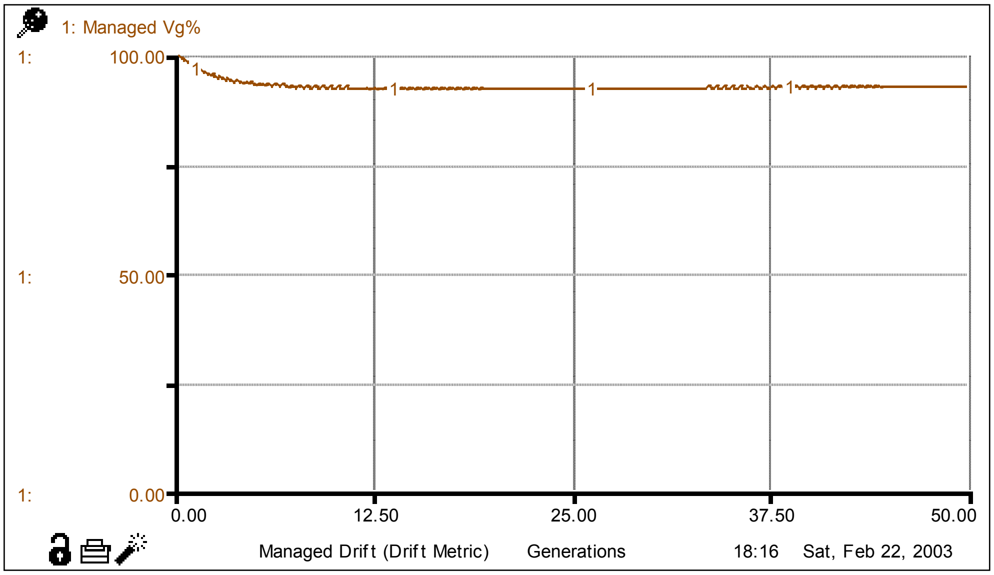


Figure 4.10 Genetic Variation, 10 Pairs, No Replacement, 2 Pairs @ 0.5

minor initial decline, the genetic variation is maintained at a nearly constant value of almost 93% with such a management strategy.

The final two figures provided are done so to illustrate the dynamic relationship between the demographic benefit of translocation and the countering effect of genetic drift. Figure 4.11 shows a population beginning with 25 pairs. The "sawtooth" effect is due to the translocation of one female every two generations without replacement. Using this technique, the population sustained over 50 generations. However, note the curved trend of the population with a decreasing slope beginning near 25 generations. Genetic drift has countered the demographic benefit of translocating individuals and has put the population in a decline. A manager may not react to such a slight decline and continue with the status quo of bringing one female every other generation. Such an action, or more accurately, lack of action, will result in further declining the population as the genetic variation continues to decrease, as shown in Figure 4.12. The important thing for natural resource managers to keep in mind is that while a slight decline may simply be a

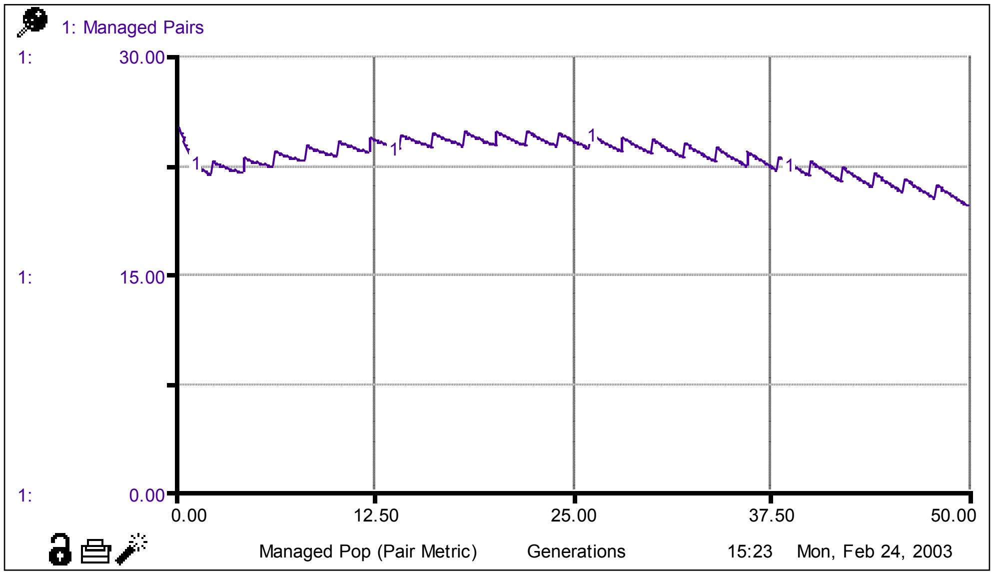


Figure 4.11 Population, 25 pairs, No Replacement, 1 Female @ 2

cyclical variation, it is also quite possible that the decline is signaling the start of a trend towards extirpation due to genetic drift.

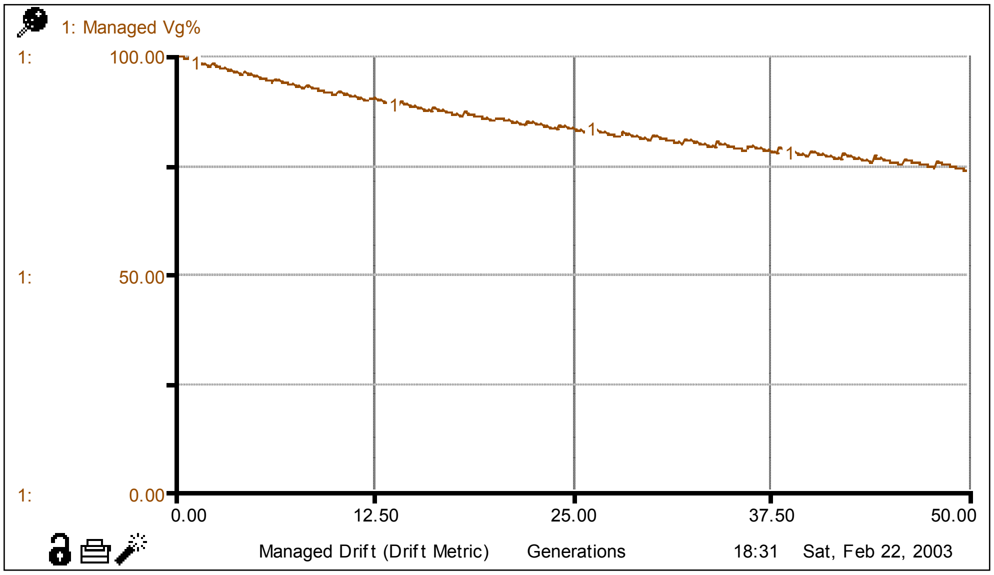


Figure 4.12 Genetic Variation, 25 pairs, No Replacement, 1 Female @ 2

5. Findings and Conclusions

Addressing Research Objective

Table 5.1 summarizes the results of those management scenarios that kept the managed population genetically healthy, as determined by maintaining the genetic variation at 90% or above. The “do nothing” scenario for each managed population size was included for comparison purposes. Note that the final value of the genetic variation of the source population was also genetically healthy for all management scenarios.

Table 5.1 Effective Management Scenarios

	Variables			Managed Population		Source Population	
	Initial Pair #	RCW per Trans	Trans Interval	Final Pair #	% V_g/V_{g0}	Final Pair #	% V_g/V_{g0}
With Replacement	10	0	0	0	0.0	480	96.6
		4	0.5	10	94.1	312	95.8
	25	0	0	6	35.7	480	96.6
		2	0.5	23	91.6	396	96.2
		4	0.5	25	94.4	312	95.8
	50	0	0	26	68.6	480	96.6
		1	0.5	47	90.8	437	96.4
		2	0.5	52	93.8	396	96.2
		4	1	48	92.3	397	96.2
		4	0.5	54	95.8	312	95.8
Without Replacement	10	0	0	0	0.0	480	96.6
		2	0.5	79	92.9	396	96.2
		4	1	75	91.7	397	96.2
		4	0.5	165	96.2	312	95.8
	25	0	0	6	35.7	480	96.6
		1	0.5	63	92.2	437	96.4
		2	1	57	90.0	438	96.4
		2	0.5	105	95.0	396	96.2
		4	1	96	93.1	397	96.2
		4	0.5	188	96.7	312	95.8
	50	0	0	26	68.6	480	96.6
		1	0.5	96	95.4	437	96.4
		2	1	91	94.5	438	96.4
		2	0.5	146	97.7	396	96.2
		4	2	84	92.2	439	96.4
		4	1	137	96.3	397	96.2
		4	0.5	235	98.6	312	95.8

It is evident that the smaller the managed population, the greater the impact of genetic drift and the greater the magnitude and frequency of translocation necessary to mitigate the effects of genetic drift. Populations that are constrained by the amount of habitat available are at an even greater disadvantage, having to utilize translocation with replacement to maintain genetic variation. The good news is that the model indicates that it is possible to keep a population as small as 10 pairs genetically healthy with the translocation of two RCW pairs twice per generation.

For those locations which can provide additional habitat, translocations without replacement make the natural resource manager's job of maintaining genetic health significantly easier. Introduction of a single pair twice per generation is sufficient to mitigate the effects of genetic drift for a population initially consisting of 10 pairs. For the modeled initial populations of 25 and 50 pairs, a single female translocated every half-generation is a viable management option.

The results of this effort confirm that larger red-cockaded woodpecker populations are more genetically robust. The scale is relative however; while a population of 50 pairs is larger and more robust than a population of 10 pairs, it is still a small population that requires active management in the form of translocations to maintain its genetic health. For the larger of the small populations, the increased genetic robustness does allow for a greater number of translocation options, but translocation definitely remains a necessary management technique.

For the natural resource managers tasked with the management of the endangered red-cockaded woodpecker on both DoD and non-DoD lands, this effort has provided insight into the management and mitigation of genetic drift. Those management scenarios that were shown to be effective in Table 5.1 are suitable to serve as the basis for translocation guidelines intended to maintain the genetic health of small RCW populations. Further, natural resource managers possessing much larger populations of RCW on their lands can be assured that their populations can serve as sources for translocation without significant harm to the genetic health of the source population.

The following is a concise summary of the relevant conclusions of this effort:

- The smaller the population, the more vulnerable it is to the effects of genetic drift, and the more intensive the translocation management strategies must be to counter those detrimental effects.

- A large population can support a significant number of translocations without harm to its genetic health.

- Translocation in habitat constrained areas (translocation with replacement) can maintain the level of genetic variation in populations initially as small as 10 pairs.

- A translocation program set up to simply maintain the number of individuals in a local population may not be adequate enough to maintain the genetic health of that population and still may ultimately result in extirpation of that population due to genetic drift.

Model Limitations

As with any modeling effort, there were a number of assumptions necessary to simplify the real system the model represents. By definition, a model is a simplification and in making simplifications, inaccuracy is introduced. The challenge for the modeler is to determine how much inaccuracy is appropriate.

In researching genetic drift in the RCW population, very little literature was discovered as to the specific effects of genetic drift and the relationship between it and demographic parameters. It was decided to model the effect of genetic drift as applying only to the mortality rates of the modeled populations. This was done through a graphical interface in STELLA and these graphs are shown in Appendix C. Given the lack of literature, the range of mortality rates utilized could be greater or less. Additionally, genetic drift could have other effects not incorporated into the model such as decreased foraging or hatching rates.

The use of Lande's quantitative equations to express genetic drift and the assumptions associated with those equations are important to understand. First and foremost, the equations provide mechanistic approximations for what is in reality, a stochastic process. Further, a number of assumptions apply to the equations. Lande assumed the effective population size remained constant (1995:321). He also assumed that the quantitative character V_g would remain constant in what he termed the "wild" population, whereas here was termed the source population. The features of the STELLA modeling software allowed the modeler to treat these parameters not as constants, but as variables. While the equations should apply regardless, it is may be that in violating some of Lande's assumptions, that the resulting genetic drift approximations are altered. However, the output generated in this effort is indeed consistent with other studies that used other methods of approximating genetic drift, such as Lacy (1987), Berger (Stiling, 2002:27), and Mills and Allendorf (USFWS, 2000:28).

Average values gathered from the literature were used in defining parameters used in the model. Certainly, many of these values vary based on many factors to include geographic region and habitat characteristics. One such parameter is the length of time between when an RCW is hatched and when it becomes a breeder or helper. In the model, this was assumed to be one year, thereby indicating generations are equal to one year. In reality, generation length in the RCW varies and one year may be an optimistic assumption. Other factors that vary in reality are natality and mortality rates as well as the number of pairs that actually nest. In the model, 10% of pairs were assumed not to nest, but the range varies from 3 to 21 percent according to field observations (USFWS, 2000:12). A potential solution for incorporating such variation is through the use of probability distributions in STELLA. Such distributions are not typically used in system dynamics, but the software does allow for their creation and use.

Another limitation of this model is that environmental and habitat parameters were not incorporated.   It was simply assumed that if a population grew, there would be habitat of sufficient quality to support it. This is of course not the case in the real world and in fact, the quantity and quality of habitat is a major focus natural resource managers work hard to address. For instance, the type, quantity, and distribution of the preferred species of pine, the Longleaf, was not incorporated. Other environmental factors not included were competitor interaction, predator effects, and food availability.

Because natural environmental and habitat factors were beyond the scope of this effort and not incorporated into the model, the management techniques associated with improving such factors could not be incorporated either. It was assumed that other habitat management techniques were indeed being performed, but they were not explicitly modeled.   Such techniques include prescribed burning to remove understory hardwoods, translocations within a population to improve spatial arrangement, conversion from a less desirable ecosystem type to Longleaf pine forest, artificial cavity construction, and predator and competitor prevention.

.Another simplification was that the modeled populations were not sufficiently close enough to other populations of RCW for natural immigration to occur. While this is true throughout much of the southeast, there are certainly a number of populations where natural immigration does occur. For these populations, the work of this effort can still lend some insight if the natural rate of immigration can be determined.

.Translocation failures were not included in the model, but commonly occur in actual populations. The effect of including such a component into the model would certainly require more translocations to be performed for the same results. Natural resource managers using the translocation guidelines established through this effort must keep in mind that if a translocation fails, a successful one must be performed in its place.

There was no consideration given to spatial arrangement and movement of the RCWs within the modeled populations. Fragmentation within a population was neglected and this can have a significant detrimental effect. Small populations are more persistent when movement of helpers can occur between groups within a population to replace breeders who die off. This modeling effort assumed that there was no fragmentation of the habitat and that individual RCWs were free to move, occupying vacancies when and where they occurred. Given that much of the actual habitat of the RCW is indeed fragmented, thereby preventing such free movement, the actual situation is more tenuous for small populations than the model predicts.

Suggestions for Further Study

The continued development of the model through the incorporation of some or all of the complexities detailed above is worthy of further effort. Certainly establishing a habitat component of the model would be the next step. With such a component, biological factors such as the foraging ability of the RCW could be linked to the effect of genetic drift (if a literature review supported such a link). Further, establishing habitat capacities would allow for more realistic scenarios in which translocation without replacement could not occur without bound.

A habitat model component would also allow for the investigation of additional management techniques in conjunction with translocation. It might be found that a number of techniques would work together synergistically to boost small populations and maintain genetic health. Additionally, the long-term effects of habitat conversion and expansion could be explored.

A system dynamics model incorporating many of these features was constructed by another graduate student of the Air Force Institute of Technology, then 1Lt Chad Schroeder. The model he developed is specific to the Poinsett Weapons Range (PWR) of Shaw AFB in South Carolina and is based on actual habitat data to spatially model the small RCW population there (Schroeder, 2001:8-9). It is possible that components of his model could be combined with the model developed in this effort to further aid natural resource managers of the PWR in maintaining their RCW population over the long-term. Perhaps a greater challenge would be to create a model with more general habitat parameters that could be altered to apply to any number of specific RCW populations. While the possibilities for future research are certainly vast, any and every effort on the part of researchers and managers to ensure the continued existence and ultimate recovery of the red-cockaded woodpecker is certainly an important one.

Appendix A: Flow Diagrams

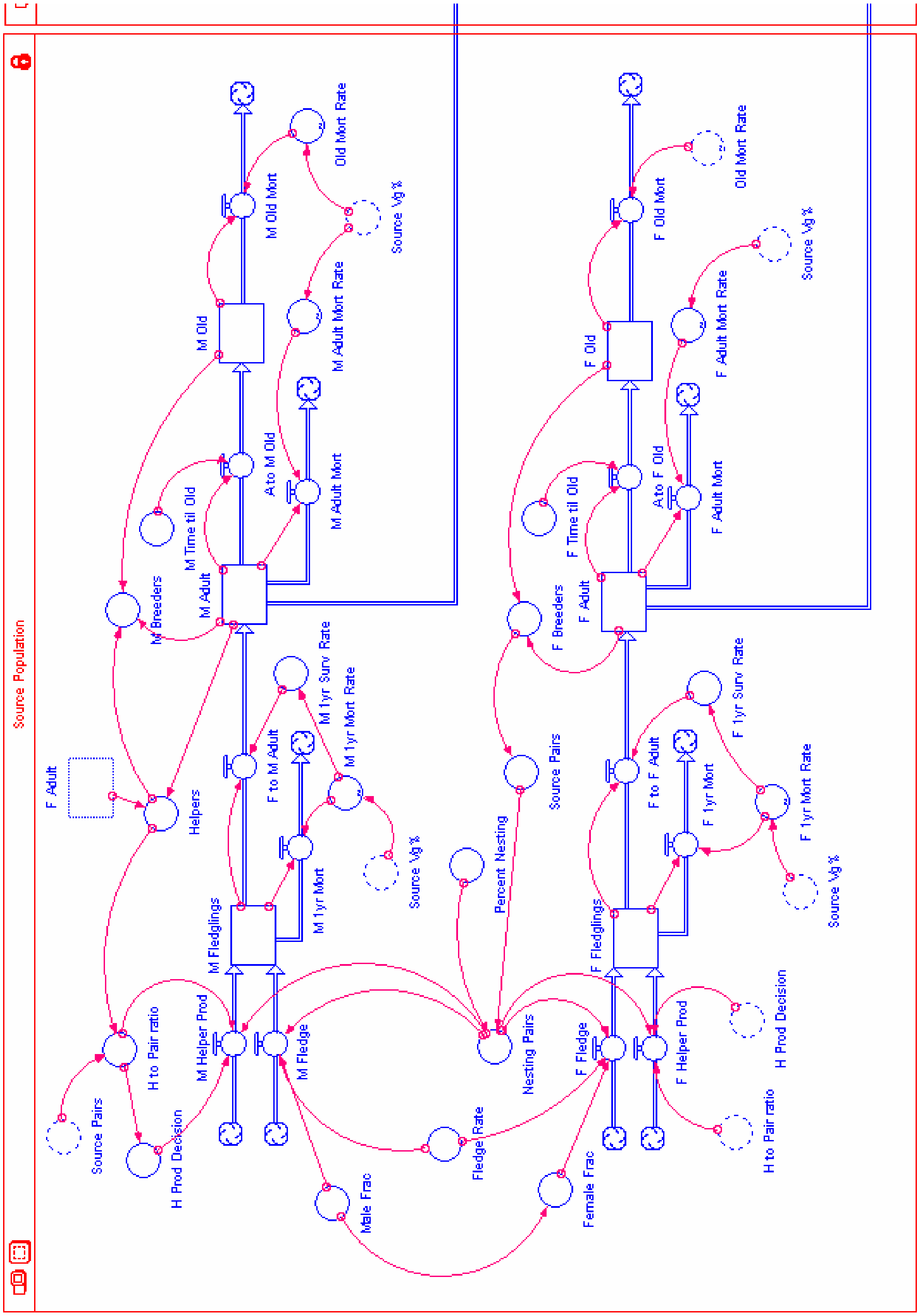


Figure A.1 Source Population Sector

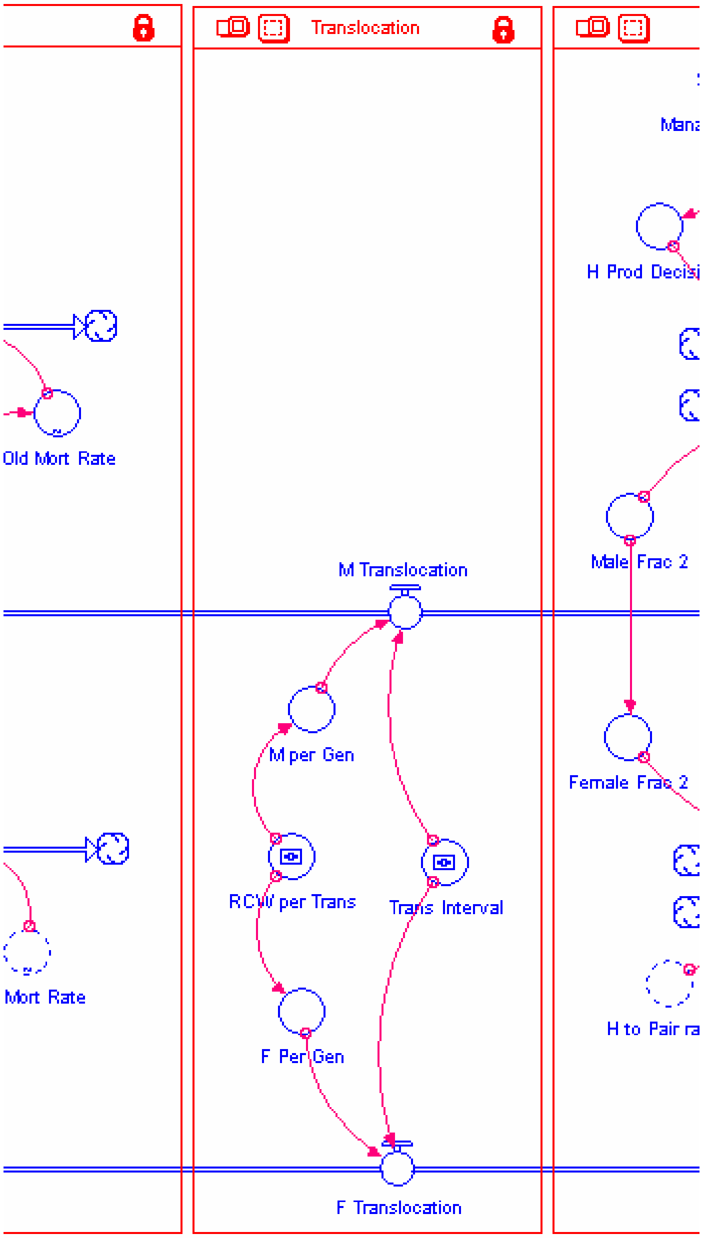


Figure A.2 Translocation Sector

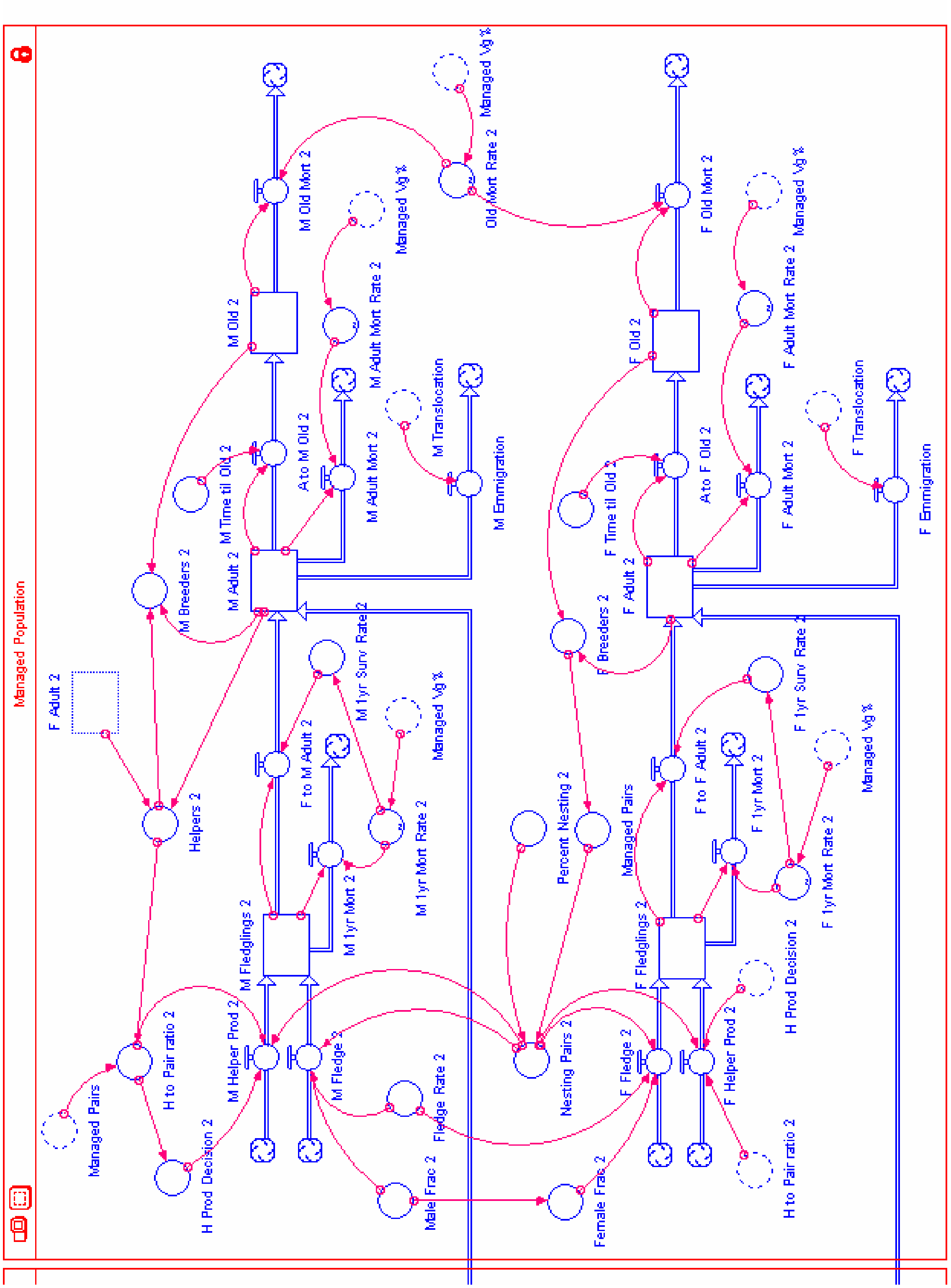


Figure A.3 Managed Population Sector, With Replacement

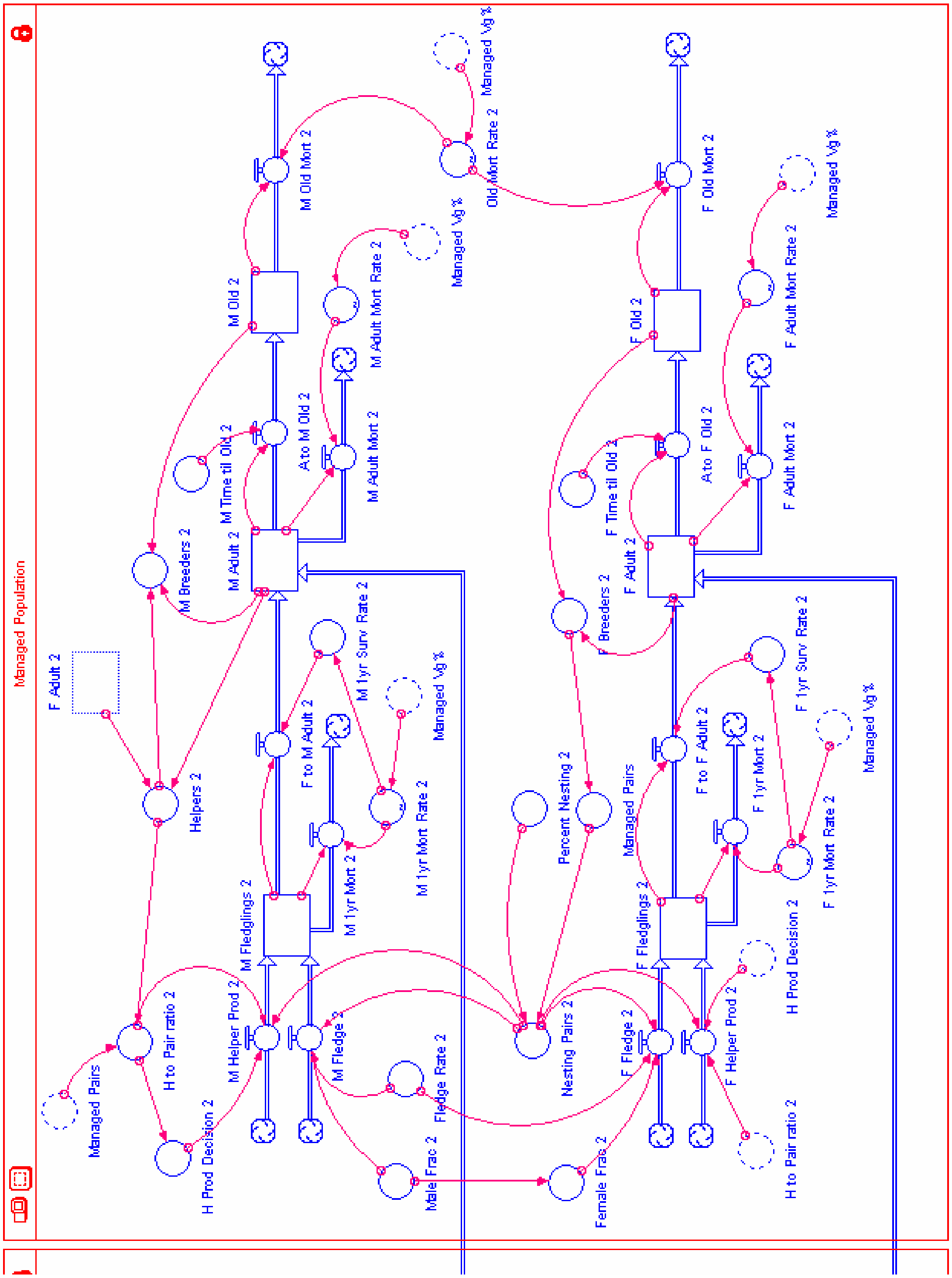


Figure A.4 Managed Population Sector, Without Replacement

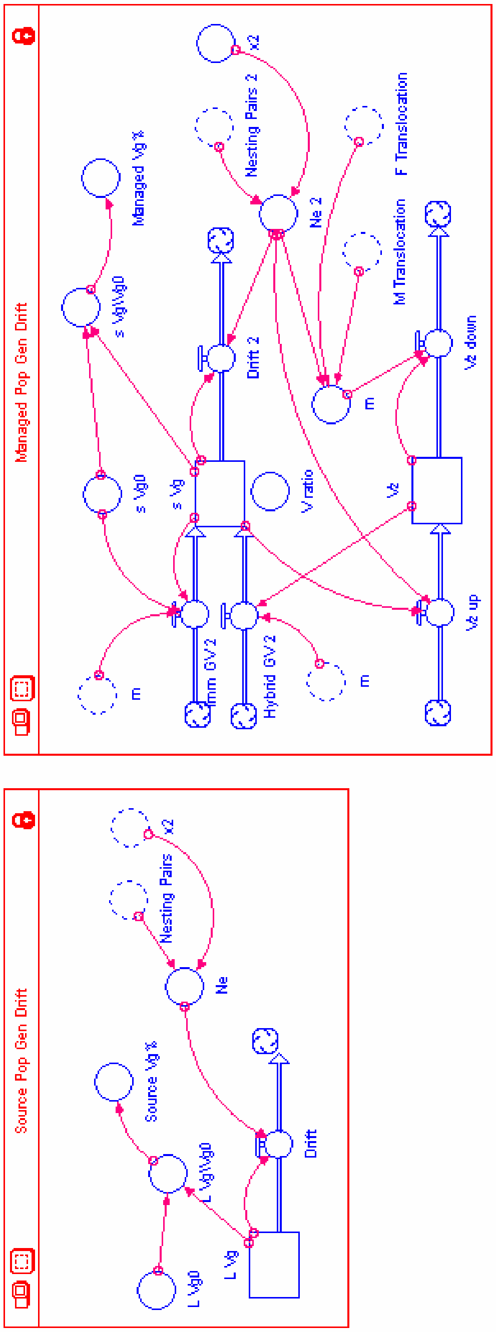


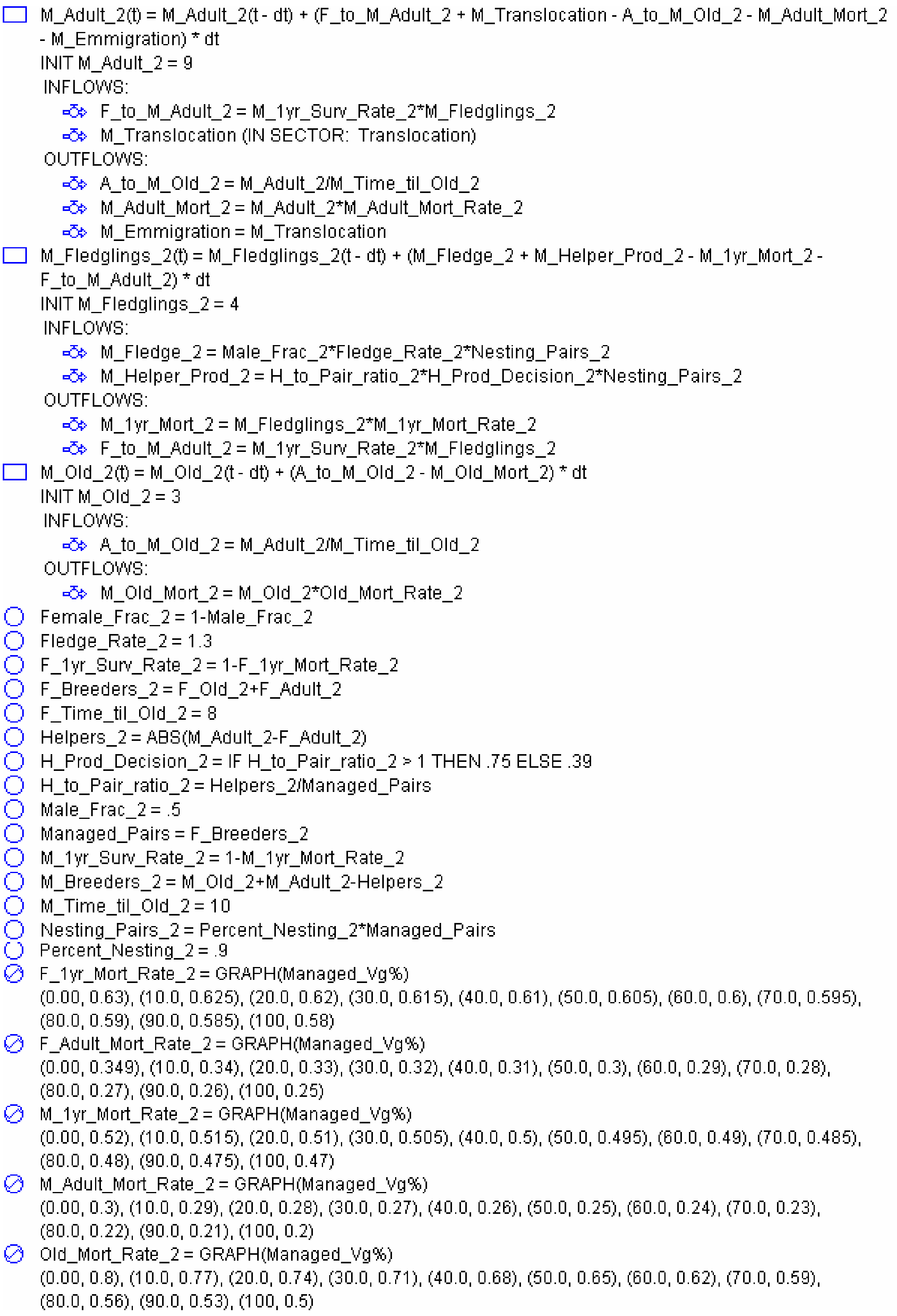
Figure A.5 Genetic Drift Sectors

Appendix B: Model Equations

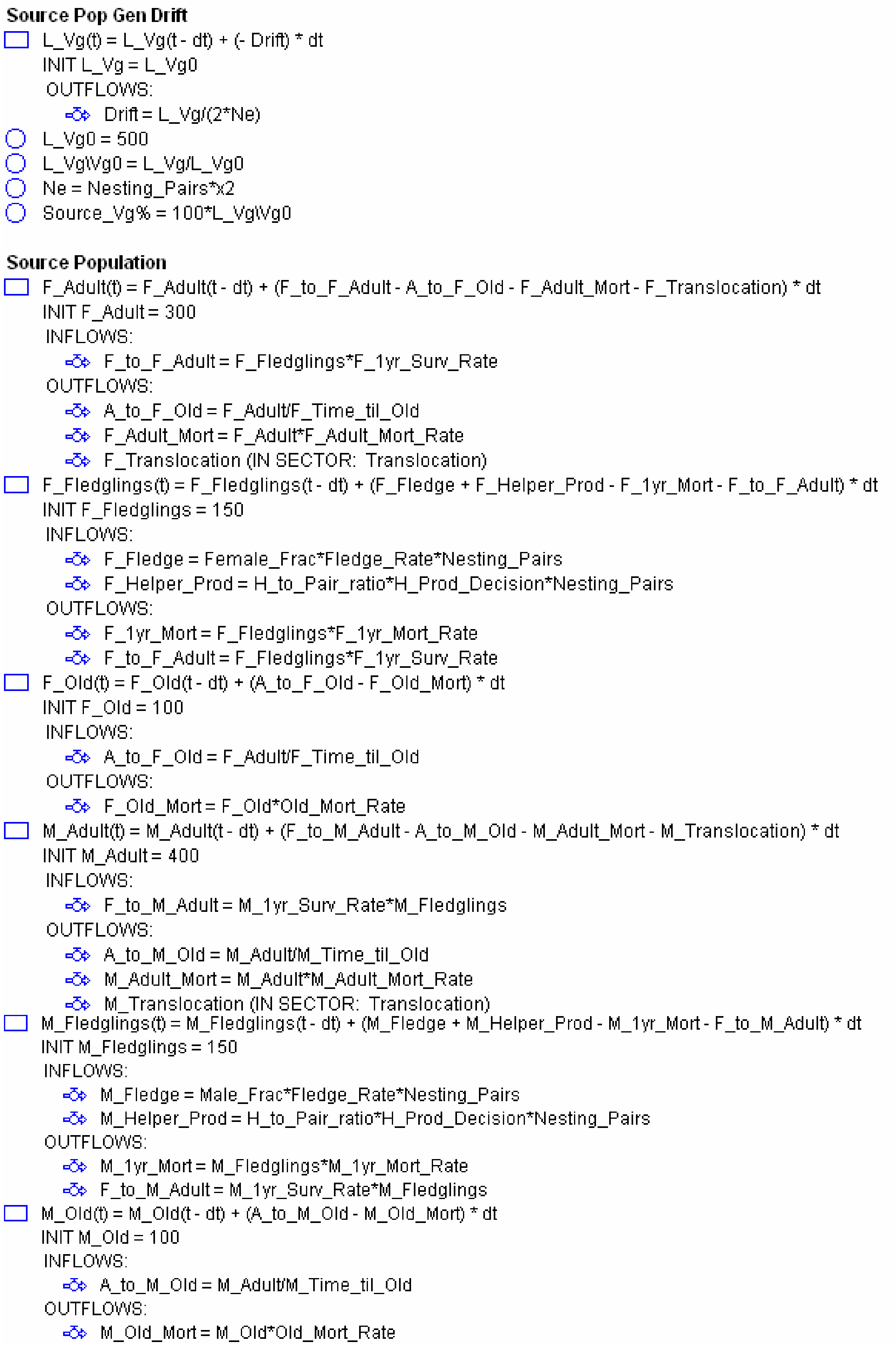
With Replacement

```
Managed Pop Gen Drift
☐ s_Vg(t) = s_Vg(t - dt) + (Imm_GV_2 + Hybrid_GV_2 - Drift_2) * dt
    INIT s_Vg = s_Vg0
    INFLOWS:
      ⇨ Imm_GV_2 = m*(s_Vg0-s_Vg)
      ⇨ Hybrid_GV_2 = (m*(1-m))*Vz/2
    OUTFLOWS:
      ⇨ Drift_2 = s_Vg/(2*Ne_2)
☐ Vz(t) = Vz(t - dt) + (Vz_up - Vz_down) * dt
    INIT Vz = s_Vg*V_ratio
    INFLOWS:
      ⇨ Vz_up = s_Vg/Ne_2
    OUTFLOWS:
      ⇨ Vz_down = 2*m*Vz
○ m = (F_Translocation+M_Translocation)/Ne_2
○ Managed_Vg% = 100*s_Vg\Vg0
○ Ne_2 = Nesting_Pairs_2*x2
○ s_Vg0 = 100
○ s_Vg\Vg0 = s_Vg/s_Vg0
○ V_ratio = .25
○ x2 = 2

Managed Population
☐ F_Adult_2(t) = F_Adult_2(t - dt) + (F_to_F_Adult_2 + F_Translocation - A_to_F_Old_2 - F_Adult_Mort_2 -
    F_Emmigration) * dt
    INIT F_Adult_2 = 7
    INFLOWS:
      ⇨ F_to_F_Adult_2 = F_Fledglings_2*F_1yr_Surv_Rate_2
      ⇨ F_Translocation (IN SECTOR:  Translocation)
    OUTFLOWS:
      ⇨ A_to_F_Old_2 = F_Adult_2/F_Time_til_Old_2
      ⇨ F_Adult_Mort_2 = F_Adult_2*F_Adult_Mort_Rate_2
      ⇨ F_Emmigration = F_Translocation
☐ F_Fledglings_2(t) = F_Fledglings_2(t - dt) + (F_Fledge_2 + F_Helper_Prod_2 - F_1yr_Mort_2 -
    F_to_F_Adult_2) * dt
    INIT F_Fledglings_2 = 4
    INFLOWS:
      ⇨ F_Fledge_2 = Female_Frac_2*Fledge_Rate_2*Nesting_Pairs_2
      ⇨ F_Helper_Prod_2 = H_to_Pair_ratio_2*H_Prod_Decision_2*Nesting_Pairs_2
    OUTFLOWS:
      ⇨ F_1yr_Mort_2 = F_Fledglings_2*F_1yr_Mort_Rate_2
      ⇨ F_to_F_Adult_2 = F_Fledglings_2*F_1yr_Surv_Rate_2
☐ F_Old_2(t) = F_Old_2(t - dt) + (A_to_F_Old_2 - F_Old_Mort_2) * dt
    INIT F_Old_2 = 3
    INFLOWS:
      ⇨ A_to_F_Old_2 = F_Adult_2/F_Time_til_Old_2
    OUTFLOWS:
      ⇨ F_Old_Mort_2 = F_Old_2*Old_Mort_Rate_2
```

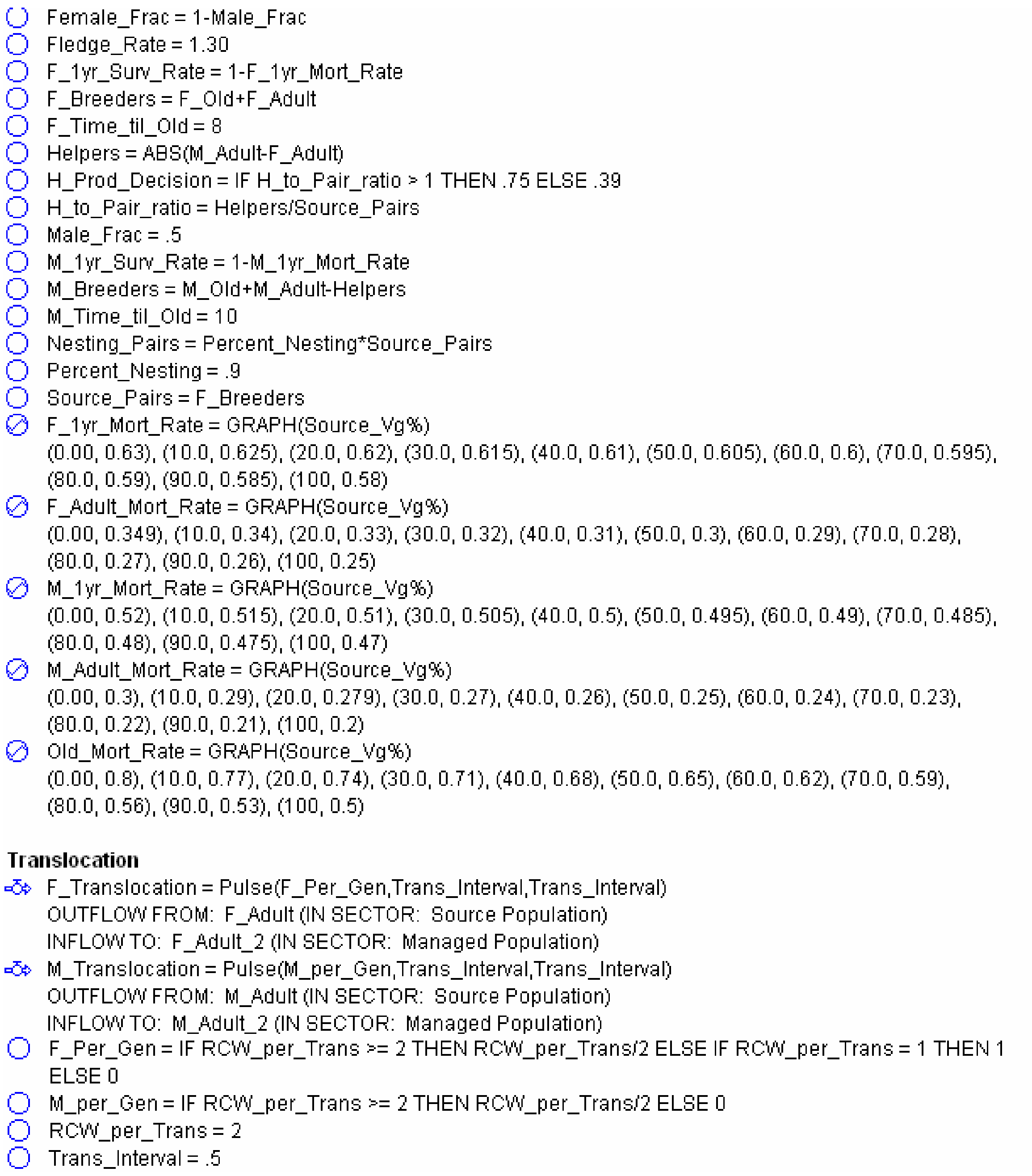


```
M_Adult_2(t) = M_Adult_2(t - dt) + (F_to_M_Adult_2 + M_Translocation - A_to_M_Old_2 - M_Adult_Mort_2
- M_Emmigration) * dt
INIT M_Adult_2 = 9
 INFLOWS:
   F_to_M_Adult_2 = M_1yr_Surv_Rate_2*M_Fledglings_2
   M_Translocation (IN SECTOR:  Translocation)
 OUTFLOWS:
   A_to_M_Old_2 = M_Adult_2/M_Time_til_Old_2
   M_Adult_Mort_2 = M_Adult_2*M_Adult_Mort_Rate_2
   M_Emmigration = M_Translocation
M_Fledglings_2(t) = M_Fledglings_2(t - dt) + (M_Fledge_2 + M_Helper_Prod_2 - M_1yr_Mort_2 -
F_to_M_Adult_2) * dt
INIT M_Fledglings_2 = 4
 INFLOWS:
   M_Fledge_2 = Male_Frac_2*Fledge_Rate_2*Nesting_Pairs_2
   M_Helper_Prod_2 = H_to_Pair_ratio_2*H_Prod_Decision_2*Nesting_Pairs_2
 OUTFLOWS:
   M_1yr_Mort_2 = M_Fledglings_2*M_1yr_Mort_Rate_2
   F_to_M_Adult_2 = M_1yr_Surv_Rate_2*M_Fledglings_2
M_Old_2(t) = M_Old_2(t - dt) + (A_to_M_Old_2 - M_Old_Mort_2) * dt
INIT M_Old_2 = 3
 INFLOWS:
   A_to_M_Old_2 = M_Adult_2/M_Time_til_Old_2
 OUTFLOWS:
   M_Old_Mort_2 = M_Old_2*Old_Mort_Rate_2
Female_Frac_2 = 1-Male_Frac_2
Fledge_Rate_2 = 1.3
F_1yr_Surv_Rate_2 = 1-F_1yr_Mort_Rate_2
F_Breeders_2 = F_Old_2+F_Adult_2
F_Time_til_Old_2 = 8
Helpers_2 = ABS(M_Adult_2-F_Adult_2)
H_Prod_Decision_2 = IF H_to_Pair_ratio_2 > 1 THEN .75 ELSE .39
H_to_Pair_ratio_2 = Helpers_2/Managed_Pairs
Male_Frac_2 = .5
Managed_Pairs = F_Breeders_2
M_1yr_Surv_Rate_2 = 1-M_1yr_Mort_Rate_2
M_Breeders_2 = M_Old_2+M_Adult_2-Helpers_2
M_Time_til_Old_2 = 10
Nesting_Pairs_2 = Percent_Nesting_2*Managed_Pairs
Percent_Nesting_2 = .9
F_1yr_Mort_Rate_2 = GRAPH(Managed_Vg%)
(0.00, 0.63), (10.0, 0.625), (20.0, 0.62), (30.0, 0.615), (40.0, 0.61), (50.0, 0.605), (60.0, 0.6), (70.0, 0.595),
(80.0, 0.59), (90.0, 0.585), (100, 0.58)
F_Adult_Mort_Rate_2 = GRAPH(Managed_Vg%)
(0.00, 0.349), (10.0, 0.34), (20.0, 0.33), (30.0, 0.32), (40.0, 0.31), (50.0, 0.3), (60.0, 0.29), (70.0, 0.28),
(80.0, 0.27), (90.0, 0.26), (100, 0.25)
M_1yr_Mort_Rate_2 = GRAPH(Managed_Vg%)
(0.00, 0.52), (10.0, 0.515), (20.0, 0.51), (30.0, 0.505), (40.0, 0.5), (50.0, 0.495), (60.0, 0.49), (70.0, 0.485),
(80.0, 0.48), (90.0, 0.475), (100, 0.47)
M_Adult_Mort_Rate_2 = GRAPH(Managed_Vg%)
(0.00, 0.3), (10.0, 0.29), (20.0, 0.28), (30.0, 0.27), (40.0, 0.26), (50.0, 0.25), (60.0, 0.24), (70.0, 0.23),
(80.0, 0.22), (90.0, 0.21), (100, 0.2)
Old_Mort_Rate_2 = GRAPH(Managed_Vg%)
(0.00, 0.8), (10.0, 0.77), (20.0, 0.74), (30.0, 0.71), (40.0, 0.68), (50.0, 0.65), (60.0, 0.62), (70.0, 0.59),
(80.0, 0.56), (90.0, 0.53), (100, 0.5)
```



```
Source Pop Gen Drift
☐ L_Vg(t) = L_Vg(t - dt) + (- Drift) * dt
    INIT L_Vg = L_Vg0
    OUTFLOWS:
      ⇨ Drift = L_Vg/(2*Ne)
○ L_Vg0 = 500
○ L_Vg\Vg0 = L_Vg/L_Vg0
○ Ne = Nesting_Pairs*x2
○ Source_Vg% = 100*L_Vg\Vg0

Source Population
☐ F_Adult(t) = F_Adult(t - dt) + (F_to_F_Adult - A_to_F_Old - F_Adult_Mort - F_Translocation) * dt
    INIT F_Adult = 300
    INFLOWS:
      ⇨ F_to_F_Adult = F_Fledglings*F_1yr_Surv_Rate
    OUTFLOWS:
      ⇨ A_to_F_Old = F_Adult/F_Time_til_Old
      ⇨ F_Adult_Mort = F_Adult*F_Adult_Mort_Rate
      ⇨ F_Translocation (IN SECTOR:  Translocation)
☐ F_Fledglings(t) = F_Fledglings(t - dt) + (F_Fledge + F_Helper_Prod - F_1yr_Mort - F_to_F_Adult) * dt
    INIT F_Fledglings = 150
    INFLOWS:
      ⇨ F_Fledge = Female_Frac*Fledge_Rate*Nesting_Pairs
      ⇨ F_Helper_Prod = H_to_Pair_ratio*H_Prod_Decision*Nesting_Pairs
    OUTFLOWS:
      ⇨ F_1yr_Mort = F_Fledglings*F_1yr_Mort_Rate
      ⇨ F_to_F_Adult = F_Fledglings*F_1yr_Surv_Rate
☐ F_Old(t) = F_Old(t - dt) + (A_to_F_Old - F_Old_Mort) * dt
    INIT F_Old = 100
    INFLOWS:
      ⇨ A_to_F_Old = F_Adult/F_Time_til_Old
    OUTFLOWS:
      ⇨ F_Old_Mort = F_Old*Old_Mort_Rate
☐ M_Adult(t) = M_Adult(t - dt) + (F_to_M_Adult - A_to_M_Old - M_Adult_Mort - M_Translocation) * dt
    INIT M_Adult = 400
    INFLOWS:
      ⇨ F_to_M_Adult = M_1yr_Surv_Rate*M_Fledglings
    OUTFLOWS:
      ⇨ A_to_M_Old = M_Adult/M_Time_til_Old
      ⇨ M_Adult_Mort = M_Adult*M_Adult_Mort_Rate
      ⇨ M_Translocation (IN SECTOR:  Translocation)
☐ M_Fledglings(t) = M_Fledglings(t - dt) + (M_Fledge + M_Helper_Prod - M_1yr_Mort - F_to_M_Adult) * dt
    INIT M_Fledglings = 150
    INFLOWS:
      ⇨ M_Fledge = Male_Frac*Fledge_Rate*Nesting_Pairs
      ⇨ M_Helper_Prod = H_to_Pair_ratio*H_Prod_Decision*Nesting_Pairs
    OUTFLOWS:
      ⇨ M_1yr_Mort = M_Fledglings*M_1yr_Mort_Rate
      ⇨ F_to_M_Adult = M_1yr_Surv_Rate*M_Fledglings
☐ M_Old(t) = M_Old(t - dt) + (A_to_M_Old - M_Old_Mort) * dt
    INIT M_Old = 100
    INFLOWS:
      ⇨ A_to_M_Old = M_Adult/M_Time_til_Old
    OUTFLOWS:
      ⇨ M_Old_Mort = M_Old*Old_Mort_Rate
```



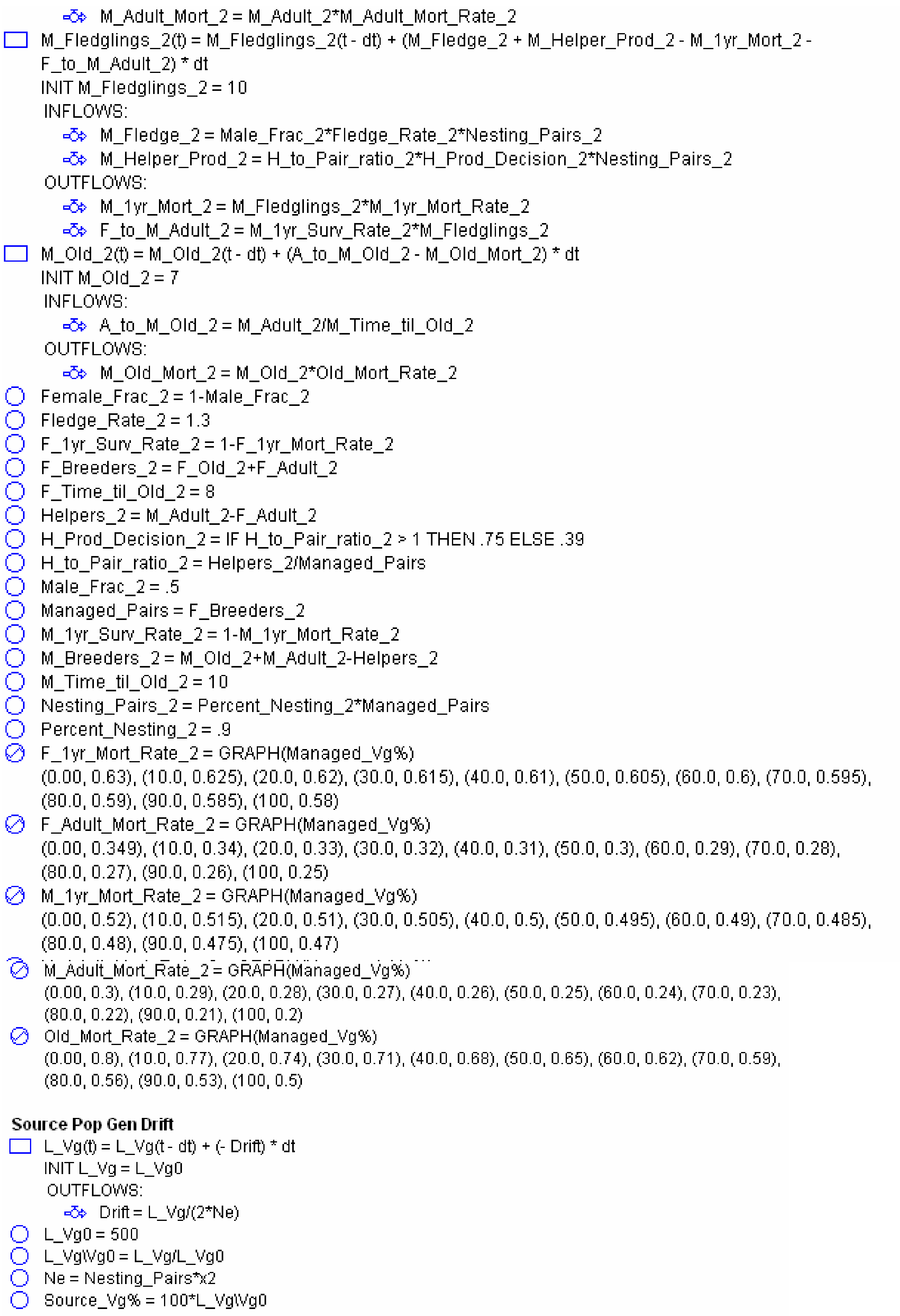
```
○ Female_Frac = 1-Male_Frac
○ Fledge_Rate = 1.30
○ F_1yr_Surv_Rate = 1-F_1yr_Mort_Rate
○ F_Breeders = F_Old+F_Adult
○ F_Time_til_Old = 8
○ Helpers = ABS(M_Adult-F_Adult)
○ H_Prod_Decision = IF H_to_Pair_ratio > 1 THEN .75 ELSE .39
○ H_to_Pair_ratio = Helpers/Source_Pairs
○ Male_Frac = .5
○ M_1yr_Surv_Rate = 1-M_1yr_Mort_Rate
○ M_Breeders = M_Old+M_Adult-Helpers
○ M_Time_til_Old = 10
○ Nesting_Pairs = Percent_Nesting*Source_Pairs
○ Percent_Nesting = .9
○ Source_Pairs = F_Breeders
⊘ F_1yr_Mort_Rate = GRAPH(Source_Vg%)
  (0.00, 0.63), (10.0, 0.625), (20.0, 0.62), (30.0, 0.615), (40.0, 0.61), (50.0, 0.605), (60.0, 0.6), (70.0, 0.595),
  (80.0, 0.59), (90.0, 0.585), (100, 0.58)
⊘ F_Adult_Mort_Rate = GRAPH(Source_Vg%)
  (0.00, 0.349), (10.0, 0.34), (20.0, 0.33), (30.0, 0.32), (40.0, 0.31), (50.0, 0.3), (60.0, 0.29), (70.0, 0.28),
  (80.0, 0.27), (90.0, 0.26), (100, 0.25)
⊘ M_1yr_Mort_Rate = GRAPH(Source_Vg%)
  (0.00, 0.52), (10.0, 0.515), (20.0, 0.51), (30.0, 0.505), (40.0, 0.5), (50.0, 0.495), (60.0, 0.49), (70.0, 0.485),
  (80.0, 0.48), (90.0, 0.475), (100, 0.47)
⊘ M_Adult_Mort_Rate = GRAPH(Source_Vg%)
  (0.00, 0.3), (10.0, 0.29), (20.0, 0.279), (30.0, 0.27), (40.0, 0.26), (50.0, 0.25), (60.0, 0.24), (70.0, 0.23),
  (80.0, 0.22), (90.0, 0.21), (100, 0.2)
⊘ Old_Mort_Rate = GRAPH(Source_Vg%)
  (0.00, 0.8), (10.0, 0.77), (20.0, 0.74), (30.0, 0.71), (40.0, 0.68), (50.0, 0.65), (60.0, 0.62), (70.0, 0.59),
  (80.0, 0.56), (90.0, 0.53), (100, 0.5)

Translocation
⇨ F_Translocation = Pulse(F_Per_Gen,Trans_Interval,Trans_Interval)
  OUTFLOW FROM:  F_Adult (IN SECTOR:  Source Population)
  INFLOW TO:  F_Adult_2 (IN SECTOR:  Managed Population)
⇨ M_Translocation = Pulse(M_per_Gen,Trans_Interval,Trans_Interval)
  OUTFLOW FROM:  M_Adult (IN SECTOR:  Source Population)
  INFLOW TO:  M_Adult_2 (IN SECTOR:  Managed Population)
○ F_Per_Gen = IF RCW_per_Trans >= 2 THEN RCW_per_Trans/2 ELSE IF RCW_per_Trans = 1 THEN 1
  ELSE 0
○ M_per_Gen = IF RCW_per_Trans >= 2 THEN RCW_per_Trans/2 ELSE 0
○ RCW_per_Trans = 2
○ Trans_Interval = .5
```

Without Replacement

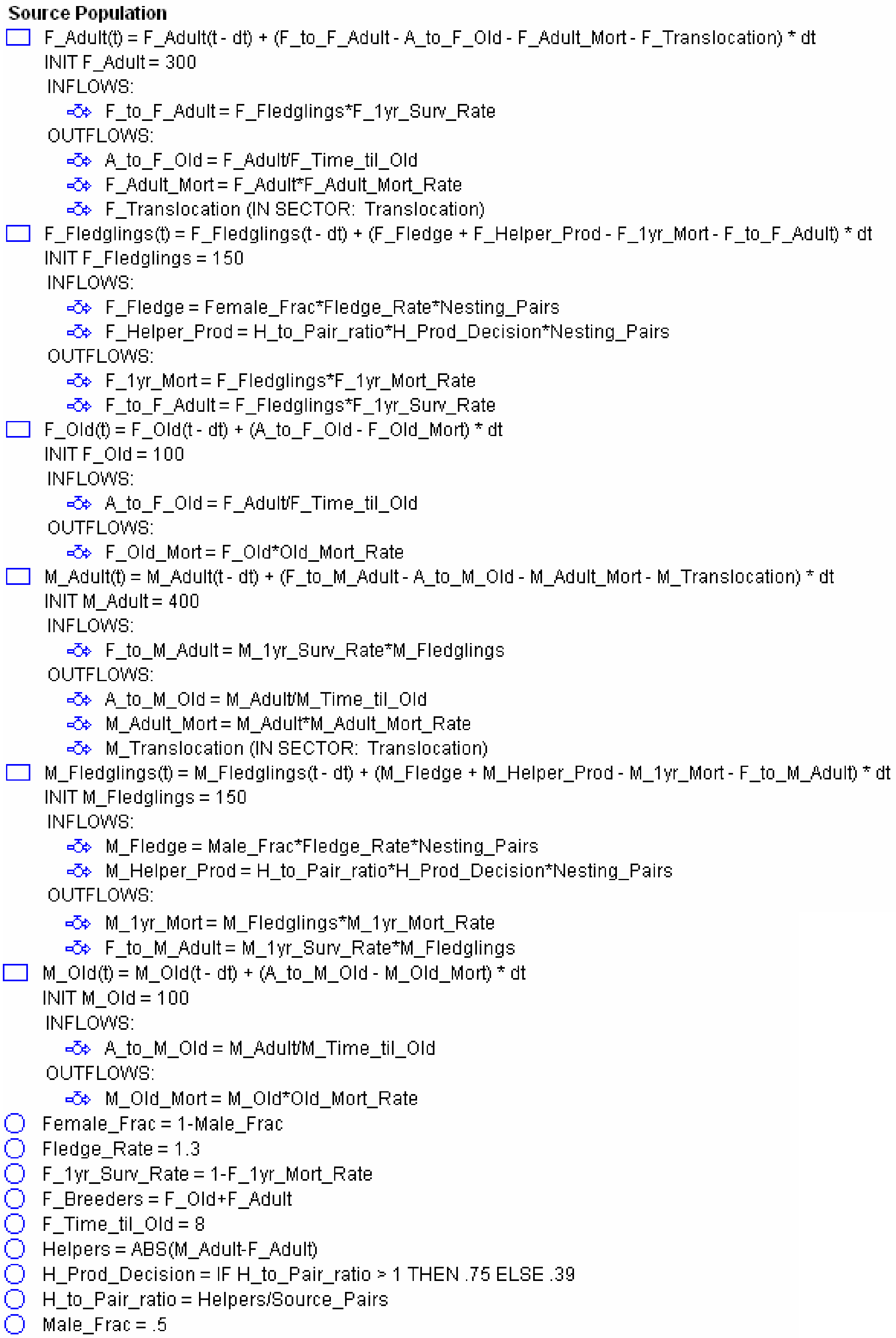
```
Managed Pop Gen Drift
☐ s_Vg(t) = s_Vg(t - dt) + (Imm_GV_2 + Hybrid_GV_2 - Drift_2) * dt
    INIT s_Vg = s_Vg0
    INFLOWS:
      ⇨ Imm_GV_2 = m*(s_Vg0-s_Vg)
      ⇨ Hybrid_GV_2 = (m*(1-m))*Vz/2
    OUTFLOWS:
      ⇨ Drift_2 = s_Vg/(2*Ne_2)
☐ Vz(t) = Vz(t - dt) + (Vz_up - Vz_down) * dt
    INIT Vz = s_Vg*V_ratio
    INFLOWS:
      ⇨ Vz_up = s_Vg/Ne_2
    OUTFLOWS:
      ⇨ Vz_down = 2*m*Vz
○ m = (F_Translocation+M_Translocation)/Ne_2
○ Managed_Vg% = 100*s_Vg\Vg0
○ Ne_2 = Nesting_Pairs_2*x2
○ s_Vg0 = 100
○ s_Vg\Vg0 = s_Vg/s_Vg0
○ V_ratio = .5
○ x2 = 2

Managed Population
☐ F_Adult_2(t) = F_Adult_2(t - dt) + (F_to_F_Adult_2 + F_Translocation - A_to_F_Old_2 - F_Adult_Mort_2) *
    dt
    INIT F_Adult_2 = 18
    INFLOWS:
      ⇨ F_to_F_Adult_2 = F_Fledglings_2*F_1yr_Surv_Rate_2
      ⇨ F_Translocation (IN SECTOR:  Translocation)
    OUTFLOWS:
      ⇨ A_to_F_Old_2 = F_Adult_2/F_Time_til_Old_2
      ⇨ F_Adult_Mort_2 = F_Adult_2*F_Adult_Mort_Rate_2
☐ F_Fledglings_2(t) = F_Fledglings_2(t - dt) + (F_Fledge_2 + F_Helper_Prod_2 - F_1yr_Mort_2 -
    F_to_F_Adult_2) * dt
    INIT F_Fledglings_2 = 10
    INFLOWS:
      ⇨ F_Fledge_2 = Female_Frac_2*Fledge_Rate_2*Nesting_Pairs_2
      ⇨ F_Helper_Prod_2 = H_to_Pair_ratio_2*H_Prod_Decision_2*Nesting_Pairs_2
    OUTFLOWS:
      ⇨ F_1yr_Mort_2 = F_Fledglings_2*F_1yr_Mort_Rate_2
      ⇨ F_to_F_Adult_2 = F_Fledglings_2*F_1yr_Surv_Rate_2
☐ F_Old_2(t) = F_Old_2(t - dt) + (A_to_F_Old_2 - F_Old_Mort_2) * dt
    INIT F_Old_2 = 7
    INFLOWS:
      ⇨ A_to_F_Old_2 = F_Adult_2/F_Time_til_Old_2
    OUTFLOWS:
      ⇨ F_Old_Mort_2 = F_Old_2*Old_Mort_Rate_2
☐ M_Adult_2(t) = M_Adult_2(t - dt) + (F_to_M_Adult_2 + M_Translocation - A_to_M_Old_2 -
    M_Adult_Mort_2) * dt
    INIT M_Adult_2 = 25
    INFLOWS:
      ⇨ F_to_M_Adult_2 = M_1yr_Surv_Rate_2*M_Fledglings_2
      ⇨ M_Translocation (IN SECTOR:  Translocation)
    OUTFLOWS:
      ⇨ A_to_M_Old_2 = M_Adult_2/M_Time_til_Old_2
```



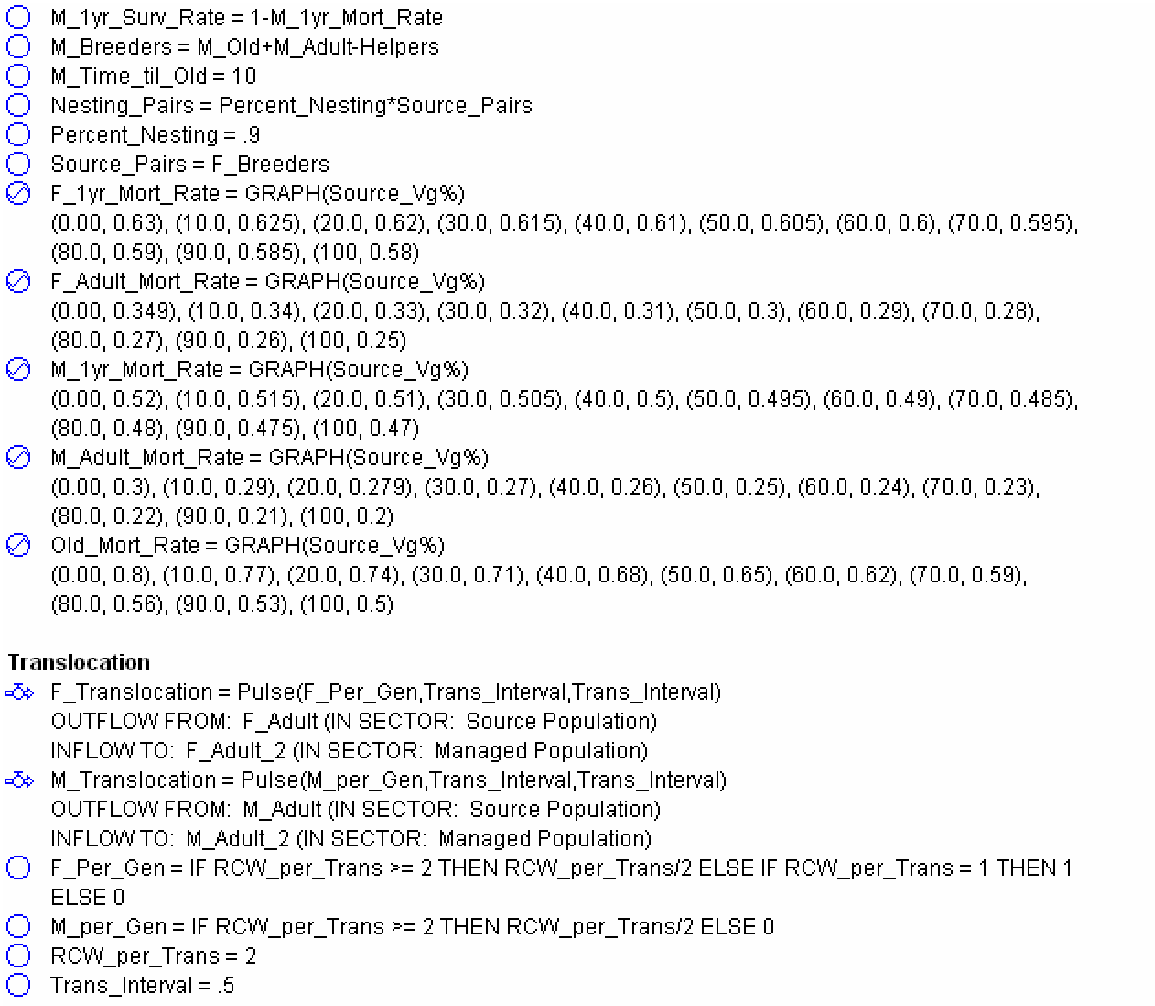
```
    → M_Adult_Mort_2 = M_Adult_2*M_Adult_Mort_Rate_2
▭ M_Fledglings_2(t) = M_Fledglings_2(t - dt) + (M_Fledge_2 + M_Helper_Prod_2 - M_1yr_Mort_2 -
  F_to_M_Adult_2) * dt
  INIT M_Fledglings_2 = 10
  INFLOWS:
    → M_Fledge_2 = Male_Frac_2*Fledge_Rate_2*Nesting_Pairs_2
    → M_Helper_Prod_2 = H_to_Pair_ratio_2*H_Prod_Decision_2*Nesting_Pairs_2
  OUTFLOWS:
    → M_1yr_Mort_2 = M_Fledglings_2*M_1yr_Mort_Rate_2
    → F_to_M_Adult_2 = M_1yr_Surv_Rate_2*M_Fledglings_2
▭ M_Old_2(t) = M_Old_2(t - dt) + (A_to_M_Old_2 - M_Old_Mort_2) * dt
  INIT M_Old_2 = 7
  INFLOWS:
    → A_to_M_Old_2 = M_Adult_2/M_Time_til_Old_2
  OUTFLOWS:
    → M_Old_Mort_2 = M_Old_2*Old_Mort_Rate_2
○ Female_Frac_2 = 1-Male_Frac_2
○ Fledge_Rate_2 = 1.3
○ F_1yr_Surv_Rate_2 = 1-F_1yr_Mort_Rate_2
○ F_Breeders_2 = F_Old_2+F_Adult_2
○ F_Time_til_Old_2 = 8
○ Helpers_2 = M_Adult_2-F_Adult_2
○ H_Prod_Decision_2 = IF H_to_Pair_ratio_2 > 1 THEN .75 ELSE .39
○ H_to_Pair_ratio_2 = Helpers_2/Managed_Pairs
○ Male_Frac_2 = .5
○ Managed_Pairs = F_Breeders_2
○ M_1yr_Surv_Rate_2 = 1-M_1yr_Mort_Rate_2
○ M_Breeders_2 = M_Old_2+M_Adult_2-Helpers_2
○ M_Time_til_Old_2 = 10
○ Nesting_Pairs_2 = Percent_Nesting_2*Managed_Pairs
○ Percent_Nesting_2 = .9
⊘ F_1yr_Mort_Rate_2 = GRAPH(Managed_Vg%)
  (0.00, 0.63), (10.0, 0.625), (20.0, 0.62), (30.0, 0.615), (40.0, 0.61), (50.0, 0.605), (60.0, 0.6), (70.0, 0.595),
  (80.0, 0.59), (90.0, 0.585), (100, 0.58)
⊘ F_Adult_Mort_Rate_2 = GRAPH(Managed_Vg%)
  (0.00, 0.349), (10.0, 0.34), (20.0, 0.33), (30.0, 0.32), (40.0, 0.31), (50.0, 0.3), (60.0, 0.29), (70.0, 0.28),
  (80.0, 0.27), (90.0, 0.26), (100, 0.25)
⊘ M_1yr_Mort_Rate_2 = GRAPH(Managed_Vg%)
  (0.00, 0.52), (10.0, 0.515), (20.0, 0.51), (30.0, 0.505), (40.0, 0.5), (50.0, 0.495), (60.0, 0.49), (70.0, 0.485),
  (80.0, 0.48), (90.0, 0.475), (100, 0.47)
⊘ M_Adult_Mort_Rate_2 = GRAPH(Managed_Vg%)
  (0.00, 0.3), (10.0, 0.29), (20.0, 0.28), (30.0, 0.27), (40.0, 0.26), (50.0, 0.25), (60.0, 0.24), (70.0, 0.23),
  (80.0, 0.22), (90.0, 0.21), (100, 0.2)
⊘ Old_Mort_Rate_2 = GRAPH(Managed_Vg%)
  (0.00, 0.8), (10.0, 0.77), (20.0, 0.74), (30.0, 0.71), (40.0, 0.68), (50.0, 0.65), (60.0, 0.62), (70.0, 0.59),
  (80.0, 0.56), (90.0, 0.53), (100, 0.5)

Source Pop Gen Drift
▭ L_Vg(t) = L_Vg(t - dt) + (- Drift) * dt
  INIT L_Vg = L_Vg0
  OUTFLOWS:
    → Drift = L_Vg/(2*Ne)
○ L_Vg0 = 500
○ L_Vg\Vg0 = L_Vg/L_Vg0
○ Ne = Nesting_Pairs*x2
○ Source_Vg% = 100*L_Vg\Vg0
```



Source Population

```
☐ F_Adult(t) = F_Adult(t - dt) + (F_to_F_Adult - A_to_F_Old - F_Adult_Mort - F_Translocation) * dt
    INIT F_Adult = 300
    INFLOWS:
        F_to_F_Adult = F_Fledglings*F_1yr_Surv_Rate
    OUTFLOWS:
        A_to_F_Old = F_Adult/F_Time_til_Old
        F_Adult_Mort = F_Adult*F_Adult_Mort_Rate
        F_Translocation (IN SECTOR:  Translocation)
☐ F_Fledglings(t) = F_Fledglings(t - dt) + (F_Fledge + F_Helper_Prod - F_1yr_Mort - F_to_F_Adult) * dt
    INIT F_Fledglings = 150
    INFLOWS:
        F_Fledge = Female_Frac*Fledge_Rate*Nesting_Pairs
        F_Helper_Prod = H_to_Pair_ratio*H_Prod_Decision*Nesting_Pairs
    OUTFLOWS:
        F_1yr_Mort = F_Fledglings*F_1yr_Mort_Rate
        F_to_F_Adult = F_Fledglings*F_1yr_Surv_Rate
☐ F_Old(t) = F_Old(t - dt) + (A_to_F_Old - F_Old_Mort) * dt
    INIT F_Old = 100
    INFLOWS:
        A_to_F_Old = F_Adult/F_Time_til_Old
    OUTFLOWS:
        F_Old_Mort = F_Old*Old_Mort_Rate
☐ M_Adult(t) = M_Adult(t - dt) + (F_to_M_Adult - A_to_M_Old - M_Adult_Mort - M_Translocation) * dt
    INIT M_Adult = 400
    INFLOWS:
        F_to_M_Adult = M_1yr_Surv_Rate*M_Fledglings
    OUTFLOWS:
        A_to_M_Old = M_Adult/M_Time_til_Old
        M_Adult_Mort = M_Adult*M_Adult_Mort_Rate
        M_Translocation (IN SECTOR:  Translocation)
☐ M_Fledglings(t) = M_Fledglings(t - dt) + (M_Fledge + M_Helper_Prod - M_1yr_Mort - F_to_M_Adult) * dt
    INIT M_Fledglings = 150
    INFLOWS:
        M_Fledge = Male_Frac*Fledge_Rate*Nesting_Pairs
        M_Helper_Prod = H_to_Pair_ratio*H_Prod_Decision*Nesting_Pairs
    OUTFLOWS:
        M_1yr_Mort = M_Fledglings*M_1yr_Mort_Rate
        F_to_M_Adult = M_1yr_Surv_Rate*M_Fledglings
☐ M_Old(t) = M_Old(t - dt) + (A_to_M_Old - M_Old_Mort) * dt
    INIT M_Old = 100
    INFLOWS:
        A_to_M_Old = M_Adult/M_Time_til_Old
    OUTFLOWS:
        M_Old_Mort = M_Old*Old_Mort_Rate
○ Female_Frac = 1-Male_Frac
○ Fledge_Rate = 1.3
○ F_1yr_Surv_Rate = 1-F_1yr_Mort_Rate
○ F_Breeders = F_Old+F_Adult
○ F_Time_til_Old = 8
○ Helpers = ABS(M_Adult-F_Adult)
○ H_Prod_Decision = IF H_to_Pair_ratio > 1 THEN .75 ELSE .39
○ H_to_Pair_ratio = Helpers/Source_Pairs
○ Male_Frac = .5
```

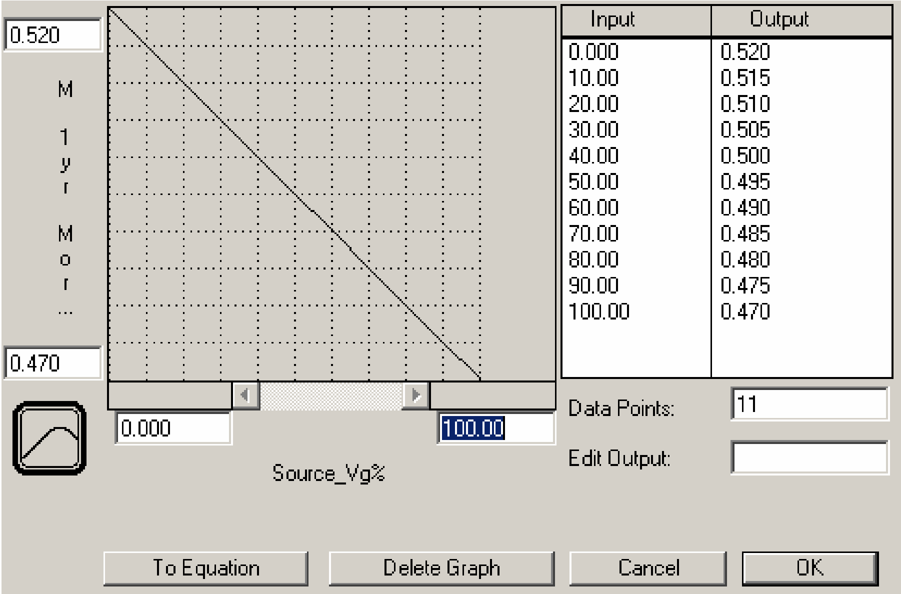


○ M_1yr_Surv_Rate = 1-M_1yr_Mort_Rate
○ M_Breeders = M_Old+M_Adult-Helpers
○ M_Time_til_Old = 10
○ Nesting_Pairs = Percent_Nesting*Source_Pairs
○ Percent_Nesting = .9
○ Source_Pairs = F_Breeders
⊘ F_1yr_Mort_Rate = GRAPH(Source_Vg%)
(0.00, 0.63), (10.0, 0.625), (20.0, 0.62), (30.0, 0.615), (40.0, 0.61), (50.0, 0.605), (60.0, 0.6), (70.0, 0.595), (80.0, 0.59), (90.0, 0.585), (100, 0.58)
⊘ F_Adult_Mort_Rate = GRAPH(Source_Vg%)
(0.00, 0.349), (10.0, 0.34), (20.0, 0.33), (30.0, 0.32), (40.0, 0.31), (50.0, 0.3), (60.0, 0.29), (70.0, 0.28), (80.0, 0.27), (90.0, 0.26), (100, 0.25)
⊘ M_1yr_Mort_Rate = GRAPH(Source_Vg%)
(0.00, 0.52), (10.0, 0.515), (20.0, 0.51), (30.0, 0.505), (40.0, 0.5), (50.0, 0.495), (60.0, 0.49), (70.0, 0.485), (80.0, 0.48), (90.0, 0.475), (100, 0.47)
⊘ M_Adult_Mort_Rate = GRAPH(Source_Vg%)
(0.00, 0.3), (10.0, 0.29), (20.0, 0.279), (30.0, 0.27), (40.0, 0.26), (50.0, 0.25), (60.0, 0.24), (70.0, 0.23), (80.0, 0.22), (90.0, 0.21), (100, 0.2)
⊘ Old_Mort_Rate = GRAPH(Source_Vg%)
(0.00, 0.8), (10.0, 0.77), (20.0, 0.74), (30.0, 0.71), (40.0, 0.68), (50.0, 0.65), (60.0, 0.62), (70.0, 0.59), (80.0, 0.56), (90.0, 0.53), (100, 0.5)

Translocation

⇨ F_Translocation = Pulse(F_Per_Gen,Trans_Interval,Trans_Interval)
OUTFLOW FROM: F_Adult (IN SECTOR: Source Population)
INFLOW TO: F_Adult_2 (IN SECTOR: Managed Population)
⇨ M_Translocation = Pulse(M_per_Gen,Trans_Interval,Trans_Interval)
OUTFLOW FROM: M_Adult (IN SECTOR: Source Population)
INFLOW TO: M_Adult_2 (IN SECTOR: Managed Population)
○ F_Per_Gen = IF RCW_per_Trans >= 2 THEN RCW_per_Trans/2 ELSE IF RCW_per_Trans = 1 THEN 1 ELSE 0
○ M_per_Gen = IF RCW_per_Trans >= 2 THEN RCW_per_Trans/2 ELSE 0
○ RCW_per_Trans = 2
○ Trans_Interval = .5

Appendix C: Drift-Mortality Graphs

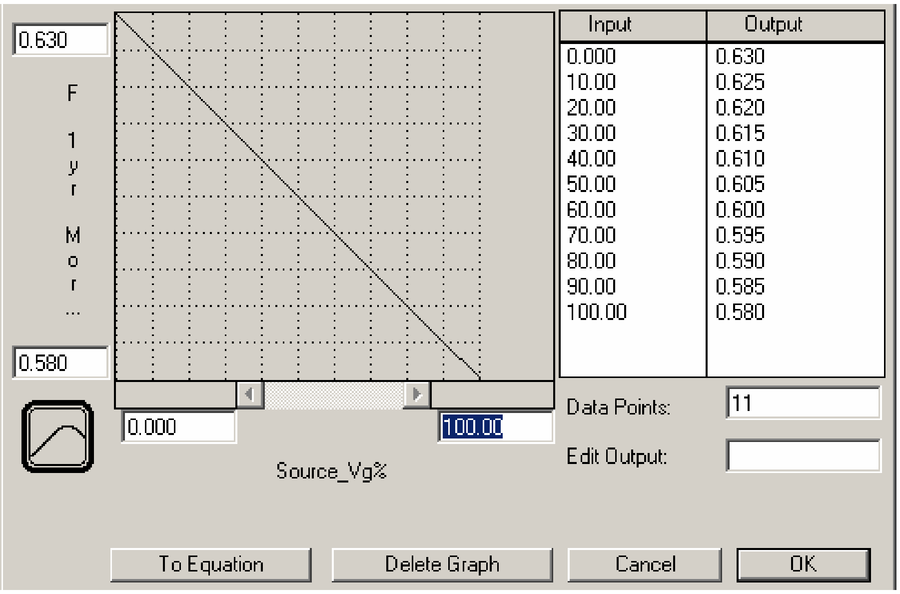


Input	Output
0.000	0.520
10.00	0.515
20.00	0.510
30.00	0.505
40.00	0.500
50.00	0.495
60.00	0.490
70.00	0.485
80.00	0.480
90.00	0.475
100.00	0.470

Data Points: 11

Edit Output:

Figure C.1 Male Fledgling Mortality Rate vs. % Genetic Variation Remaining

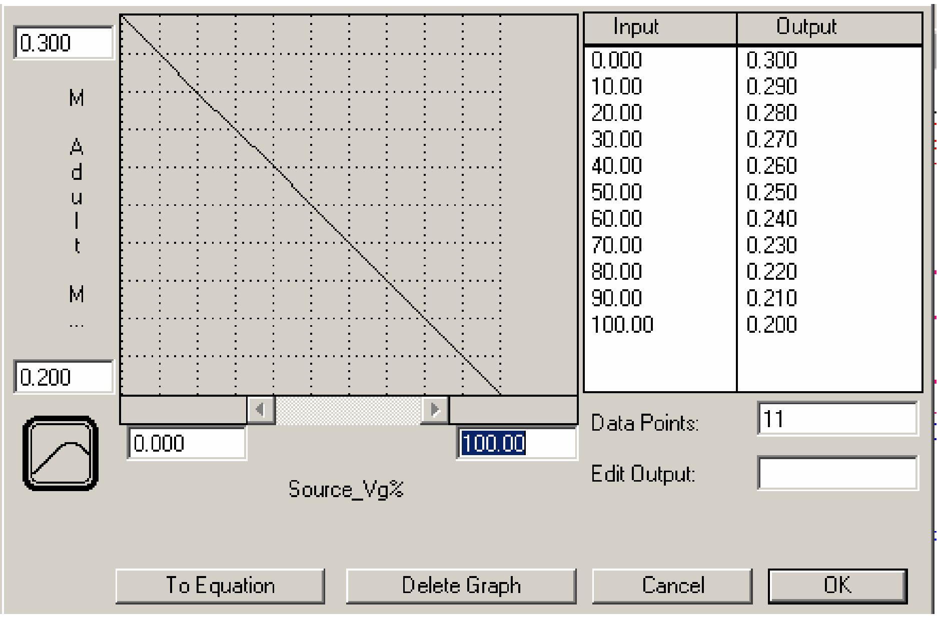


Input	Output
0.000	0.630
10.00	0.625
20.00	0.620
30.00	0.615
40.00	0.610
50.00	0.605
60.00	0.600
70.00	0.595
80.00	0.590
90.00	0.585
100.00	0.580

Data Points: 11

Edit Output:

Figure C.2 Female Fledgling Mortality Rate vs. % Genetic Variation Remaining

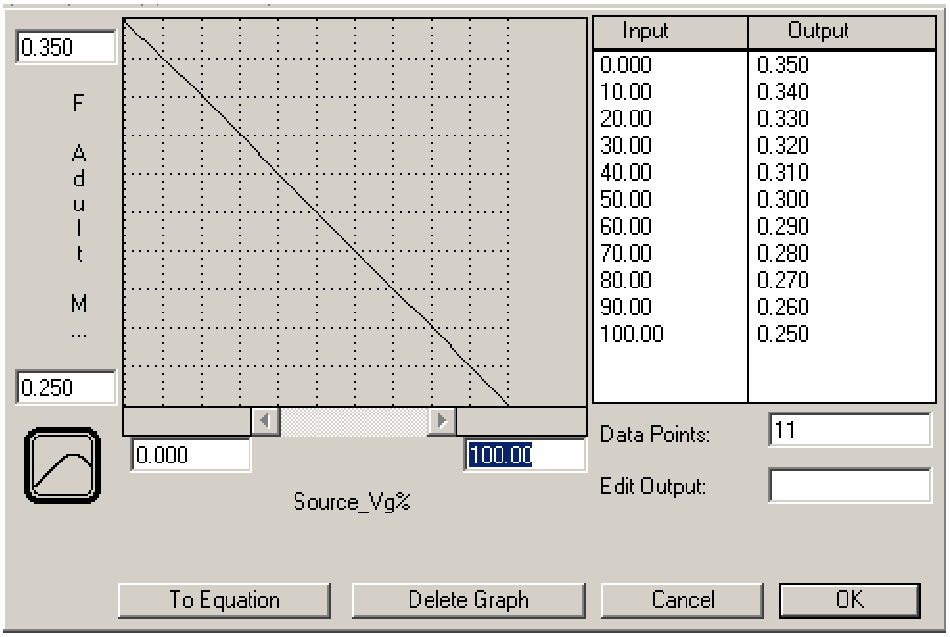


Input	Output
0.000	0.300
10.00	0.290
20.00	0.280
30.00	0.270
40.00	0.260
50.00	0.250
60.00	0.240
70.00	0.230
80.00	0.220
90.00	0.210
100.00	0.200

Data Points: 11

Edit Output:

Figure C.3 Male Adult Mortality Rate vs. % Genetic Variation Remaining

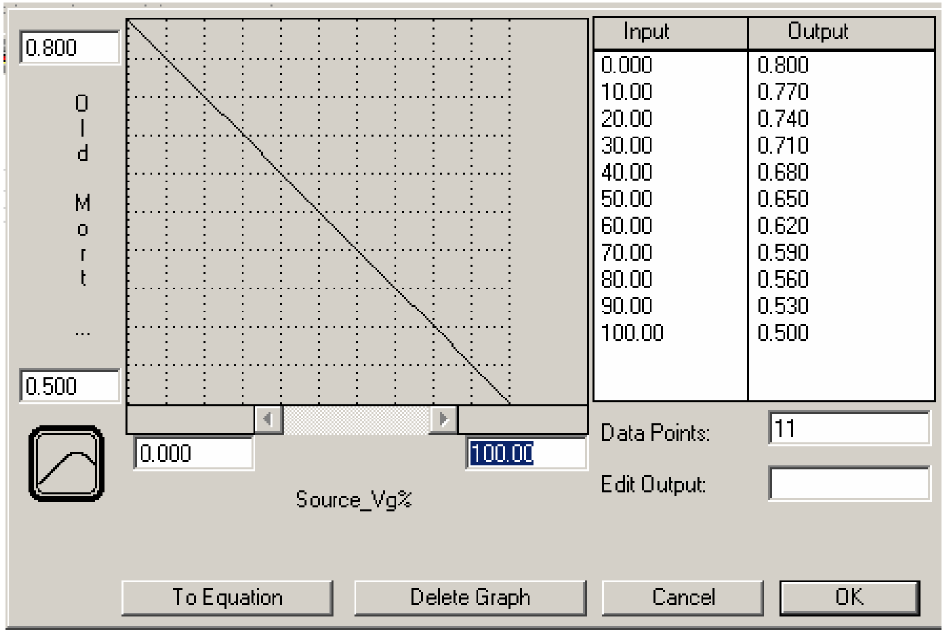


Input	Output
0.000	0.350
10.00	0.340
20.00	0.330
30.00	0.320
40.00	0.310
50.00	0.300
60.00	0.290
70.00	0.280
80.00	0.270
90.00	0.260
100.00	0.250

Data Points: 11

Edit Output:

Figure C.4 Female Adult Mortality Rate vs. % Genetic Variation Remaining



Input	Output
0.000	0.800
10.00	0.770
20.00	0.740
30.00	0.710
40.00	0.680
50.00	0.650
60.00	0.620
70.00	0.590
80.00	0.560
90.00	0.530
100.00	0.500

Data Points: 11

Edit Output:

Figure C.4 Old Mortality Rate vs. % Genetic Variation Remaining

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Vita

Captain Jason E. Yates was born and raised in Grand Ronde, Oregon. He graduated from Willamina High School in Willamina, Oregon. He entered undergraduate studies at Oregon State University in Corvallis, Oregon where he graduated Cum Laude with a Bachelor of Science degree in Civil Engineering in June 1998. During his years at OSU, he was a Air Force ROTC cadet and was commissioned upon graduation through Detachment 685 AFROTC at Oregon State University.

His first assignment was Nellis AFB in Las Vegas, Nevada in the 99th Civil Engineer Squadron starting in August 1998. While stationed at Nellis, he wed a fellow Oregonian in March of 2000. In August 2001, he entered the Graduate School of Engineering Management, Air Force Institute of Technology. Upon graduation, he will be assigned to the 51st Civil Engineer Squadron, Osan ABS, South Korea.

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14. ABSTRACT

The red-cockaded woodpecker (Picoides borealis) is classified under the Endangered Species Act of 1973 as an endangered species. As such, the red-cockaded woodpecker (RCW) is afforded strict protection in an effort to return the RCW population to a self-sustainable level. Endemic to southeastern United States mature pine forests, the presence of the RCW impacts the operations of many Department of Defense (DoD) installations to include testing and training ranges. A particular challenge in sustaining what are often small populations of RCW at these locations is the loss of genetic variation due to genetic drift. The optimal method for mitigating the loss of genetic variation due to genetic drift is through the artificial immigration, termed translocation, of individual RCWs from nother populations. The research objective of this effort was to quantify the translocation rate that would counter genetic drift in small populations though the modeling of RCW populations using a system dynamics approach. Both source and target populations utilizing various magnitudes and frequencies of translocations were modeled over a time period of 50 generations. While the optimal translocation rate is dependent on the initial population size, the results of this research indicate that it is possible to counter the effects of genetic drift in RCW populations as small as 10 mating pairs with the translocation of two pairs of red-cockaded woodpeckers twice per generation.

15. SUBJECT TERMS

Natural Resources Management, System Dynamics, Red-Cockaded Woodpecker, Genetic Drift, Translocation, Endangered Species

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