DISSERTATION

POPULATION DYNAMICS OF TOWNSEND'S GROUND SQUIRRELS IN SOUTHWESTERN IDAHO

Submitted by

Gail S. Olson

Department of Fishery and Wildlife Biology

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY GAIL S. OLSON ENTITLED POPULATION DYNAMICS OF TOWNSEND'S GROUND SQUIRRELS IN SOUTHWESTERN IDAHO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Advisor

Department Head

ABSTRACT OF DISSERTATION

POPULATION DYNAMICS OF TOWNSEND'S GROUND SQUIRRELS IN SOUTHWESTERN IDAHO

Townsend's ground squirrels (*Spermophilus townsendii*, or TGS) are a conspicuous component of the desert shrub-steppe ecosystem of southwestern Idaho. In 1991, a large-scale research project was initiated to assess the impacts of habitat alterations on TGS populations located within the Snake River Birds of Prey National Conservation Area (SRBPNCA), where TGS are the primary prey of the raptors for which the area is named. During 4 years (1991-1994), > 5,000 TGS were live-trapped on 20 study sites to answer questions about whether TGS density, survival and productivity were affected by either the recent large-scale conversion of native shrub habitat to grassland by wildfires, or the use of a portion of the SRBPNCA by the Idaho Army National Guard for military tank training. Capture-recapture methods were used to estimate abundance and survival of TGS.

Abundance was estimated using the no recruitment special case of the Jolly-Seber model, with the additional feature of modeling of capture and survival probabilities. These methods have never been combined in a study of this magnitude. I was able to estimate abundance in cases with small sample sizes, where the Jolly-Seber model is generally ineffective, by pooling data from more than one study site and estimating joint

capture and survival probabilities. Ground squirrel densities were highest in 1992, immediately before a population crash caused by a severe late spring drought in that year. Declines in density were greater among populations in grassland habitats than in shrub habitats. Very few juveniles born in 1992 survived to become adults. Following the crash, populations remained low, but made modest recoveries in 1994 on grassland sites.

Per-day survival rates were estimated for adults in 1991-1993 during 3 seasons of the year, using Cormack-Jolly-Seber methods and parameter modeling techniques. Random effects model analyses found differences in survival rates attributable to study year in all 3 seasons. These differences were assumed to reflect varying weather conditions occurring within those years. The effects of these conditions differed by habitat during the early part of the ground squirrel active season, and by sex during the late active season. Variability in survival rates during the inactive season was due to a complex interaction among all factors: year, sex, and habitat. Although lowered survival rates during and immediately following the 1992 drought were expected, survival rates remained low much later in 1993 despite apparently good environmental conditions. This was attributed to carry-over effects from the drought, but the exact mechanisms for those effects are unknown.

Dispersal patterns of juvenile ground squirrels were measured in a radio-telemetry study conducted in 1993-1994. Nearly 60 juveniles (38 males, 20 females) were radio-collared over the 2 years on 4 study sites selected to represent 2 habitat types: shrub and grass. Male-predominant dispersal rates, typical for *Spermophilus* spp., were confirmed, as nearly 60% of males dispersed whereas only 1 female did. No differences between

habitats was noted in the proportion of juveniles dispersing, the fates of dispersers, nor the patterns of dispersers; low sample sizes may have been responsible for the inability to detect any such differences. Dispersal distances (which averaged 515 m) fit a truncated exponential distribution, and the direction of dispersal did not differ from random.

A spatially explicit population model for TGS on the SRBPNCA was constructed to integrate the population parameters estimated in other portions of this research and to investigate potential impacts of habitat patterns on population dynamics of Townsend's ground squirrels. This population model is intended to be included in a more comprehensive model of habitat, prey, and raptors on the SRBPNCA. In the TGS population model, the model area was divided into 2.25 ha cells, within which population process of reproduction and survival take place, and between which dispersal occurs. Population parameters vary by environmental conditions (assessed 2 times during each model year) and habitat. Population parameter values were estimated from data collected during the TGS demography study. Model simulations of the TGS population model were conducted on a 10,000 cell test area of the SRBPNCA. In model simulations under random environmental conditions, TGS populations experienced population growth, and growth was higher in grass habitats than in shrub habitats. Population densities in grass habitats reached unrealistic levels (i.e., the mean of all cell populations was >50 animals/ha) at least once during model simulation in most cases, yet they remained at more modest levels in shrub habitats. In addition, populations tended to become increasingly aggregated, with highest densities concentrated in large areas of grass habitat, and lowest densities (and sometimes local extinction) in large areas of shrub

habitat. If model assumptions are realistic, these patterns may indicate that intermingling of the 2 habitats is required for TGS populations to remain stable. However, an important model assumption is that there are no density dependent regulation mechanisms operating; this assumption is likely unrealistic. Therefore, future research should be concentrated on determining the means by which TGS populations are regulated, as well as on studying more closely the response of TGS population parameters to environmental conditions.

Gail S. Olson
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins, CO 80523
Spring 1999

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PREFACE

Being a part of a well-funded, large-scale research project can be both beneficial and challenging. The benefits are obvious: manpower and equipment are readily available, the opportunities exist to collaborate with professional colleagues, and the magnitude of the data collected during such efforts is greater than for most wildlife studies. The challenge is in how to define individual contributions among the many parts of the whole. Such was the case for me, relative to a large scale demography study of Townsend's ground squirrels (TGS) conducted on the Snake River Birds of Prey National Conservation Area, Idaho, in 1991-1994. In 1990, Bureau of Land Management contract YA651-CTO-340032 was awarded to Dr. Beatrice Van Horne of the Biology Department at Colorado State University for a study to examine TGS abundance, productivity and habitat relationships. Although the primary researcher on this project, Dr. Van Horne enlisted the aid of several persons to address the objectives of this study. They included: Dr. Kenneth P. Burnham, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Robert L. Schooley, Department of Biology, Colorado State University, several doctoral students (including myself), and dozens of field assistants. My role and responsibilities in this effort were sometimes difficult to define exclusively, but were primarily concerned with the demographic aspects of the study, and particularly

the large-scale capture-recapture effort. In Chapter 1 of this dissertation, I describe the demography study, including the overall study design and details of the field methods employed. Much of that material is not exclusively my own, but is essential background for the subsequent chapters, which are my own. I then relate how I used data from this study, supplemented by my own radio-telemetry study, to estimate the key population parameters of abundance (Chapter 2), survival (Chapter 3) and dispersal (Chapter 4), and integrated these parameters into a spatially explicit population model (Chapter 5). In the final chapter (6) I draw conclusions from this work and summarize my thoughts on priorities for future research.

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CHAPTER ONE

BACKGROUND

TOWNSEND'S GROUND SQUIRREL BIOLOGY

Townsend's ground squirrels (Order Rodentia, Family Sciuridae, Genus *Spermophilus*, species *townsendii*, hereafter known as TGS) are found in high desert shrub habitats of the Great Basin and Columbia Plateau, in parts of the states of Washington, Oregon, Idaho, California, Nevada, and Utah (Rickart 1987). Rickart (1987) recognized 7 subspecies of TGS, of which the one I studied was *S.t. idahoensis*. Although Hoffmann et al. (1993) included this population of TGS in *S. mollis* based on chromosomal grounds, I have chosen to use the older designation for consistency with other publications based upon the same research project that supported this dissertation.

Townsend's ground squirrels are one of the smaller members of the *Spermophilus* genus, and body size is one of its distinguishing features, along with short tail length, small ears, and pale gray-tan unmarked pelage (Rickart 1987). Adults are <300 mm total length, with hind foot <39 mm, with males slightly larger overall (Davis 1939). Adult mass varies seasonally, with an average low of ca. 165 g in late winter, and an average high of >190 g in late spring (unpublished data).

Well-named, ground squirrels spend most of their lives underground. Townsend's ground squirrels build extensive burrow systems, which may have several burrow

entrances (Alcorn 1940). Several TGS researchers have used counts of burrow entrances as an indicator of TGS density (Nydegger and Smith 1986, Yensen et al. 1992) although Van Horne et al. (1997b) found such counts to be unreliable.

As with other *Spermophilus* spp., TGS are dormant during most of the calender year. They emerge from hibernation in late January-mid February, with males generally emerging 1-3 weeks prior to females. Adults immerge into estivation in May, with males again preceding females by about 2-3 weeks. There is no evidence that TGS emerge in the fall despite occasional anecdotal reports. Therefore, the average time spent in estivation/hibernation by adult TGS is about 8 ½ months per year.

The reproductive potential of TGS is high. Most TGS mature as yearlings, and pregnancy rates are usually high (nearly 100% of adults and >50% of yearlings; Smith and Johnson 1985, Van Horne et al. 1997a). A notable exception occurred in 1977, when there was a total suspension of reproduction due to a severe winter drought (Smith and Johnson 1985). Although only 1 litter per year is produced, embryo counts as high as 16 have been reported (Rickart 1982). Rickart (1982) also reported mean litter sizes to be 7-10, with yearlings having smaller litters than older ground squirrels. However, litter size also appears to be affected by environmental conditions, and can be substantially less in years following severe drought (Van Horne et al. 1997a).

To endure their lengthy hibernation period, TGS must build sufficient fat reserves prior to immergence. Adult males begin this process after breeding is complete, generally by late February. Adult females must wait until after weaning of litters, about a month later, and therefore must put on fat for hibernation at the same time as their offspring are

consuming food for growth and hibernation. Given the reliance of TGS on fat reserves, and the short time in which they must acquire those reserves, diet must play an important role in TGS's survival.

TGS diets have been studied by several authors (Rogers and Gano 1980, Rickart 1982, Yensen and Quinney 1992, Van Horne et al. 1998), but the results of these studies have been somewhat contradictory. All have found that TGS eat a wide variety of food items but mostly green vegetation early in the active season, and seeds of grasses and forbs later in the year. Van Horne et al. (1998) found they apparently prefer native food sources, especially Sandberg's bluegrass (*Poa secunda*), and winterfat (*Ceretoides lanata*), and they avoid exotic plants such as cheatgrass (*Bromus tectorum*), and Russian thistle (*Salsola iberica*), yet Yensen and Quinney (1992) found no avoidance of exotics.

Townsend's ground squirrels serve as an important food resource for several predators. These include badgers (*Taxidea taxus*), coyotes (*Canis latrans*), western rattlesnakes (*Crotalus viridis*), gopher snakes (*Pituophis melanoleucus*), and several raptors: prairie falcons (*Falco mexicanus*), red-tailed hawks (*Buteo jamaicensis*), and ferruginous hawks (*B. regalis*) (Messick and Hornocker 1981, Diller and Johnson 1988, Steenhof and Kochert 1988, Marzluff et al. 1997) . There have been no studies of competition between TGS and other herbivores. Townsend's ground squirrels are thought to be subordinate to *S. armatus* and *S. beldingi* where their range overlaps, as TGS are restricted to the most arid habitats in those areas. Other small mammals, such as Ord's kangaroo rat (*Dipodomys ordii*), Great Basin pocket mouse (*Perognathus parvus*), western harvest mouse (*Reithrodontomys megalotis*) and the least chipmunk (*Eutamias*

minimus) also overlap in distribution with TGS. Although these potential competitors may eat similar foods and/or construct or use similar burrow systems, nothing is known about how they may impact TGS. Competition with cattle and sheep has been inferred, yet Rogers and Gano (1980) felt that cattle grazing had little impact on ground squirrel diets. It is more likely that large grazers have an indirect impact on TGS via habitat modification than a direct impact through a shared food resource, since most grazing takes place during the time ground squirrels are in torpor.

The limited time in which TGS must reproduce and replenish fat reserves no doubt imposes severe constraints on their ability to respond to changes in factors that may lengthen these activities. The most likely interfering factors are environmental conditions and habitat alterations. The former will act on an annual basis virtually at random, and could be anything from an unusually long, cold winter to an extended drought. These are conditions that TGS are likely to have evolved under and could probably cope with over a number of years. Alterations of habitat, and specifically changes to the food base of ground squirrels, probably have more long-term effects. If alterations are major, and not of a type or scale previously encountered by TGS, they may have serious impacts on the long-term viability of ground squirrel populations. Therefore, evaluating the effects of habitat alterations on TGS is a key component of this study.

STUDY AREA

The 195,325 ha Snake River Birds of Prey National Conservation Area (SRBPNCA) is U.S. public land managed by the Bureau of Land Management (BLM), and is located in southwestern Idaho, approximately 50 km south of Boise (Figure 1.1).

Originally consisting of a 10,800 ha strip of Snake River Canyon, the area was established in 1971 as a Natural Area to protect the nesting habitat of one of the highest densities of cliff-nesting raptors in the world (U.S. Dept. of Interior 1979). Subsequent research identified the importance of the plains above the canyon in supporting the raptors' primary prey species, TGS and black-tailed jackrabbits (*Lepus californicus*) (U.S. Dept. of Interior 1979), and the remaining acreage was added to protect this area in 1980. The area's current name and status as a National Conservation Area was adopted in 1993.

Within the SRBPNCA is the 55,770 ha Orchard Training Area (OTA), used by the Idaho Army National Guard (IDARNG) for tank training activities since the 1950's. In 1986, the IDARNG filed a request to upgrade their facilities and expand their activities within the SRBPNCA. This prompted the BLM to initiate research into the effects of IDARNG use, and other habitat alterations, on raptors and their prey populations. In particular, fire and grazing are known to have changed vegetative characteristics on large portions of the SRBPNCA (Yensen 1982). The SRBPNCA has been subject to grazing for over 100 years (Yensen 1982), while wildfires have recently (since 1980) burned over half of the area (105,000 ha : Kochert and Pellant 1986).

The climate in this region is generally dry, with annual precipitation ranging from 11- 35 cm, the majority of which falls between November and April (Yensen et al. 1992). Temperatures are extremely variable; mean daily temperatures range from -26 - 32° C and are highest in July, and lowest in January (NOAA National Climate Center Data, 1946-1994). The elevation of the area ranges from 700 - 1067 m but the topography is mostly flat or slightly rolling with a few tall volcanic buttes and cones (Nydegger and

Smith 1986). The land is a broad basalt plain with aridosol soils developed in loess or silty alluvium (Knick 1996).

Historically, the vegetation of the area was dominated by shrubs, particularly big sagebrush (*Artemesia tridentata*), winterfat (*Ceratoides lanata*), and several *Atriplex* spp. Forbs, such as balsamroot (*Balsamorhiza sagittata*) and perennial bunchgrasses (primarily *Poa secunda*) covered the understory (Yensen 1982). Grazing, intentional burning by ranchers, and wildfires, have caused several changes to the vegetative community, especially the proliferation of exotic annuals such as cheatgrass (*Bromus tectorum*) and Russian thistle (*Salsola iberica*) (Yensen 1982). In general, however, vegetation is sparse, as nearly 50% of the area is bare ground, with an additional 25-30% of coverage by litter (Van Horne et al. 1991).

TOWNSEND'S GROUND SQUIRREL DEMOGRAPHY STUDY

The TGS demography study was part of the research efforts funded by the BLM to determine the impacts of tank tracking and other habitat modifications on raptors and prey populations. The objectives of that study that directly related to my research were to determine whether TGS densities, survival, and productivity differ:

1. among habitat types,
2. between areas that have been subjected to tracked vehicle operations over a long period of time and those that have not been tracked,
3. between burned and unburned areas, and
4. between burned areas that have been seeded and those that have not been seeded.

Field work for this study was initiated in January 1991 and was conducted during January-June in each of the years 1991-1994. Through the 1991 field season, decisions about the design of the capture-recapture study, including site selection and trapping protocol, were made by Dr. Bea Van Horne, Dr. Ken Burnham, Bob Schooley, and Susan White. Subsequently, I replaced Ms. White in this group of primary researchers, and in the remainder of this chapter, I use "we" to refer to this group. Briefer descriptions of these methods have been published elsewhere (Schooley et al. 1993, Van Horne et al. 1997a).

Study sites

Twenty 10 ha. study sites were selected in early 1991 to represent 10 habitat and treatment combinations. (Table 1.1; Figure 1.1). Sites were selected based on accessibility and the homogeneity of habitat within and around the site. Two sites (3A and 3B), located in shadscale habitat in 1991, were dropped from the study and replaced by 2 winterfat-sagebrush mosaic sites in 1992-1994. On each site, a 300 × 300 m permanent grid was established using 25 metal fenceposts set out 75 m apart and numbered 1-25 starting at the NW corner, with pole 13 at the center. The UTM coordinates of the center of each study site were determined by using a Global Positioning System (GPS) unit, with a 2-5 m circular error probable (i.e., 50% of measurements taken repeatedly would be within that radius). The fenceposts remained in place throughout the study and defined the maximum boundaries of the sites. Within these boundaries, live-trapping was conducted.

Trapping protocol

The placement of traps varied from year to year and from site to site within a year. In 1991, traps were placed at burrow entrances (hole-based trapping) because this was thought to be the most efficient way to capture ground squirrels. This turned out not to be the case, as this method was not sufficiently effective at targeting animals using the burrows where traps were placed, and was very labor-intensive to apply. Beginning in 1992, we placed traps in a grid arrangement (grid-based trapping) and used this system for the remainder of the study. Our choices of grid areas, trap numbers, and trap spacing were always made based on what we thought would be optimally efficient at capturing sufficient numbers of ground squirrels for capture-recapture estimation of population parameters. We felt that the capture-recapture estimation methods we used should be robust to these changes in trap placement patterns because of their ability to cope with variable capture probabilities.

In 1991, burrow entrances which appeared to be actively used by ground squirrels were identified and, starting from the center of the study sites (Pole 13), were uniquely numbered (up to 200 per site), and labeled using aluminum tags placed flush on the ground and secured with a 75 mm nail. The location of each hole was mapped in relation to the center to the grid. Up to 39 traps (per site) were placed at randomly selected burrow entrances, with traps shifted every day to new randomly selected locations. Each site was trapped for 4-12 consecutive days (called a cycle), until few new captures were made. With this design, and rotating between all 20 sites, there was at least 1 month intervening between cycles on the same site. All sites were trapped at least twice (2

cycles), most sites were trapped for 3 cycles, and 1 site was trapped 4 times (Table 1.2). With this design, the area covered by traps (in the naive sense, i.e., not accounting for animals being drawn to traps from outside the area where traps were actually placed) varied from 0.71 - 5.75 ha.

In 1992, we changed the timing of trapping among sites. Although the cycle pattern was affective in gathering appropriate data for population parameter estimation within a site, the asynchronous timing of the cycles made it difficult to make direct comparisons among sites. Therefore, we modified our trapping protocol so that we trapped each site for 1 day only, before moving on to another site. With 5 trapping crews working simultaneously, this allowed us to trap all 20 sites within 4 days under optimal conditions. We continually rotated through the study sites in this manner throughout the ground squirrel active season. Trapping was suspended or discontinued on some sites when no adult ground squirrels were captured prior to juvenile emergence, and additional trapping effort was sometimes added to other sites to enhance efforts there. The result was 5-24 trapping occasions on each site in a given year (Table 1.3).

In 1991, there had been problems with trap saturation on sites with high population densities. Consequently, in 1992, we trapped smaller grids on these sites (2.25 ha), trapped intermediate sized grids (4.50 ha) on sites with moderate densities, and trapped the entire site area (9.00 ha) on sites with low densities. Our determination of grid size was based on our expectation of the area needed to trap ≥25 adult female ground squirrels, based on 1991 density estimates. However, because 1 adult female can give birth to up to 11 juveniles, we had to further reduce grid areas when juveniles emerged.

We based this grid shrinkage on the number of adult females that were captured as of 15 March 92. All sites that were 2.25 ha were reduced to 1.0 ha, and all but 1 site that was 4.50 ha was reduced to 2.25; the exception was site 10B which was reduced from 4.5 to 1.0 ha. (Figure 1.2). Sites that were 9.00 ha were not reduced upon emergence of juveniles.

The number of traps per grid also varied, from 49-66. Despite this, traps were spaced farther apart on larger sites. To compensate, we used 2 trap placement patterns on the 2 larger grid areas, and shifted traps between these patterns on alternate trapping occasions (Figure 1.3). Therefore, the maximum distance from any point within the grid to a trap was 53.0 m on 9.00 ha sites, 41.9 m on 4.50 ha sites, and 35.4 m on 2.25 ha sites. We also placed additional traps on larger grids in areas where unmarked animals were observed, and mapped the locations of these supplemental traps.

In 1993 and 1994, grid size and configuration was the same for all study sites (Figure 1.4). We chose the 4.50 ha grid size because: 1) we expected ground squirrel densities to be substantially reduced because of a severe late spring drought in 1992, and that trap saturation would not be a problem, and 2) we felt that it took too much time to check all traps on larger sites and that this was detrimental to the ground squirrels captured. The same grid size was maintained throughout both years (93 and 94). We did not shrink trapping grids when juveniles emerged because their appearance did not increase density appreciably in those years. The minimum number of traps used (66) was the same on all sites, with additional traps added in areas where juveniles were captured to facilitate capturing multiple animals from the same litter.

Capturing and handling procedures

Although the timing of trapping and pattern of trap placement varied among sites and years, the procedures used to capture and handle ground squirrels remained consistent throughout the study. Each site was live-trapped with Tomahawk cage traps (Model 201, Tomahawk Live Trap Co., Tomahawk, WI) throughout the TGS active season. We began trapping each year in early-mid February, soon after adults emerged from hibernation. After an initial period for training technicians (at which time only 1-2 sites were trapped per day), we began trapping up to 5 sites per day. All traps were opened at about 0800 (nearer to 0700 when weather was hot in June), baited with small pieces of apple (approximately 1 g), and checked 1 hour later. This entire procedure was repeated, for up to 3 trapping sessions within a site per day. No trapping was conducted during inclement weather (snow or rain) because TGS are not active under such conditions, and trapping was sometimes stopped before 3 trapping sessions were completed because of rain or high winds (>30 kph). If only 1 session was completed, we generally returned to that site the next day to complete the remaining sessions. We did not trap when snow cover was >8-10 cm , and at times could not reach all study sites because of poor road conditions.

Upon first capture, all TGS were marked by inserting a uniquely encoded Passive Integrated Transponder (PIT) tag (Model TX 1400, Detron IDI, Boulder, CO) subcutaneously just posterior to the cranium. This allowed for subsequent recaptures to be identified by scanning animals with a PIT tag reader (Model HS 5101 Destron IDI), which displayed the 10-digit hexadecimal code of the tag. A more complete description

of the entire PIT-tagging procedure may be found in Schooley et al. (1993). At each capture, age (adult or juvenile) , sex, and capture history (first capture or recapture) were recorded. Weight (to the nearest 1 g) was recorded the first time an individual was captured during the day, and any special conditions were noted, such as the presence of ecto-parasites or other anomalies. On some sites, additional handling procedures were applied to collect data for other research studies. These included: marking animals with visible black dye codes for behavioral observations, collection of fecal material for diet and parasite analyses, and collection of tail segments (tip only) for DNA-based genetic identification (in 1993 only). On 6 sites, at certain times during the season, captured animals were removed briefly from study sites for measurement of body composition for a fat dynamics study, and most juveniles captured on 4 sites in 1993 and 1994 were radio-collared for a dispersal study (see Chapter 4). Sites used in each of these other studies are identified in Table 1.1.

Other data collection procedures

In addition to the data collected on TGS, measurements of environmental variables were also recorded. Weather data were collected during each trapping session at locations adjacent to the trapping grid. Weather measurements included air temperature at 2 heights (15 cm, or "ground squirrel height", and 125 cm) both shaded (if taken on shrub sites) and in direct sunlight, air speed (at the same 2 heights), and percent cloud cover (recorded as 1 of 5 categories). Vegetation was measured on each site at 2-3 times during the season using a 3.0 × 0.5 m point frame (Floyd and Anderson 1982) as the basic sampling unit. On all sites, vegetation measurements included species

composition, frequency, canopy cover, plant status (live vs. dead or senescent), and substrate. On shrub sites, we also measured shrub density and mean and maximum shrub height (in meters), and presence/absence of canopy from 3.14 m^2 circular plots (on 3 sites) and 7.07 m^2 circular plots on 17 sites, established at the end of the vegetation transects. Trapping was suspended on all sites while vegetation measurements were being taken. Weather and vegetation data were little used in subsequent sections of this dissertation; some results from analyses of these data were reported by Van Horne et al. (1997a, 1998) and Van Horne and Sharpe (1998).

Experimental treatments of study sites

The objectives for the TGS study called for controlled tracking by a military M-1 tank on 4 of the study sites (Table 1.1). In addition, 2 sites (7A and 8A) were selected in 1993 to test theories on the effects of supplemental feeding on TGS population responses to a severe drought in 1992. Details of application and results of these treatments are reported elsewhere (Van Horne and Sharpe 1998 and Van Horne et al. in prep). In summary, the conclusions of those studies were that the experimental tank tracking had no discernable effects on TGS populations, and that supplemental feeding treatments had substantial effects on several population parameters. Therefore, the tracking treatments were subsequently ignored with respect to the analyses within this dissertation but the supplemental feeding treatments were not. I excluded data from sites 7A and 8A collected in 1993 and 1994 from most analyses, and assigned them to a separate habitat type when they were not excluded. The specific handling of these data are noted for each analysis.

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Table 1.1. Townsend's ground squirrel study sites established on the Snake River Birds of Prey National Conservation Area, identified by designation code, habitat type, whether the site was located within the Orchard Training Area (OTA) and treatment type, if any. All sites were used for the demography study. Some sites were used for related studies; these are designated as: B, behavior study; F, fat dynamics study; P, parasite study; D, dispersal study; and G, genetics study.

Site	Habitat	OTA	Treatment	Other studies
1A	Winterfat	NO	None	B,F,P
1B	Winterfat	NO	None	F,P
2A	Sagebrush	NO	None	P
2B	Sagebrush	NO	None	P
3A	Winterfat-Sagebrush Mosaic[a]	NO	None	
3B	Winterfat-Sagebrush Mosaic[a]	NO	None	B
4A	Burned sagebrush	YES	None	B,F,P,G
4B	Burned sagebrush	YES	None	F,P,G
5A	Sagebrush	YES	None	F,P
5B	Sagebrush	YES	None	B,F,P,D,G
6A	Burned winterfat	NO	None	
6B	Burned winterfat	NO	None	G
7A	Burned sagebrush	NO	Supplemental feeding[b]	
7B	Burned sagebrush	NO	None	
8A	Burned winterfat	NO	Seeded[c], Supplemental feeding[b]	B,F
8B	Burned winterfat	NO	Seeded[c]	F
9A	Sagebrush	YES	Tracked[d]	
9B	Sagebrush	YES	Tracked[d]	B,D,G
10A	Burned sagebrush	YES	Tracked[d]	B,D,G
10B	Burned sagebrush	YES	Tracked[d]	D,G

[a]In 1991, sites 3A and 3B were located in shadscale habitat location outside of the OTA. In 1992, these were replaced by sites located in winterfat-sagebrush mosaic habitat, and remained so until the end of the study.
[b]In 1993 and 1994, sites 7A and 8A received food supplementation as part of an experimental study.
[c]Sites 8A and 8B had been seeded by the BLM in an attempt to re-establish shrubs on areas that had burned.
[d]Sites 9A, 9B, 10A, and 10B were experimentally tracked by an M-1 tank after the 1992 field season was completed.

Table 1.2. Dates for each trapping cycle conducted on TGS study sites in 1991, with number of successful trapping occasions per cycle (days in which >0 animals were caught) in parentheses (from Van Horne et al. 1991).

Site	Cycle 1	Cycle 2	Cycle 3
1A	26 FEB - 9 MAR (9)	13 APR - 18 APR (4)	12 MAY - 19 MAY (4)[a]
1B	12 MAR - 18 MAR (5)	21 APR - 4 MAY (4)	25 JUN - 26 JUN (2)
2A	19 FEB - 9 MAR (12)	13 APR - 18 APR (4)	
2B	13 MAR - 18 MAR (2)	6 MAY - 16 MAY (4)	
3A	27 MAR - 31 MAR (0)	7 MAY - 21 MAY (1)	
3B	3 APR - 8 APR (4)	5 MAY - 21 MAY (5)	
4A	23 MAR - 28 MAR (4)	30 APR - 5 MAY (4)	27 JUN - 28 JUN (2)
4B	2 APR - 7 APR (5)	6 MAY - 16 MAY (5)	19 JUN - 21 JUN (3)
5A	12 MAR - 18 MAR (6)	20 APR - 23 APR (4)	
5B	26 FEB - 9 MAR (10)	8 APR - 18 APR (5)	22 MAY - 27 MAY (4)
6A	12 MAR - 18 MAR (1)	6 MAY - 7 MAY (1)	
6B	23 MAR - 28 MAR (4)	20 APR - 23 APR (4)	
7A	2 APR - 7 APR (5)	28 APR - 5 MAY (5)	26 MAY - 29 MAY (4)
7B	16 FEB - 7 MAR (9)	13 APR - 18 APR (4)	27 MAY - 29 MAY (3)
8A	23 MAR - 28 MAR (4)	20 APR - 23 APR (4)	19 MAY - 22 MAY (4)
8B	2 APR - 5 APR (4)	28 APR - 5 MAY (5)	20 MAY - 26 MAY (4)
9A	31 MAR - 5 APR (6)	5 MAY - 16 MAY (6)	
9B	23 MAR - 28 MAR (4)	28 APR - 4 MAY (5)	
10A	26 FEB - 9 MAR (9)	13 APR - 18 APR (4)	19 MAY - 22 MAY (4)
10B	12 MAR - 18 MAR (6)	21 APR - 28 APR (4)	25 MAY - 28 MAY (4)

[a]Site 1A was also trapped in Cycle 4, 22 JUN - 24 JUN (3)

Table 1.3. Number of days each site was trapped in 1992 - 1994, with number of successful trapping occasions (days when > 0 TGS were captured) in parentheses.

Site	1992	1993	1994
1A	20 (18)	10 (3)	5 (0)
1B	19 (18)	9 (1)	5 (1)
2A	11 (4)	7 (2)	5 (0)
2B	12 (11)	14 (8)	6 (0)
3A	11 (7)	11 (1)	19 (8)
3B	19 (18)	14 (12)	18 (13)
4A	17 (17)	21 (19)	20 (18)
4B	18 (18)	20 (16)	21 (17)
5A	21 (21)	19 (18)	20 (17)
5B	20 (20)	19 (19)	23 (21)
6A	12 (6)	13 (2)	7 (0)
6B	19 (19)	16 (12)	20 (14)
7A	16 (16)	22 (21)	23 (21)
7B	18 (17)	21 (12)	19 (11)
8A	19 (18)	20 (20)	25 (25)
8B	18 (17)	21 (19)	20 (6)
9A	20 (20)	16 (16)	19 (16)
9B	19 (19)	17 (16)	21 (16)
10A	18 (17)	17 (16)	24 (22)
10B	19 (19)	17 (16)	26 (24)

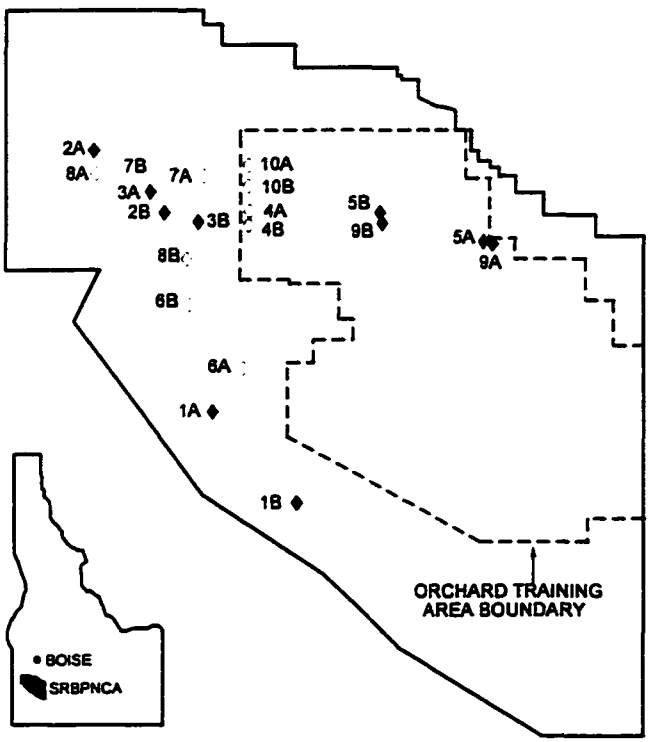

Figure 1.1. Location of study sites within the Snake River Birds of Prey National Conservation Area (SRBPNCA) in southwestern Idaho (only a portion of the SRBPNCA is shown). Closed diamonds are shrub sites and open diamonds are non-shrub sites. Labels indicate site pairs, with habitat descriptions given in Table 1.1. Sites 3A and 3B depicted on this map are the sites used in 1992-1994. Scale is 1:300,000. (Modified from Van Horne et al. 1992).

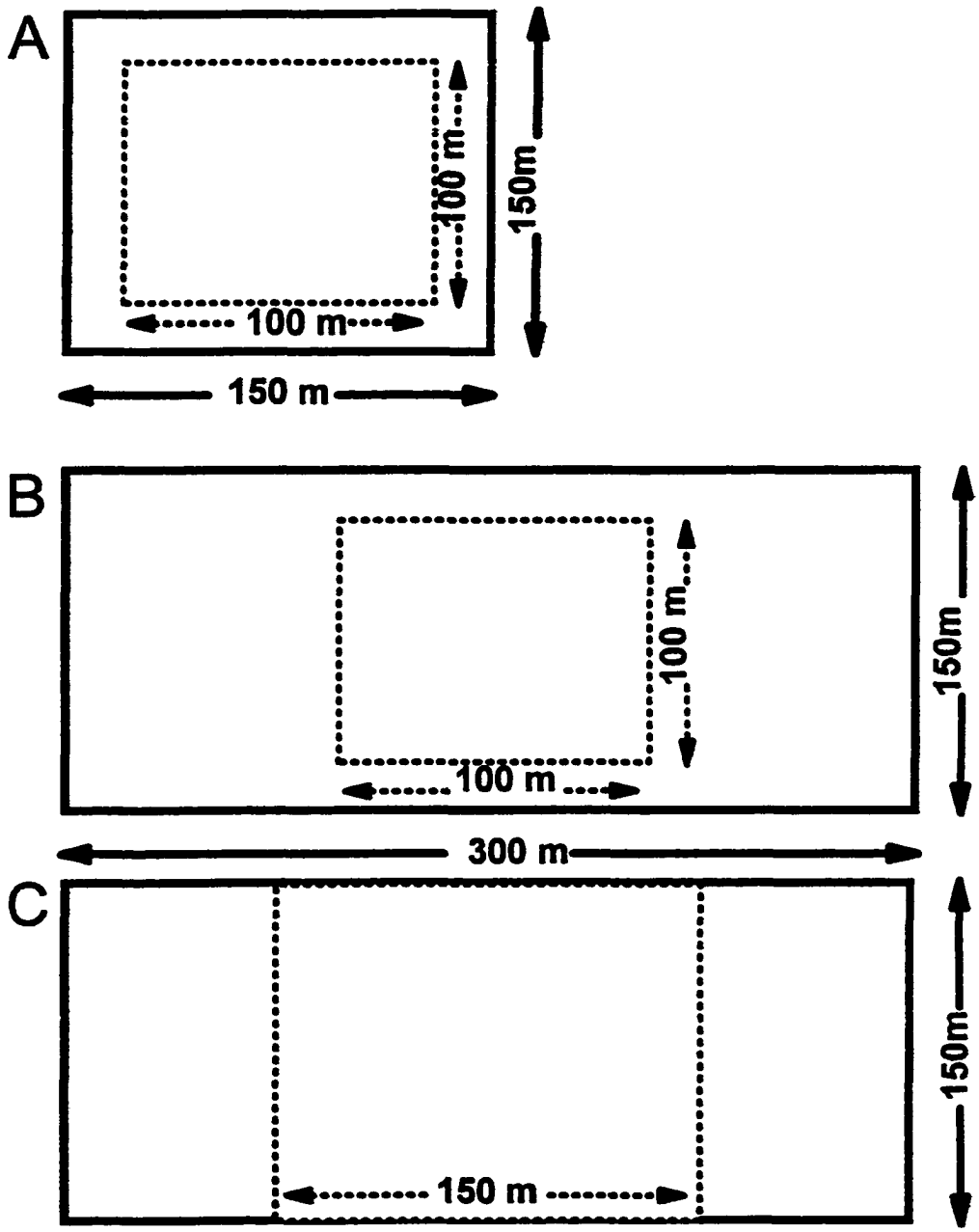

Figure 1.2. Diagram of trapping grid areas used for live-trapping Townsend's ground squirrels on study sites in 1992. Solid lines are the boundaries of grid areas used prior to emergence of juveniles, and dashed lines are the boundaries used after emergence of juveniles. A shows the grid configuration for sites 4A, 4B, 7A, 7B, 8A, 8B, and 10A; the area within the solid lines is 2.25 ha and the area within dashed lines is 1.00 ha. B shows the grid configuration for site 10B; the area within the solid lines is 4.50 ha, and the area within the dashed line is 1.00 ha. C shows the grid configuration for sites 5A, 5B, 6B, and 9B; the area within the solid lines is 4.50 ha and the area within the dashed lines is 2.25 ha. Not shown is the 9.00 ha area trapping grid used for sites 1A, 1B, 2A, 2B, 3A, 3B, and 6A, which were not reduced in size after emergence of juveniles.

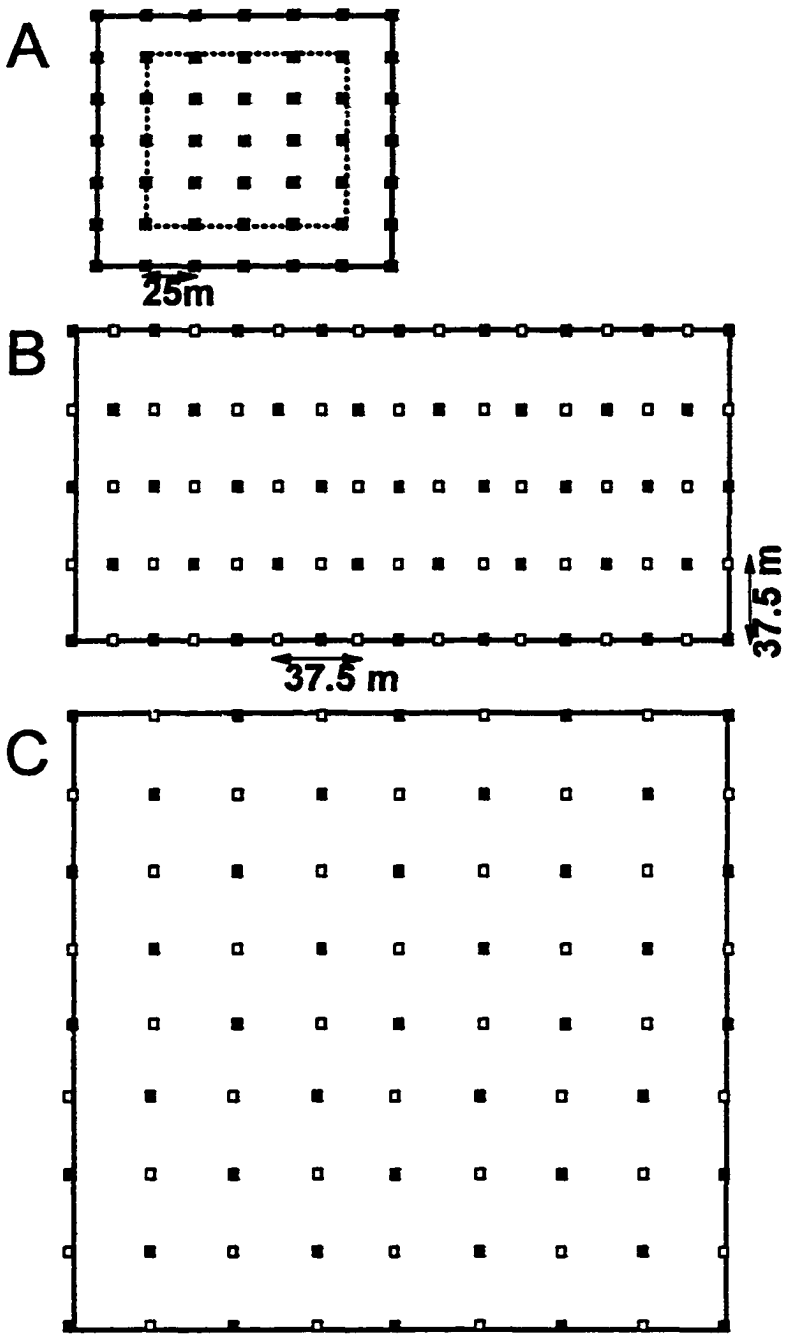

Figure 1.3. Diagram of trap locations within grids used for live-trapping Townsend's ground squirrels on study sites in 1992. Solid boxes depict the original trap placement pattern, and open boxes depict the alternate trap placement pattern, if any. A shows the trap locations for trapping grids that were 2.25 ha (area within solid lines) and 1.00 ha (area within dashed lines). B shows the location of traps for grids that were 4.50 ha, and C shows the location of traps for grids that were 9.00 ha.

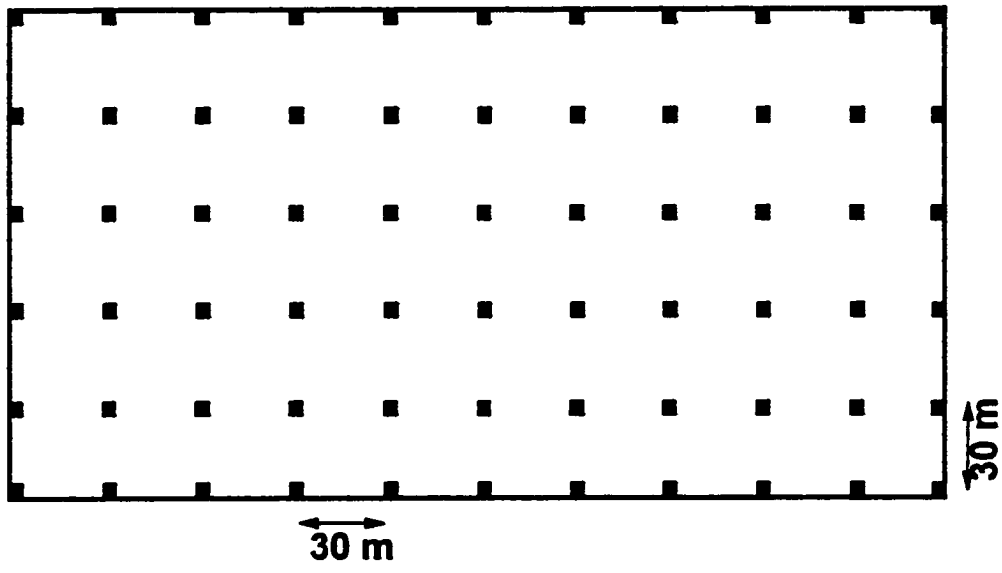

Figure 1.4. Diagram of trap locations within trapping grids used for live-trapping Townsend's ground squirrels on all study sites in 1993 and 1994. The area within the solid lines is 4.50 ha.

CHAPTER TWO

ABUNDANCE AND DENSITY ESTIMATION

Population size, or abundance, was one of the key attributes of interest in the TGS demography study. In all years, capture-recapture data were used to estimate abundance. In 1991, population closure (i.e., no losses or gains to the population) between capture occasions within a trapping cycle could reasonably be assumed and therefore the methods of Otis et al. (1978) were used to estimate abundance (Van Horne et al. 1997). In 1992-1994, the intervals between successive capture occasions was sufficiently large that population closure could no longer be assumed as losses from deaths, especially, were likely to have occurred. Therefore, it was necessary to use an abundance estimation method suitable for open populations.

For many years, open population abundance estimation required the use of the general Jolly-Seber model (Jolly 1965, Seber 1965, Pollock et al. 1990). This model contains $5k$-3 inter-related parameters (Table 2.1), where k is the number of capture occasions. Although not all of these parameters must be estimated from the data directly (some can be computed once estimates for the others have been calculated), in many cases the number of animals in the population under study is insufficient to compute realistic and precise estimates. This was the case for the TGS study, particularly after a

severe drought in 1992 substantially reduced population numbers in 1993 and 1994 (Van Horne et al. 1997).

To improve estimates of abundance for the TGS study, I eliminated some parameters by using the no recruitment special case of the Jolly-Seber model (called the death only model by Pollock et al. 1990) and combined it with parameter modeling techniques as have been used for survival rate estimation (cf. Lebreton et al. 1992, Schwarz and Arnason 1996). Although the no recruitment model was first described over 30 years ago (Jolly 1965), it has received little attention in general, and only recently has anyone considered combining the use of the no recruitment model with parameter modeling techniques to estimate abundance (Schwarz and Arnason 1996).

METHODS

The no recruitment model

As its name implies, under the no recruitment model the assumption is made that no animals are added to the population, i.e., that only death, or permanent emigration occurs. Because it is a special case of the Jolly-Seber model, the assumptions of that model also apply to the no recruitment model (from Pollock et al. 1990): 1) every animal present in the population at the time of the sample has the same probability of capture, 2) every animal present has the same probability of survival, 3) that marks are not lost or overlooked, and 4) all samples are instantaneous and each release is made immediately following the sample.

The fully specified no recruitment model has $3k$-1 inter-related parameters (Table 2.1). Of these, $2k$-1 are separately estimable, a reduction of k-2 parameters over the

general Jolly-Seber model. Because of the no recruitment assumption, the k-1 recruitment parameters (B_i) are all = 0. The k population size parameters (N_i) are thus reduced to functions of N_1, the population size at time 1, and the k-1 survival probabilities (ϕ_i). For example, if an estimate of the population size at time 3 is desired, it may be obtained by multiplying $\hat{N}_1$ by the survival probabilities $\hat{\phi}_1$ and $\hat{\phi}_2$. Generally the number of marked animals, M_i, are not of interest and can be ignored as their expected values are functions of the known number of animals marked at each occasion and the survival probabilities. This leaves N_1, k-2 survival probabilities (ϕ_i), k-1 capture probabilities (p_i), and the combination parameter ($\phi_{k-1}p_k$) as the $2k$-1 parameters to be estimated.

The number of model parameters can be further reduced by specifying constraints on the capture and survival probabilities, using modeling techniques such as described by Lebreton et al. (1992). Such modeling also allows the relaxation of the homogeneity assumptions regarding survival and capture probabilities (listed as assumptions 1 and 2 of the Jolly-Seber model, above). As has been advocated for survival rate analyses (cf. Lebreton et al. 1992, Burnham and Anderson 1992, Schwarz and Arnason 1996), several a priori considered models are tried for each dataset to be analyzed with the best model selected according to some standardized criteria.

Once a model is selected, the population size at the time of the 1st trapping occasion, N_1, is estimated as:

$$\hat{N}_1 = \frac{M_{t+1}}{\hat{p}_1 + (1-\hat{p}_1)\hat{\lambda}_1} = \frac{M_{t+1}}{\hat{\lambda}_0}$$

where: M_{t+1} is the total number of animals ever marked,

$\hat{p}_1$ is the estimated capture probability for the first trapping occasion,

$\hat{\lambda}_1$ is the estimated probability of recapture after the first occasion, given that the animal was marked and released on the first occasion, and

$\hat{\lambda}_0$ is the estimated probability of ever being caught, given that the animal was present in the population when trapping was initiated.

The approximate theoretical variance of $\hat{N}_1$ is :

$$\mathrm{Var}(\hat{N}_1) = N_1^2 \left[\frac{\mathrm{Var}(M_{t+1})}{(N_1\lambda_0)^2} + \frac{\mathrm{Var}(\hat{\lambda}_0)}{\lambda_0^2} \right]$$

where:

$$\mathrm{Var}(M_{t+1}) = N_1\lambda_0(1-\lambda_0) \quad ,$$

and:

$$\mathrm{Var}(\hat{\lambda}_0) = \left(\frac{\partial\lambda_0}{\partial\theta} \right)' \mathrm{Var}(\hat{\theta}) \left(\frac{\partial\lambda_0}{\partial\theta} \right),$$

where: $\hat{\theta}$ is the vector of model-specific parameter estimates and $\mathrm{Var}(\hat{\theta})$ is their variance-covariance matrix. (The above formulae are based on results from Burnham 1997 in which he derives the explicit probability distribution for the no recruitment special case of the Jolly-Seber model).

A 95% CI for N_1 (assuming a log-normal distribution for $\hat{N}_1 - M_{t+1}$; Chao 1989) is:

$$\left(M_{t+1} + \frac{(\hat{N}_1 - M_{t+1})}{C} \; , \; M_{t+1} + (\hat{N}_1 - M_{t+1})C \right),$$

where:

$$C = e^{1.96\sqrt{\ln(1+CV(\hat{N}_1)^2)}}, \qquad \text{and} \qquad CV(\hat{N}_1) = \frac{SE(\hat{N}_1)}{\hat{N}_1 - M_{t+1}}.$$

Use of the no recruitment model also allows for combining of data from multiple study sites, which is especially useful when capture numbers are small. In this case, the above formulae are also appropriate, using the number of animals marked at each site (M_{t+1}) and the site-specific $\hat{\lambda}_0$. The M_{t+1} are assumed to be independent among sites, but estimation of the $\hat{\lambda}_0$ from data combined over multiple sites induces a covariance among the site-specific $\hat{N}_1$, the magnitude of which depends on the number of shared (non-site specific) parameters in the model. This covariance between any pair of i, j sites is estimated as:

$$Cov(\hat{N}_{1i}, \hat{N}_{1j}) = \hat{N}_{1i}\hat{N}_{1j}\left[\frac{Cov(\hat{\lambda}_{0i}, \hat{\lambda}_{0j})}{\lambda_{0i}\lambda_{0j}}\right], \text{ where}$$

$$Cov(\hat{\lambda}_{0i}, \hat{\lambda}_{0j}) = \left(\frac{\partial\lambda_{0i}}{\partial\theta}\right)' Var(\hat{\theta})\left(\frac{\partial\lambda_{0j}}{\partial\theta}\right).$$

The no recruitment model appeared to be a good choice for use in estimating TGS abundance as there are identifiable periods of the TGS active season during which the no recruitment assumption may be satisfied. For adults, this period begins with emergence from hibernation burrows and may last until immergence. Events such as a major spring drought may cause late-season dispersal by adults (unpublished data), but dispersal by adults in general is though to be rare. Juveniles are readily distinguishable from adults

until after the time most adults have begun estivation and thus would not be mistakenly considered as recruited into the adult segment of the population.

For juveniles, the period during which the no recruitment assumption may be satisfied is much shorter: from emergence from natal burrows until the initiation of dispersal. Natal dispersal by ground squirrels may be substantial (Holekamp 1984). In a radio-telemetry study of juvenile dispersal patterns (Chapter 4) I found that 58% of juvenile male Townsend's ground squirrels radio-collared in 1993 and 1994 dispersed. The earliest date of dispersal in either year was 15 April, but most dispersal (75%) took place after 1 May. Therefore, there is a short, and variable, time period during which the no recruitment assumption may be considered satisfied for juveniles.

Abundance estimation

For the TGS demography study, age-specific (juvenile or adult) estimates of abundance for each trapping site within year were needed to satisfy study objectives. For adults, sex-specific estimates were also desired. Whenever possible, capture datasets were analyzed separately for each year, site, sex (for adults), and age-class. However, small sample sizes sometimes made it necessary to combine data across groups to obtain reasonable estimates of abundance. I first combined data from both sexes within a study site, but when this was not successful, I combined data over multiple sites for a single sex. The selection of sites to combine was based on geographical proximity and habitat similarity.

For both age groups, it was necessary to determine a date after which the no recruitment assumption was likely to have been violated, and use only capture data

collected prior to that truncation date. In 1992, reduction of the trapping grid area after emergence of juveniles on some sites made it necessary to confine the data used for estimating adult abundance to the period from the initiation of trapping until grid reduction. For sites where grids were not reduced, the first date of juvenile emergence was used as the truncation date for data used in adult abundance estimates. These truncation dates also eliminated any late-season adult immigrants due to the 1992 drought. Datasets for adults in 1993 and 1994 were truncated at 1 May to remove complications of modeling capture and survival probabilities during the period of immergence into hibernation.

For juveniles, I aimed to truncate datasets at a point before most dispersal had occurred. The structure of the sampling design did not allow detection of immigration onto each site and therefore determination of an appropriate site-specific truncation date. Overly conservative truncation dates would have resulted in too few numbers of individuals and capture occasions to compute estimates on some sites. Based on radio-telemetry data collected on 4 study sites (2 shrub sites and 2 non-shrub sites) in 1993 and 1994 (Chapter 4), I chose 1 May as the truncation date for juvenile datasets for all sites in 1992, and for non-shrub sites in 1993 and 1994, and 10 May and 5 May, respectively, as truncation dates for shrub sites in 1993 and 1994.

Since my primary objective was to estimate abundance ($\hat{N}_1$), I considered survival and capture probabilities to be nuisance parameters. That is, I was not interested in the estimates of these parameters, nor in testing hypotheses about them (except see Chapter 3). Therefore, I tried to reduce the number of these nuisance parameters by employing

models with a few simple constraints on capture and survival probabilities. I modeled survival probabilities using a log-link function (Table 2.2), thereby accounting for varying time intervals between capture occasions by modeling daily survival. Per-day survival probabilities were then modeled as either constant throughout the entire trapping season, or as a linear function of the number of days elapsed since the start of the trapping season (i.e., either declining or increasing per-day survival rates). I modeled capture probabilities using a logit-link function (Table 2.2), which constrains those probabilities to be between 0 and 1. Capture probabilities were constrained to be either: 1) constant for all capture occasions, 2) a linear function of days elapsed, 3) a quadratic function of days elapsed, or 4) time-specific. For analyses where I combined data from >1 sites, I included a site effect in the candidate models for both survival and capture probabilities, allowing several additional constraints that included site-specific terms and interactions between site and time. Time-specific models for capture probabilities were not examined when data from different sites were combined. Table 2.2 shows a complete list and description of the candidate models.

Model selection

Selection of the best model for abundance estimation from among the candidate models was primarily based on the models' Akaike's Information Criterion (AIC; Akaike 1973, 1985) value. The use of AIC and other information theoretic criteria in model selection has received much attention recently (Anderson et al. 1994, Burnham et al. 1995, Burnham and Anderson 1998). In this approach, the model with the lowest AIC value is selected from among the many candidate models as the most appropriate, given

the data. Often, lowest AIC identified a clear choice of a best model, but at times there were several models with very similar AIC values (i.e., ≤ 2 units apart). When this occurred I compared the parameter estimates from those models. If some resulted in parameter estimates that were unrealistic (for example, if survival estimates were >>1) or were not biologically credible, such as when population estimates were less than the total number of animals that were captured, these models were rejected in favor of those with more realistic results. When parameter estimates were reasonable, and abundance estimates were similar among models, I chose the one that had the best precision on the abundance estimates. If abundance estimates were very different among models with similar AIC values, model averaging (Buckland et al. 1997, Stanley and Burnham 1998) was used. In this approach I weighted estimates of $\hat{N}_1$ from all models within 2 units of the model with the lowest AIC based on their AIC values, and computed a weighted average estimate of abundance as:

$$\hat{N}_w = \sum_{j=1}^{n} w_j \hat{N}_j \ ,$$

where: $\hat{N}_j$ is the estimate of abundance from model j. The weights (w_j) were computed as:

$$w_j = \frac{e^{-\frac{1}{2}\Delta AIC_j}}{\sum_{j=1}^{n} e^{-\frac{1}{2}\Delta AIC_j}},$$

where $\Delta AIC_j = AIC_j - AIC_{min}$, AIC_j is the AIC from model j, and AIC_{min} is the smallest computed AIC from among the n models. The variance of $\hat{N}_w$ was estimated as:

$$\hat{Var}(\hat{N}_w) = \left\{ \sum_{j=1}^{n} w_j \sqrt{\hat{Var}(\hat{N}_j) + \hat{\beta}_j^2} \right\}^2$$

where:

$$\hat{\beta}_j = \hat{N}_j - \hat{N}_w.$$

Finally, for datasets where all models with lowest AIC values had biologically unreasonable results, I looked for possible violations of model assumptions, especially the no recruitment assumption, and sought explanations for why violations may have occurred.

Computer programs

When I conducted these analyses, no computer software package was available for estimation of abundance for the no recruitment model that allows for datasets to be combined across groups with differing number of trapping occasions and varying time intervals between occasions. Program MARK can now compute estimates of abundance for this model, and allows for combining data among groups, but does not readily handle asynchrony in capture occasions (G.C. White, personal communication). Program JOLLY (Pollock et al. 1990) computes single group estimates only for the no recruitment model where survival and capture probabilities are time-specific, that is, the ϕ_t and p_t are all estimated. POPAN-4 (Arnason and Schwarz 1995) can provide single group estimates under the no recruitment model, and also allows modeling of capture and

survival probabilities. Other computer programs, such as SURGE (Pradel and Lebreton 1991) and SURVIV (White 1983, 1986), allow modeling of survival and recapture probabilities and combining data across groups when trapping occasions coincide, but do not compute estimates of abundance.

I therefore wrote a series of SAS® Macro Language (SAS Institute Inc. 1990a) modules that enabled me to format capture-recapture data for input into a SAS® Proc NLIN (SAS Institute Inc. 1989) program to compute maximum likelihood estimates for survival and capture probabilities under the no recruitment model. This program was modified from one previously described by Burnham (1989) for population estimation for the general Jolly-Seber model to allow for additional constraints to be placed on the capture and survival parameters of the no recruitment model. For site-specific estimates, capture history matrices for animals within site were summarized into minimum sufficient statistics that were concatenated prior to entry in the Proc NLIN program. Model parameter estimates were then passed through a series of SAS steps, including SAS/IML® (SAS Institute 1990b), to calculate $\hat{N}_1$ and associated statistics (standard error, CV, etc.) and to compute the model deviance (used to calculate AIC by adding 2 times the number of parameters in the model).

Density and area estimation

Differences in trapping grid areas within and among years meant that conversion of abundance estimates to density was necessary before comparisons could be made among the groups for which abundance was estimated. Therefore, some estimate of the effective area trapped was required. It has long been known that animals are generally

drawn to traps from an area that exceeds that within the physical boundaries of the trapping grid (Dice 1938). Consequently, use of that area (sometimes called the naive grid area) is inappropriate, and it is necessary to add to the naive grid area the area of an additional strip of width *w*, (presumably the distance from which animals may travel to traps) to compute an effective trapping grid area.

To date, the methodology for estimating this additional strip area has been somewhat inconsistent, and largely untested. A common method in small mammal trapping is the use of assessment lines (cf. Swift and Steinhorst 1976, Van Horne 1982). Assessment lines were employed in the TGS study in 1991-93, but in 1993 there were too few captures of animals on assessment lines for area estimates to be computed, and in 1994, assessment lines were not used at all. Therefore, to use a consistent methodology for area estimation in all years, I used a movement based estimator known as Mean Maximum Distance Moved (MMDM; Wilson and Anderson 1985), in which *w* is estimated as one half the mean of the maximum distance moved within the trapping grid for individuals captured >1 times. This method was also used by Johnson et al. (1987) to adjust TGS densities as estimated by Smith and Johnson (1985).

Movement distances may be affected by many factors, including sex and age of the animal, habitat, and trapping grid configuration. There is also a tendency for the maximum movement distance recorded to increase as the number of captures increase. Therefore, I first investigated whether this relationship was true for the TGS study by examining plots of the maximum distance moved vs. number of captures, to see if there was an appropriate cut-off point whereby distance no longer increased with increasing

captures. I then used Analysis of Variance (ANOVA) to test for factors that may have affected movement distances. Finally, I computed the MMDM for each factor identified as significant in the ANOVA. For the ANOVAs and estimation of *w* values, I used the same capture data used to compute abundance estimates, employing the same temporal truncation points, if any.

The estimated strip width, $\hat{w}$, was computed as MMDM/2, with $SE(\hat{w})$ = SE(MMDM)/2. The adjusted grid area (in ha) was estimated as:

$$\hat{A} = \frac{(L+2\hat{w})(W+2\hat{w})-(4-\pi)\hat{w}^2}{10{,}000},$$

where L and W are the length and width (in meters), respectively, of the trapping grid boundaries. The standard error of the adjusted grid area was computed as:

$$\hat{SE}(\hat{A}) = \frac{2(L+W)+2\pi\hat{w}}{10{,}000}\,\hat{SE}(\hat{w}).$$

Density was estimated in the usual way: $\hat{D} = \frac{\hat{N}_1}{\hat{A}}$, with standard errors of density estimates computed based on the relationship:

$$\hat{CV}(\hat{D})^2 = \hat{CV}(\hat{N}_1)^2 + \hat{CV}(\hat{A})^2 + [\hat{CV}(\hat{N}_1)^2 \hat{CV}(\hat{A})^2],$$

where CV is the coefficient of variation. Prior to hypothesis testing, site-specific density estimates for adult males and females were summed for a single site-specific estimate of

density for adults. Standard errors of the total adult density estimates were computed simply as the square root of the sum of the sex-specific variances, since the sex-specific estimates were independent of each other.

In some cases, especially in 1993 and 1994, numbers of captures were too few (or nonexistent) to estimate abundance. Exclusion of these sites from hypothesis tests would have biased the results. Therefore, I chose to use the number of distinct animals captured (sometimes known as the Minimum Number Alive or MNA) as an estimate of abundance on these sites. When no animals were captured, I used 0.0 as the estimated abundance. I then computed density for these sites as given above.

A problem with using MNA is that the sampling variance associated with it is unknown, and probably not estimable. However, I had to provide some estimate of sample variances to construct the density variance-covariance matrix used in hypothesis testing. Therefore, I constructed ad hoc sampling standard errors for density based on the average proportion: $\frac{\mathrm{CV}(\hat{A})}{\mathrm{CV}(\hat{D})}$ from sites where numbers of captures were ≤ 5, yet abundance estimates (and their standard errors) were calculable. I then back-calculated $\mathrm{CV}(\hat{D})$ for sites where I used MNA as the estimate of abundance using these average proportions (separately calculated for each year and age class, and sex-specific for adults) and the estimated $\mathrm{CV}(\hat{A})$. Standard errors were then computed in the usual fashion except when the density estimate was 0.0. Then I used 0.1 as the density estimate for the purpose of computing standard errors only.

Hypothesis testing

The main hypotheses of interest for the TGS study relative to population density were whether site-specific differences in adult densities could be attributed to habitat type (shrub or grass), or location (OTA or off-OTA). In addition, study year was considered a relevant factor. (Although juvenile densities were computed, the main hypotheses of interest for juveniles were regarding production, computed as juveniles per reproductive female. The analyses I conducted on production are reported in Chapter 5). In the main analysis, the supplemental feeding treatment was not of interest, but since including data from the supplementally fed sites would have confound the results, I did not use data from sites 7A and 8A in any years.

By pooling data from >1 site (as was done for all area estimates and some abundance estimates), I induced correlation between the site-specific estimates, and therefore they were not independent. This violates a major assumption of most statistical tests. Whenever possible, I tried to minimize the correlation between sites, but the effect the induced correlations would have on hypothesis tests that assume independence was unknown. Therefore, I used SAS/STAT® PROC MIXED (SAS Institute Inc. 1992) to test the main hypotheses of interest. This procedure allowed me to specify the estimated sampling variance-covariance matrix associated with the site-specific estimates. This had the added benefit of removing the sampling variance component from the residual variance (normally denoted as σ^2).

The general mixed model can be specified as: $y = X\beta + Zv + \epsilon$ with variance of y: $V = ZGZ' + R$ (SAS Institute Inc. 1992). In the density analyses, y was the vector of site-

specific density estimates, X the design matrix of fixed effects (habitat, year, location, and interactions among them), β the vector of unknown fixed-effect parameters, Z the design matrix for random effects (see below), υ the unknown random error vector, G the sampling variance-covariance matrix corresponding to the site-specific density estimates, and R the residual variance matrix which was assumed to be = $\sigma^2 I$, where I is the identity matrix. To use the site-specific variance-covariance matrix for G, it was necessary to specify site (within habitat type and location) as a random effect. Since site was also the unit of replication, this resulted in a fully saturated model, yet still allowed for testing of the fixed effects.

Because using PROC MIXED was difficult and time-consuming, I also compared the results from this procedure to those from a repeated measures analysis of variance (using PROC GLM: SAS Institute Inc. 1989) to determine if similar results would be obtained if the correlations and sampling variances were ignored.

RESULTS

Abundance estimation

A total of 4,056 ground squirrels were captured on all sites in 819 capture occasions during 1992-1994. The mean number of individuals captured per site within a year was 13.6 (range: 0-69) for adults (sexes separate) and 21.4 (range: 0-122) for juveniles (sexes combined).

Estimates of TGS abundance and their 95% CI's are given in Tables 2.3 (adults) and 2.4 (juveniles), along with the number of animals captured, information on pooling

(if applicable) and the model(s) selected to estimate abundance. For adults, I was able to compute no recruitment model estimates for 87 of 120 potential cases (3 years × 20 sites × 2 sexes). Of the remaining 33 cases, 18 had 0 captures. There were 13 cases with 1-4 captures but no recaptures. For 2 cases (site 3B, adult females in 1992 and site 8A, adult females in 1993), there was a clear violation of the no recruitment assumption, for logical reasons. Site 3B was 1 of 2 sites (site 3A being the other) where grid sizes were expanded 3-4 weeks after trapping began in 1992 because captures of individuals within the original grid area were few. Thus new individuals were exposed to traps, and thereby recruited into the population being estimated. (Only 1 adult ground squirrel of either sex was trapped on Site 3A). Site 8A was 1 of 2 sites (site 7A being the other), where supplemental food was provided as an experimental treatment in 1993 and 1994. Thus it is not surprising the no recruitment assumption may have been violated there as female ground squirrels outside the trapping area took advantage of the increase in food resources. However, no apparent failure of assumptions was noted for either adult males or for adult females on site 7A in 1993 or for any age or sex class on these sites in 1994.

Estimates of juvenile abundance were computed for 36 of 60 potential datasets (3 years × 20 sites). In 16 cases, there were 0 captures, and in 7 cases there were 1-3 individuals captured but no recaptures. In 1 case there may have been a failure of the no recruitment assumption, on site 9B in 1993, where there were 23 individuals captured. This may have occurred if there were a large number of early immigrants onto that site.

In 61 cases (40 adult, 21 juvenile; or 50% of the cases for which I could compute estimates using the no recruitment model) it was possible to estimate abundance without

combining data from >1 site. When a single best model could be determined (see below), I found the number of parameters was often related to the number of animals captured; i.e., the more individuals caught, the more parameters in the model. Also, model selection favored models with more structure (i.e., more parameters) in the capture probabilities than the survival probabilities. For adults, in all but 5 cases I selected models with constant per-day survival probabilities, whereas capture probabilities were nearly evenly distributed between constant, linear on time, quadratic on time, and time-specific models.

For juveniles, models with constant per-day survival were always selected in 1993 and 1994 (when numbers of captures were small), but only half the time in 1992, with the remaining models favoring survival probabilities linear through time. Models for capture probabilities were quite variable, with the most frequently selected structure (in 10 cases) being linear through time. Time-specific models were selected 5 times, constant probabilities selected 3 times, and quadratic through time selected twice. In 3 cases (sites 7B and 8B in 1992 and site 7A in 1994), sex-specific models were an improvement over the sexes-combined model. Therefore, sex-specific estimates were summed to give overall juvenile abundance estimates for these sites.

For 62 cases, it was necessary to combine data over multiple sites. Although I first examined models where data from both sexes were combined within a site, I found that for adults, those models were never better than models where data from one sex were combined with data from the same sex on a different site. For the sites-combined models, survival probabilities were selected as site-specific in only 1 case, but capture

probabilities included site-specific parameters 8 times. In all cases, models tended to have simpler structure (constant per-day survival and either constant or linear capture probabilities) than the single-site models, but this was most likely due to the small sample sizes which made combining sites necessary to begin with.

In 19 total cases I was unable to select a single best model and therefore used the model averaging approach. Only models ≤ 2 units of the lowest AIC were used in these analyses because the weights for other values were so small that they figured insignificantly in the results.

In general, population estimates ranged from 1.0 - 4.0 times the number of animals captured on each site. Coefficients of variation (CV: a relative indicator of precision) for these estimates ranged from 5.1 - 105.0%, with a median of 25.2%.

Density and area estimation

Examination of plots of maximum distance moved vs. number of captures confirmed a positive relationship between the two, but there was no obvious point at which the movement distances leveled off. I decided that using MMDM for all animals with >1 captures would be more reasonable than limiting the data to those from animals with large numbers of captures, because the latter would reduce sample sizes considerably. Using the mean distance moved, uncorrected for number of captures, may have resulted in an underestimate of MMDM, but this potential bias was at least partially offset by limiting the estimate to animals that were captured in at least 2 separate traps, thus eliminating all recorded maximum distances of 0 m.

Grid configuration (a combination of size and spacing) did have an effect on the

mean maximum distance moved in 1992 ($F_{2,363} = 61.39$, $P \leq 0.001$), and the pattern of this effect differed by age ($F_{2,363} = 7.49$, $P \leq 0.001$). This was especially true for juveniles, for which the smallest trapped grid areas were 1.0 ha. MMDM calculated for juveniles was considerably lower on the smallest grids (1.00 ha: $\bar{x} = 29.2$, SE = 1.5, n = 148) than on larger sized grids (2.25 ha: $\bar{x} = 51.5$, SE = 5.0, n = 44; 9.00 ha: $\bar{x} = 88.2$, SE = 16.2, n = 11). For adults (for which larger grid areas were trapped, in general, prior to shrinkage), there were much greater movements recorded on the largest grids (9.00 ha: $\bar{x} = 120.1$, SE = 21.5, n = 11), but little difference between the smaller grids (2.25 ha: $\bar{x} = 40.5$, SE = 2.3, n = 107; 4.50 ha: $\bar{x} = 39.4$, SE = 3.7, n = 53). However, since the sample size for the 9.00 ha grids was small, inclusion of these data had relatively little effect on the MMDM estimate. It appeared, then, that recorded movements of juveniles from the 1.00 ha sites were biased low, and so I excluded data from the 1.00 ha sites from subsequent analyses of MMDM.

For each year, I also examined the possible effect of the major habitat/treatment combinations (OTA grass, OTA shrub, off OTA grass, off OTA shrub and, in 1993 and 1994, supplemental feeding sites) on MMDM, and found they were not significant (92: $F_{3,363} = 0.56$, $P = 0.642$; 93: $F_{4,280} = 0.83$, $P = 0.506$; 94: $F_{4,164} = 1.14$, $P = 0.337$).

I combined the data from 1992 - 1994 and tested for year, age, and sex effects (including interactions), and found that the age × year interaction to be significant ($F_{2,634} = 5.07$, $P = 0.006$) and the age × sex × year interaction to be nearly so ($F_{4,634} = 2.17$, $P = 0.071$). Therefore, I ran separate ANOVAs for each age group. For adults, there was a significant year and sex interaction ($F_{2,502} = 4.25$, $P = 0.015$), but for juveniles there

were no differences in movement distances attributable to sex ($F_{1,132} = 1.34$, $P = 0.250$), year ($F_{2,132} = 0.58$, $P = 0.564$), or their interaction ($F_{2,132} = 0.30$, $P = 0.739$). Therefore, I computed year- and sex-specific strip widths for adults, but calculated a single w for juveniles for all years. Estimates of w, A, and density, and their standard errors, are given in Tables 2.5 (adults) and 2.6 (juveniles).

Hypothesis tests

The results of the PROC MIXED analysis of the effects of habitat, location, and year on adult TGS density estimates, and the corresponding repeated measures analysis using PROC GLM is given in Table 2.7. Both analyses had similar test results, and nearly identical P-values, except for the 3-way interaction, which had $P < 0.05$ in the GLM analysis, but not in the MIXED analysis. Otherwise, all factors were highly significant except for the location × habitat interaction. Mean densities were consistently highest in 1992 (pre-drought) and declined in each of the years following, but those declines were greater for sites within the OTA (Figure 2.1), and in the grass habitat (Figure 2.2).

DISCUSSION

Abundance estimation methodology

The no recruitment model worked well for the ground squirrel problem, where time periods could be identified for which this key assumption could be met. When this assumption was clearly violated, models either did not converge or gave unrealistic results. More formal goodness-of-fit (GOF) tests for the no recruitment model are possible, but somewhat complex to compute. For each selected model, the test consists

of the sum of χ^2 GOF components for the general Jolly-Seber model and the general no recruitment model (see Stanley and Burnham in press), plus an additional χ^2 component for the constrained model vs. the unconstrained no recruitment model. In the ground squirrel example, the data were often too sparse for results from these tests to be useful, and constructing GOF tests for each of the 126 models where estimates were computed were beyond the scope of this study. A χ^2 test for the no recruitment model over the general Jolly-Seber model has been known for some time (Pollock et al. 1974, and see also Stanley and Burnham in press), but when I attempted to apply this test to the ground squirrel data, I found the results to be of doubtful validity when used on small samples.

Among the general Jolly-Seber model assumptions, it was difficult to assess whether the homogeneity assumptions (1 and 2) were met, but assumptions 3 and 4 were met by the field methodology employed (see Chapter 1). Potential violations of homogeneity assumptions were at least partially avoided by analyzing data separately by age and sex classes. In their review of the effects of heterogeneity on Jolly-Seber estimators of population size, Hwang and Chao (1995) listed 2 conclusions: 1) that biases due to heterogeneity in capture probabilities are generally negative, and are dependent on the average capture probability and the CV of the capture probability distribution; 2) that heterogeneity in capture probabilities is largely unimportant when capture probabilities are high (> 0.5). Although I did not actually compute estimates of capture probabilities when analyzing the ground squirrel data, the proportion of animals captured (based on the number of animals marked, M_{t+1}, divided by the estimated population size ($\hat{N}_1$) was almost always >0.5 for adults, and usually >0.5 for juveniles. However, since most of the

variability in $\hat{N}_1$ is due to variability in capture probabilities, the relatively large standard errors estimated for $\hat{N}_1$ may indicate that capture probabilities are indeed heterogeneous among individuals. Therefore, point estimates of $\hat{N}_1$ are possibly negatively biased, but these biases should be minimal because of the relatively high capture probabilities. The use of parameter modeling, model selection, and model averaging should also reduce the potential for biased results due to heterogeneity in both survival and capture probabilities.

Because of the large number of estimates required, and somewhat high variability in capture-recapture design, the TGS example illustrates many important aspects of the use of the no recruitment case with the use of parameter modeling. Most importantly, I was able to use these methods to estimate population abundance for open populations even when few animals were captured. Often, in small mammal studies in particular, researchers that have been unable to compute Jolly-Seber estimates of abundance have resorted to using the number of animals captured (MNA) as the population estimate, although the problems with MNA have been pointed out by numerous authors (cf. Hilborn et al. 1976, Jolly and Dickson 1983, Pollock et al. 1990, Efford 1992). Modeling capture and survival probabilities, and combining data across sites to improve sample sizes, is one viable alternative to the often impractical full Jolly-Seber model methods. Although population estimates were often similar to the MNA when few individuals were captured, the methodology I used had the advantage of providing measures of the uncertainty of the estimates. While I used MNA in some cases, the frequency of usage of this usually biased estimator was much reduced, and I was able to provide some estimate of its sampling error, albeit an ad hoc one.

Although estimated CV's may have been sometimes higher than may be desired for wildlife studies, they are much smaller than CV's that would be obtained using the more general case of the Jolly-Seber model. Direct comparisons with Jolly-Seber model estimates are somewhat difficult, but Pollock et al. (1990) did several simulations that demonstrated the increased precision of estimates using the no recruitment model. The additional feature of modeling capture and survival probabilities allows for even greater reduction in CV's. Some examples are given in Table 2.7 where, for arbitrarily selected datasets, estimates were calculated for the Jolly-Seber model, for the no-recruitment model with no modeling, and for the no recruitment model with modeling as used in this study. For that comparison, estimates of $\hat{N}_1$ from the no recruitment model with and without modeling were compared to maximum estimates of N_t from the Jolly-Seber model because for the Jolly-Seber model no estimate of N_1 is obtainable, and under the assumption of the no recruitment model N_1 is the maximum population. Not only are the standard errors much reduced using the no recruitment with modeling methods, but for situations with small samples (the majority of the ground squirrel cases in 1993 and 1994) Jolly-Seber model estimates of precision could not even be calculated.

Another benefit of the methods I used was that I was able to combine data across classes to improve sample sizes for estimation. Using AIC model selection criteria, I could determine when this was appropriate, and often gain biological insight in the process. For instance, in most cases for adults, models combining data across sexes within a site were rejected (i.e., had greater AIC values) in favor of those combining data from >1 site for a given sex. This indicated that capture and/or survival probabilities

differ between sexes more than they do among members of the same sex among sites, and that estimating sex ratios of the population based only on marked animals would be misleading.

The ability to combine data across groups that do not share the same pattern of trapping occasions also allows considerably more flexibility in the design and analysis of capture-recapture data than has been available previously. The critical point here is that the capture and survival parameters must be modeled as smoothed functions of time, which allows for the sharing of parameters between sites where capture occasions are asynchronous. This flexibility is not limited to abundance estimation, but also applies to estimation of survival probabilities (see Chapter 3). Although I advocate reducing sources of variation as much as possible when designing capture-recapture studies, there may be numerous reasons why standardization of trapping patterns is not feasible.

One drawback to combining data across sites is that this induces a correlation between the site-specific estimates, with the degree of correlation dependent upon the number of shared (non site-specific) parameters in the model. For the TGS example, sampling correlations between abundance estimates ranged from 0.032 to 0.774, with a median of 0.385. Although such correlations do not affect the validity of the estimates, they may be problematic when tests of hypotheses are desired. In the ground squirrel study, however, I found the induced correlations to have no effect on the tests of hypotheses regarding density.

In summary, I feel that use of the no recruitment model for estimation of abundance for open populations is a viable and under-utilized alternative to the Jolly-

Seber model, when assumptions can be met. This is especially true when constraints can be placed on capture and survival probabilities to further reduce the number of estimable parameters. Further work should be done, however, to investigate this technique, especially the use of Monte Carlo simulations to test its robustness to moderate violations of the major assumptions: no recruitment and homogeneity of survival and capture probabilities. Although Hwang and Chao (1995) used simulations to examine the biases associated with failure of the homogeneity assumptions (and proposed a new estimator of abundance for the no recruitment model), they did not consider cases using parameter modeling. Of course the ultimate test for any abundance estimator is how it compares to the true number of animals. This was not possible for the ground squirrel study, but future research should be designed with validation of the no recruitment model estimator in mind.

TGS density estimation and hypothesis tests

Perhaps the most subjective part of the methodology I used for calculating density estimates was the use of MMDM as the basis for area estimates. However, there was no better alternative, given the data that were collected. Although Otis et al. (1978) advocated the use of nested trapping grids to estimate effective trapping area, this method may be biased and very imprecise, especially for small sample sizes (K. Burnham, personal communication). Even when assessment line data are available, there is no commonly accepted, and verified, method for the use of such data in estimating the effective area trapped. Furthermore, Tanaka (1980) concluded that neither nested grid nor assessment lines methods were improvements over a method used by Dice (1938),

based on home range. Wilson and Anderson (1985) concluded that the MMDM method was an adequate substitution when home range area is unknown, and may be superior as it can take into account such factors as population density and trap spacing. In their simulation study, Wilson and Anderson (1985) found MMDM to yield density estimates with relative bias of <20%. By attempting to remove known sources of bias, and accounting for the factors influencing movement distances, I believe that the MMDM method provided reasonable estimates of area for TGS density estimates.

The most striking differences in adult TGS densities was among study years, with 1992 densities exceeding those in 1993 and 1994 by a large margin on most sites. This can be directly attributed to the late spring drought in 1992. Supportive evidence of the magnitude of the drought and its general impact on TGS populations has been provided by Van Horne et al. (1997). The analyses of density estimates showed that the immediate demographic impact of the drought may have been less in shrub habitats than in the grass habitats, given that declines in density were less in those sites between 1992 and 1993. However, density declined in both habitats about equally between 1993 and 1994, indicating that either lingering effects of the drought, or some other mechanism, was operating equally in both habitats by that time. Van Horne et al. (1997) discuss at length the possible influences of habitat on TGS response to drought conditions.

Sites located within the OTA consistently had higher densities than sites outside the OTA boundaries. Although the decline in density following the drought appeared to be greater for OTA sites, by 1994 densities on off-OTA had declined to near zero. Based on density alone, it appeared that TGS populations were better off on the study sites

located within the OTA. This may be partially due to differences in vegetation or soil characteristics, as Van Horne and Sharpe (1998) found several differences among sagebrush sites within and outside the OTA. However, they found no differences in vegetation characteristics among grassland sites due to location, although soils did differ somewhat. However, neither differences in vegetation nor TGS density can be attributed to use of the OTA by the IDARNG, as Van Horne and Sharpe (1998) point out several potential reasons why such results may be unrelated, including study site selection and spatial correlation. Therefore, my conclusion is that the significance of location as a factor affecting TGS density reflects an array of conditions, and warrants further examination.

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Table 2.1. Parameters for the Jolly-Seber model and for the no recruitment special case of the Jolly-Seber model (after Pollock et al. 1990, Table 2).

PARAMETERS OF THE JOLLY-SEBER MODEL

M_i = the number of marked animals in the population at the time the ith sample is taken ($i = 2, \ldots, k$; $M_1 = 0$).

N_i = the total number of animals in the population at the time the ith sample is taken ($i = 1, \ldots, k$).

B_i = the total number of new animals entering the population between the ith and $(i + 1)$th sample ($i = 1, \ldots, k - 1$), and still there, alive, just before the $(i + 1)$th sample is taken.

ϕ_i = the survival probability for all animals between the ith and $(i + 1)$th sample ($i = 1, \ldots, k - 1$).

p_i = the capture probability for all animals in the ith sample ($i = 1, \ldots, k$).

Total number of parameters = $5k - 3$. Number of separately estimable parameters = $3k - 3$.

PARAMETERS OF THE NO RECRUITMENT CASE OF THE JOLLY-SEBER MODEL

M_i = the number of marked animals in the population at the time the ith sample is taken ($i = 2, \ldots, k$; $M_1 = 0$).

N_1 = the total number of animals in the population at the time the 1st sample is taken.

ϕ_i = the survival probability for all animals between the ith and $(i + 1)$th sample ($i = 1, \ldots, k - 1$).

p_i = the capture probability for all animals in the ith sample ($i = 1, \ldots, k$).

Total number of parameters = $3k - 1$. Number that are separately estimable = $2k - 1$. Note that the number of parameters can be further reduced by placing constraints on ϕ_i and p_i.

Table 2.2. Constraints placed on survival and capture probabilities in the no recruitment special case of the Jolly-Seber model, used for abundance estimation of Townsend's ground squirrels. Each combination of constraints is one candidate model, and the best model was selected for each set of estimates using the selection criteria described in the text.

Model description	Notation	Model[a]
Single site analyses		
Survival probabilities:		
Constant per-day survival	$\phi.$	$\ln(\phi_i) \approx \alpha D_i$
Linear function of time	ϕ_T	$\ln(\phi_i) \approx \alpha D_i + \beta D_i T_i$
Capture probabilities:		
Same for all occasions	$p.$	$p_i = p.$
Linear function of time	p_T	$\text{logit}(p_i) = \alpha + \beta T_i$
Quadratic function of time	p_{TT}	$\text{logit}(p_i) = \alpha + \beta T_i + \gamma T_i^2$
Time specific	p_t	$p_i = p_i$
Multiple site analyses (in addition to models above)		
Survival probabilities		
Site-specific, constant per day	ϕ_S	$\ln(\phi_{Si}) \approx \alpha_S D_{Si}$
Site × Time additive model	ϕ_{T+S}	$\ln(\phi_{Si}) \approx \alpha_S D_{Si} + \beta D_{Si} T_{Si}$
Site × Time interaction model	ϕ_{T*S}	$\ln(\phi_{Si}) \approx \alpha_S D_{Si} + \beta_S D_{Si} T_{Si}$
Capture probabilities		
Site-specific, same for all occasions	p_S	$\text{logit}(p_{Si}) = \alpha_S$
Site × Time, additive model	p_{T+S}	$\text{logit}(p_{Si}) = \alpha_S + \beta T_{Si}$
Site × Time, interaction model	p_{T*S}	$\text{logit}(p_{Si}) = \alpha_S + \beta_S T_{Si}$
Site × Time^2, additive model	p_{TT+S}	$\text{logit}(p_{Si}) = \alpha_S + \beta T_{Si} + \gamma T_{Si}^2$
Site × Time^2, interaction model	p_{TT*S}	$\text{logit}(p_{Si}) = \alpha_S + \beta_S T_{Si} + \gamma_S T_{Si}^2$

[a]Subscript i denotes the interval between capture occasions (for survival probabilities, $i = 1,\ldots, k-1$) or the capture occasion (for capture probabilities, $i = 1,\ldots, k$). Subscript S denotes site-specific parameters, $S = 1,\ldots, r$, where r = the number of sites combined in the analysis. D_i is the number of days in the ith interval, and T_i is the number of days elapsed since the first capture occasion. Greek letters (α, β, γ) denote regression parameters.

Table 2.3. Results of abundance estimation using the no recruitment special case of the Jolly-Seber model, for adult Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, 1992-1994 (A-C). Estimates were computed for each site and sex. Data from some sites were pooled when sample sizes were small; those sites are indicated with the estimated correlation induced between abundance estimates. Also given is the model selected for abundance estimation when a clear choice could be made among tested models (see Table 2.2 and text). When model averaging was used, the models for which estimates were averaged are given. The resulting estimates of abundance are shown with a 95% confidence interval (C.I.). When selected model is given as "NONE", no estimates were computed from the no recruitment model due to assumptions violations; when left blank, estimates could not be calculated due to small sample sizes.

A. 1992 Adults

Site	Sex	Number marked	Pooling (Correlation)	Selected model(s)	$\hat{N}$	95% C.I.
1A	F	6	1B (0.42)	$\phi_T p.$	9.9	6.9 - 23.1
	M	3	1B (0.08)	$\phi_T p.$	3.4	3.0 - 7.9
1B	F	6	1A (0.42)	$\phi_T p.$	8.9	6.6 - 19.6
	M	4	1A (0.08)	$\phi_T p.$	4.3	4.0 - 7.8
2A	F	0			0.0	
	M	0			0.0	
2B	F	0			0.0	
	M	5	3B (0.43)	$\phi.p_S$, $\phi.p.$, $\phi.p_T$	13.6	10.2 - 19.4
3A	F	1			1.0	
	M	1			1.0	
3B	F	8		NONE		
	M	16	2B (0.43)	$\phi.p_S$,$\phi.p.$, $\phi.p_T$	33.3	26.2 - 45.3
4A	F	45		$\phi.p_{TT}$	55.3	48.4 - 76.5
	M	22		$\phi.p_T$	26.2	22.6 - 50.1
4B	F	40		$\phi.p_{TT}$	58.8	46.6 - 93.5
	M	35		$\phi.p_{TT}$	36.5	34.6 - 45.2
5A	F	21	9A (0.49)	$\phi.p_{T+S}$	27.6	22.6 - 49.1
	M	20	9A (0.28)	$\phi.p_S$	21.0	20.1 - 27.7
5B	F	44	9B (0.16)	$\phi.p_S$	52.4	45.9 - 81.5
	M	31		$\phi.p.$	33.2	31.4 - 44.0
6A	F	0			0.0	
	M	0			0.0	
6B	F	34		$\phi.p_{TT}$	36.4	34.3 - 52.0
	M	22		$\phi.p_T$, $\phi_T p_T$, $\phi_T p_{TT}$, $\phi.p_{TT}$	34.9	24.1 - 100.8
7A	F	35		$\phi.p_{TT}$	49.0	40.1 - 73.9
	M	19		$\phi.p_{TT}$	21.1	19.4 - 31.0
7B	F	21		$\phi.p_T$	27.6	22.3 - 54.8
	M	20		$\phi.p_i$	25.7	21.4 - 43.0
8A	F	25		$\phi.p_{TT}$	29.6	25.8 - 50.0
	M	18		$\phi.p.$	23.4	19.7 - 35.2

Site	Sex	Number marked	Pooling (Correlation)	Selected model(s)	$\hat{N}$	95% C.I.
8B	F	35		$\phi . p_T$	37.3	35.4 - 48.9
	M	21		$\phi . p .$	23.4	21.5 - 33.7
9A	F	15	5A (0.49)	$\phi . p_{T+S}$	16.4	15.2 - 27.1
	M	16	5A (0.28)	$\phi . p_S$	16.4	16.0 - 21.2
9B	F	27	5B (0.16)	$\phi . p_S$	30.2	27.3 - 62.6
	M	37		$\phi . p_i$	46.8	39.5 - 74.5
10A	F	47		$\phi . p .$	55.8	50.5 - 69.2
	M	27		$\phi . p .$	28.6	27.4 - 34.4
10B	F	56		$\phi . p_i$	82.7	65.5 - 131.3
	M	43		$\phi . p_i$	48.4	44.3 - 66.0

B. 1993 Adults

Site	Sex	Number marked	Pooling (Correlation)	Selected model(s)	$\hat{N}$	95% C.I.
1A	F	2	2B (0.25),3B (0.34)	$\phi . p .$	2.6	2.1 - 8.2
	M	4		NONE	4.0	
1B	F	0			0.0	
	M	1			1.0	
2A	F	0			0.0	
	M	2			2.0	
2B	F	2	1A (0.25), 3B (0.30)	$\phi . p .$	2.6	2.1 - 8.0
	M	2	3B (0.16)	$\phi . p_{T+S}$	2.2	2.0 - 5.2
3A	F	0			0.0	
	M	1			1.0	
3B	F	4	1A (0.34), 2B (0.30)	$\phi . p .$	5.4	4.2 - 14.6
	M	5	2B (0.16)	$\phi . p_{T+S}$	6.5	5.2 - 14.6
4A	F	10	4B (0.44)	$\phi . p_T , \phi_S p_T , \phi . p_{TT} , \phi_S p_{TT}$	21.2	13.0 - 51.5
	M	13	4B (0.22)	$\phi . p_{TT+S}$	14.7	13.3 - 23.4
4B	F	7	4A (0.44)	$\phi . p_T , \phi_S p_T , \phi . p_{TT} , \phi_S p_{TT}$	13.6	8.4 - 38.6
	M	14	4A (0.22)	$\phi . p_{TT+S}$	27.2	18.0 - 57.7
5A	F	8	9A (0.03)	$\phi_S p .$	9.5	8.3 - 17.1
	M	19		$\phi . p_T$	31.0	23.3 - 52.2
5B	F	32		$\phi . p_i$	41.2	35.4 - 56.4
	M	27		$\phi . p_{TT}$	38.9	31.8 - 56.6
6A	F	0			0.0	
	M	2			2.0	
6B	F	10	7B (0.29)	$\phi . p .$	14.0	11.0 - 25.6
	M	12	7B (0.37)	$\phi . p_T$	18.8	14.2 - 33.0
7A	F	45		$\phi_T p_T$	65.4	50.6 - 119.6
	M	32		$\phi . p_T$	53.9	40.9 - 85.8

Site	Sex	Number marked	Pooling (Correlation)	Selected model(s)	$\hat{N}$	95% C.I.
7B	F	4	6B (0.29)	$\phi . p.$	5.9	4.4 - 13.6
	M	8	6B (0.37)	$\phi . p_T$	13.0	9.5 - 25.2
8A	F	69		NONE		
	M	50		$\phi . p_t$	70.3	59.7 - 92.5
8B	F	15		$\phi . p_T$,$\phi_T p_T$, $\phi_T p_{TT}$, $\phi . p_{TT}$	36.9	19.9 - 112.7
	M	19		$\phi . p.$	26.5	21.8 - 39.3
9A	F	13	5A (0.03)	$\phi_s p.$	15.8	13.7 - 24.1
	M	16		$\phi_T p_T$	26.8	19.4 - 49.8
9B	F	22		$\phi . p_t$	37.9	27.3 - 69.1
	M	27		$\phi . p_T$	32.4	28.6 - 45.4
10A	F	16		$\phi_T p_{TT}$	22.5	17.5 - 44.2
	M	21		$\phi . p.$, $\phi . p_T$, $\phi_T p.$	35.9	25.0 - 75.8
10B	F	22		$\phi_T p_T$, $\phi . p_T$, $\phi_T p_{TT}$	45.9	26.6 - 121.9
	M	20		$\phi . p.$	22.1	20.4 - 32.8

C. 1994 Adults

Site	Sex	Number marked	Pooling (Correlation)	Selected model(s)	$\hat{N}$	95% C.I.
1A	F	0			0.0	
	M	0			0.0	
1B	F	1			1.0	
	M	0			0.0	
2A	F	0			0.0	
	M	0			0.0	
2B	F	0			0.0	
	M	0			0.0	
3A	F	1			1.0	
	M	1	3B (0.13)	$\phi . p_T$	1.1	1.0 - 3.1
3B	F	4		$\phi . p.$	9.2	4.6 - 46.3
	M	4	3A (0.13)	$\phi . p_T$	4.5	4.0 - 9.1
4A	F	1	4B (0.61)	$\phi . p_T$, $\phi_T p_T$, $\phi . p_{TT}$, $\phi_{T+s} p_T$	22.8	13.8 - 77.3
	M	4	4B (0.12)	$\phi . p_T$	4.8	4.1 - 10.7
4B	F	7	4A (0.61)	$\phi . p_T$, $\phi_T p_T$, $\phi . p_{TT}$, $\phi_{T+s} p_T$	15.3	8.6 - 49.8
	M	2	4A (0.12)	$\phi . p_T$	2.4	2.0 - 6.2
5A	F	6	9A (0.51)	$\phi . p_T$	7.7	6.3 - 16.4
	M	5	9A (0.31)	$\phi . p_T$	5.8	5.1 - 11.5

Site	Sex	Number marked	Pooling (Correlation)	Selected model(s)	$\hat{N}$	95% C.I.
5B	F	9	9B (0.43)	$\phi . p_T$	14.3	10.4 - 28.4
	M	10	9B (0.27)	$\dot{\psi} . p_{T+S}$	14.9	11.3 - 29.2
6A	F	0			0.0	
	M	0			0.0	
6B	F	6	7B (0.44)	$\phi . p_{T+S}$	12.0	7.2 - 34.9
	M	2			2.0	
7A	F	16		$\phi . p .$	18.5	16.7 - 25.5
	M	8		$\phi_T p_{TT}$, $\phi . p_{TT}$	28.2	10.8 - 154.7
7B	F	4	6B (0.44)	$\phi . p_{T+S}$	6.0	4.3 - 15.8
	M	2			2.0	
8A	F	54		$\phi_T p_t$	57.6	54.5 - 81.9
	M	27		$\phi_T p_{TT}$	29.6	27.6 - 37.8
8B	F	1			1.0	
	M	2			2.0	
9A	F	9	5A (0.51)	$\phi . p_T$	11.4	9.4 - 23.4
	M	2	5A (0.31)	$\phi . p_T$	2.8	2.1 - 9.1
9B	F	5	5B (0.43)	$\phi . p_T$	10.2	6.3 - 26.0
	M	4	5B (0.27)	$\phi . p_{T+S}$	5.0	4.1 - 11.1
10A	F	6	10B (0.14)	$\phi_S p_{T+S}$	9.4	6.7 - 21.7
	M	3	10B (0.33)	$\phi_T p_{T+S}$, $\phi_T p_S$, $\phi . p_S$, $\phi .$	3.3	3.1 - 4.2
10B	F	8	10A (0.14)	$\phi_S p_{T+S}$	16.2	10.0 - 40.5
	M	8	10A (0.33)	$\phi_T p_{T+S}$, $\phi_T p_S$, $\phi . p_S$, $\phi .$	11.3	8.6 - 25.8

Table 2.4. Results of abundance estimation using the no recruitment special case of the Jolly-Seber model, for juvenile Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, 1992-1994 (A-C). Estimates were computed for each site. Data from some sites were pooled when sample sizes were small; those sites are indicated with the estimated correlation induced between abundance estimates. Also given is the model selected for abundance estimation when a clear choice could be made among tested models (see Table 2.2 and text). When model averaging was used, the models for which estimates were averaged are given. The resulting estimates of abundance are shown with a 95% confidence interval (C.I.). When selected model is given as "NONE", no estimates were computed from the no recruitment model due to assumptions violations; when left blank, estimates could not be calculated due to small sample sizes.

A. 1992 Juveniles

Site	Number marked	Pooling (correlation)	Selected model(s)	$\hat{N}$	95% C.I.
1A	28	1B (0.43)		29.5	28.0 - 71.4
1B	9	1A (0.43)		13.3	10.1 - 25.5
2A	0				
2B	0				
3A	0				
3B	27		$\phi . p_T$	41.0	28.8 - 132.8
4A	87		$\phi_T p_t$	194.1	137.3 - 314.9
4B	122		$\phi_T p_t$	163.6	134.0 - 266.6
5A	39		$\phi . p_T$	57.3	
5B	16		$\phi . p_T$	40.6	19.7 - 178.0
6A	0				
6B	96		$\phi . p_{TT}$	281.1	174.7 - 531.5
7A	96		$\phi_T p_T$	128.9	107.3 - 188.3
7B	46		F: $\phi_T p_.$, M: $\phi . p_.$	73.7	55.5 - 126.6
8A	45		$\phi_T p_t$, $\phi . p_t$	107.0	88.5 - 133.4
8B	49		F: $\phi_T p_{TT}$, M: $\phi_T p_T$	83.7	54.9 - 251.5
9A	40		$\phi . p_T$	58.4	
9B	23		NONE	23.0	
10A	106		$\phi . p_t$, $\phi_T p_t$	245.9	222.3 - 274.2
10B	79		$\phi_T p_t$	149.4	93.7 - 415.9

B. 1993 Juveniles

Site	Number marked	Pooling (correlation)	Selected model(s)	$\hat{N}$	95% C.I.
1A	0				
1B	0				
2A	0				
2B	0				
3A	0				

Site	Number marked	Pooling (correlation)	Selected model(s)	$\hat{N}$	95% C.I.
3B	1			1.0	
4A	1			1.0	
4B	15	10A (0.77)		39.7	19.1 - 162.8
5A	1			1.0	
5B	4	9B (0.39)	$\phi . p.$	5.9	4.4 - 13.7
6A	0				
6B	2				
7A	30		$\phi . p_t$	44.5	32.5 - 115.4
7B	1	8B (0.50)	$\phi . p.$	3.8	1.4 - 23.1
8A	41		$\phi . p_T$, $\phi_T p.$, $\phi . p_{TT}$, $\phi . p.$, $\phi . p_t$, $\phi_T p_t$	68.7	45.4 - 213.4
8B	9	7B (0.50)	$\phi . p.$	25.4	12.2 - 92.9
9A	2			2.0	
9B	22	5B (0.39)	$\phi . p.$	31.9	25.1 - 53.5
10A	11	4B (0.77)		44.0	15.8 - 238.2
10B	30		$\phi . p.$	58.4	33.3 - 276.6

C. 1994 Juveniles

Site	Number marked	Pooling (correlation)	Selected model(s)	$\hat{N}$	95% C.I.
1A	0				
1B	0				
2A	0				
2B	0				
3A	0				
3B	3				
4A	5	4B (0.38)	$\phi . p.$, $\phi_T p.$, $\phi . p_{TT}$, $\phi . p_T$	15.8	8.5 - 38.5
4B	20	4A (0.38)	$\phi . p.$, $\phi_T p.$, $\phi . p_{TT}$, $\phi . p_T$	25.6	21.3 - 45.0
5A	6	9A (0.49)	$\phi . p.$	6.3	6.0 - 10.3
5B	21		$\phi . p_T$	38.2	24.4 - 108.6
6A	0				
6B	4	7B (0.61) ,8B (0.58)	$\phi . p.$	8.5	4.8 - 30.1
7A	42		F: $\phi . p_T$, M: $\phi . p.$	114.9	63.8 - 285.8
7B	5	6B (0.61), 8B (0.51)	$\phi . p.$	8.7	5.5 - 30.9
8A	39		$\phi . p_T$, $\phi . p_{TT}$, $\phi_T p_T$, $\phi_T p_{TT}$	150.9	62.2 - 573.3
8B	3	6B (0.58), 7B (0.51)	$\phi . p.$	9.8	4.3 - 39.3
9A	4	5A (0.49)	$\phi . p.$	4.0	4.0 - 5.6
9B	1				
10A	24		$\phi . p_T$	27.4	24.4 - 55.3
10B	32		$\phi . p_T$	105.4	53.0 - 288.5

Table 2.5. Density estimates for adult Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, Idaho, in 1992-1994 (A-C).

A. 1992 Adults

Site	Sex	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
1A	F	6	9.9	3.41	9.00	21.78	1.77	11.76	0.24	0.84	0.29
	M	3	3.4	0.82	9.00	23.43	2.06	11.98	0.28	0.28	0.07
1B	F	6	8.9	2.68	9.00	21.78	1.77	11.76	0.24	0.76	0.23
	M	4	4.3	0.63	9.00	23.43	2.06	11.98	0.28	0.36	0.05
2A	F	0	0.0		9.00	21.78	1.77	11.76	0.24	0.00	0.01[a]
	M	0	0.0		9.00	23.43	2.06	11.98	0.28	0.00	0.02[a]
2B	F	0	0.0		9.00	21.78	1.77	11.76	0.24	0.00	0.01[a]
	M	5	13.6	8.94	9.00	23.43	2.06	11.98	0.28	1.13	0.75
3A	F	1	1.0		9.00	21.78	1.77	11.76	0.24	0.09	0.01[a]
	M	1	1.0		9.00	23.43	2.06	11.98	0.28	0.08	0.02[a]
3B	F	8	8.0		9.00	21.78	1.77	11.76	0.24	0.68	0.10[a]
	M	16	33.3	18.25	9.00	23.43	2.06	11.98	0.28	2.78	1.52
4A	F	45	55.3	6.39	2.25	21.78	1.77	3.71	0.13	14.92	1.80
	M	22	26.2	5.26	2.25	23.43	2.06	3.83	0.15	6.84	1.4
4B	F	40	58.8	10.79	2.25	21.78	1.77	3.71	0.13	15.87	2.97
	M	35	36.5	2.23	2.25	23.43	2.06	3.83	0.15	9.53	0.70
5A	F	21	27.6	5.63	4.50	21.78	1.77	6.61	0.18	4.18	0.86
	M	20	21.0	1.4	4.50	23.43	2.06	6.78	0.22	3.10	0.23
5B	F	44	52.4	7.47	4.50	21.78	1.77	6.61	0.18	7.93	1.15
	M	31	33.2	2.5	4.50	23.43	2.06	6.78	0.22	4.90	0.40

Site	Sex	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
6A	F	0	0.0		9.00	21.78	1.77	11.76	0.24	0.00	0.01[a]
	M	0	0.0		9.00	23.43	2.06	11.98	0.28	0.00	0.02[a]
6B	F	34	36.4	3.29	4.50	21.78	1.77	6.61	0.18	5.51	0.52
	M	22	34.9	14.95	4.50	23.43	2.06	6.78	0.22	5.15	2.21
7A	F	35	49.0	7.82	2.25	24.78	1.77	3.71	0.13	13.22	2.16
	M	19	21.1	2.32	2.25	23.43	2.06	3.83	0.15	5.51	0.65
7B	F	21	27.6	6.61	2.25	21.78	1.77	3.71	0.13	7.45	1.80
	M	20	25.7	4.62	2.25	23.43	2.06	3.83	0.15	6.71	1.24
8A	F	25	29.6	4.84	2.25	21.78	1.77	3.71	0.13	7.99	1.34
	M	18	23.4	3.49	2.25	23.43	2.06	3.83	0.15	6.11	0.94
8B	F	35	37.3	2.65	2.25	21.78	1.77	3.71	0.13	10.07	0.80
	M	21	23.4	2.47	2.25	23.43	2.06	3.83	0.15	6.11	0.69
9A	F	15	16.4	2.16	2.25	21.78	1.77	3.71	0.13	4.43	0.60
	M	16	16.4	0.87	2.25	23.43	2.06	3.83	0.15	4.28	0.29
9B	F	27	30.2	6.00	4.50	21.78	1.77	6.61	0.18	4.57	0.92
	M	37	46.8	7.57	4.50	23.43	2.06	6.78	0.22	6.90	1.14
10A	F	47	55.8	4.41	2.25	21.78	1.77	3.71	0.13	15.06	1.30
	M	27	28.6	1.46	2.25	23.43	2.06	3.83	0.15	7.47	0.49
10B	F	56	82.7	15.18	4.50	21.78	1.77	6.61	0.18	12.51	2.32
	M	43	48.4	4.61	4.50	23.43	2.06	6.78	0.22	7.14	0.72

B. 1993 Adults

Site	Sex	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
1A	F	2	2.6	1.07	4.50	25.58	1.71	7.01	0.18	0.37	0.15
	M	4	4.0		4.50	31.32	1.68	7.63	0.18	0.52	0.13[a]
1B	F	0	0.0		4.50	25.58	1.71	7.01	0.18	0.00	0.04[a]
	M	1	1.0		4.50	31.32	1.68	7.63	0.18	0.13	0.03
2A	F	0	0.0		4.50	25.58	1.71	7.01	0.18	0.00	0.04[a]
	M	2	2.0		4.50	31.32	1.68	7.63	0.18	0.26	0.07[a]
2B	F	2	2.6	1.04	4.50	25.58	1.71	7.01	0.18	0.37	0.15
	M	2	2.2	0.50	4.50	31.32	1.68	7.63	0.18	0.29	0.07
3A	F	0	0.0		4.50	25.58	1.71	7.01	0.18	0.00	0.04[a]
	M	1	1.0		4.50	31.32	1.68	7.63	0.18	0.13	0.03[a]
3B	F	4	5.4	1.92	4.50	25.58	1.71	7.01	0.18	0.77	0.27
	M	5	6.5	1.80	4.50	31.32	1.68	7.63	0.18	0.85	0.24
4A	F	10	21.2	8.41	4.50	25.58	1.71	7.01	0.18	3.03	1.20
	M	13	14.7	1.98	4.50	31.32	1.68	7.63	0.18	1.93	0.26
4B	F	7	13.6	6.23	4.50	25.58	1.71	7.01	0.18	1.94	0.89
	M	14	27.2	8.88	4.50	31.32	1.68	7.63	0.18	3.57	1.17
5A	F	8	9.5	1.73	4.50	25.58	1.71	7.01	0.18	1.36	0.25
	M	19	31.0	6.69	4.50	31.32	1.68	7.63	0.18	4.06	0.88
5B	F	32	41.2	4.88	4.50	25.58	1.71	7.01	0.18	5.88	0.71
	M	27	38.9	5.85	4.50	31.32	1.68	7.63	0.18	5.10	0.78
6A	F	0	0.0		4.50	25.58	1.71	7.01	0.18	0.00	0.04[a]
	M	2	2.0		4.50	31.32	1.68	7.63	0.18	0.26	0.07[a]

Site	Sex	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
6B	F	10	14.0	3.15	4.50	25.58	1.71	7.01	0.18	2.00	0.45
	M	12	18.8	4.26	4.50	31.32	1.68	7.63	0.18	2.46	0.56
7A	F	45	65.4	15.12	4.50	25.58	1.71	7.01	0.18	9.33	2.17
	M	32	53.9	10.59	4.50	31.32	1.68	7.63	0.18	7.07	1.40
7B	F	4	5.9	1.88	4.50	25.58	1.71	7.01	0.18	0.84	0.27
	M	8	13.0	3.49	4.50	31.32	1.68	7.63	0.18	1.70	0.46
8A	F	69			4.50	25.58	1.71	7.01	0.18		
	M	50	70.3	7.93	4.50	31.32	1.68	7.63	0.18	9.22	1.06
8B	F	15	36.9	19.46	4.50	25.58	1.71	7.01	0.18	5.27	2.78
	M	19	26.5	4.07	4.50	31.32	1.68	7.63	0.18	3.47	0.54
9A	F	13	15.8	2.24	4.50	25.58	1.71	7.01	0.18	2.25	0.33
	M	16	26.8	6.87	4.50	31.32	1.68	7.63	0.18	3.51	0.91
9B	F	22	37.9	9.53	4.50	25.58	1.71	7.01	0.18	5.41	1.37
	M	27	32.4	3.74	4.50	31.32	1.68	7.63	0.18	4.25	0.50
10A	F	166	22.5	5.63	4.50	25.58	1.71	7.01	0.18	3.21	0.81
	M	21	35.9	11.10	4.50	31.32	1.68	7.63	0.18	4.71	1.46
10B	F	22	45.9	20.22	4.50	25.58	1.71	7.01	0.18	6.55	2.89
	M	20	22.1	2.43	4.50	31.32	1.68	7.63	0.18	2.90	0.33

C. 1994 Adults

Site	Sex	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
1A	F	0	0.0		4.50	27.98	2.16	7.26	0.23	0.00	0.05[a]
	M	0	0.0		4.50	43.41	4.31	9.00	0.51	0.00	0.04[a]
1B	F	1	1.0		4.50	27.98	2.16	7.26	0.23	0.14	0.07[a]
	M	0	0.0		4.50	43.41	4.31	9.00	0.51	0.00	0.04[a]
2A	F	0	0.0		4.50	27.98	2.16	7.26	0.23	0.00	0.05[a]
	M	0	0.0		4.50	43.41	4.31	9.00	0.51	0.00	0.04[a]
2B	F	0	0.0		4.50	27.98	2.16	7.26	0.23	0.00	0.05[a]
	M	0	0.0		4.50	43.41	4.31	9.00	0.51	0.00	0.04[a]
3A	F	1	1.0		4.50	27.98	2.16	7.26	0.23	0.14	0.07[a]
	M	1	1.1	0.31	4.50	43.41	4.31	9.00	0.51	0.12	0.04[a]
3B	F	4	9.2	7.59	4.50	27.98	2.16	7.26	0.23	1.27	1.05
	M	4	4.5	0.87	4.50	43.41	4.31	9.00	0.51	0.50	0.10
4A	F	12	22.8	12.42	4.50	27.98	2.16	7.26	0.23	3.14	1.71
	M	4	4.8	1.21	4.50	43.41	4.31	9.00	0.51	0.53	0.14
4B	F	7	15.3	8.36	4.50	27.98	2.16	7.26	0.23	2.11	1.15
	M	2	2.4	0.72	4.50	43.41	4.31	9.00	0.51	0.27	0.08
5A	F	6	7.7	1.98	4.50	27.98	2.16	7.26	0.23	1.06	0.27
	M	5	5.8	1.16	4.50	43.41	4.31	9.00	0.51	0.64	0.13
5B	F	9	14.3	3.93	4.50	27.98	2.16	7.26	0.23	1.97	0.54
	M	10	14.9	3.88	4.50	43.41	4.31	9.00	0.51	1.66	0.44
6A	F	0	0.0		4.50	27.98	2.16	7.26	0.23	0.00	0.05[a]
	M	0	0.0		4.50	43.41	4.31	9.00	0.51	0.00	0.04[a]

Site	Sex	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
6B	F	6	12.0	5.7	4.50	27.98	2.16	7.26	0.23	1.65	0.79
	M	2	2.0		4.50	43.41	4.31	9.00	0.51	0.22	0.08[a]
7A	F	16	18.5	1.93	4.50	27.98	2.16	7.26	0.23	2.55	0.28
	M	8	28.2	26.98	4.50	43.41	4.31	9.00	0.51	3.13	3.01
7B	F	4	6.0	2.24	4.50	27.98	2.16	7.26	0.23	0.83	0.31
	M	2	2.0		4.50	43.41	4.31	9.00	0.51	0.22	0.08[a]
8A	F	54	57.6	5.08	4.50	27.98	2.16	7.26	0.23	7.93	0.74
	M	27	29.6	2.17	4.50	43.41	4.31	9.00	0.51	3.29	0.30
8B	F	1	1.0		4.50	27.98	2.16	7.26	0.23	0.14	0.07[a]
	M	2	2.0		4.50	43.41	4.31	9.00	0.51	0.22	0.08[a]
9A	F	9	11.4	2.74	4.50	27.98	2.16	7.26	0.23	1.57	0.38
	M	2	2.8	1.25	4.50	43.41	4.31	9.00	0.51	0.31	0.14
9B	F	5	10.2	4.22	4.50	27.98	2.16	7.26	0.23	1.40	0.58
	M	4	5.0	1.31	4.50	43.41	4.31	9.00	0.51	0.56	0.15
10A	F	6	9.4	3.12	4.50	27.98	2.16	7.26	0.23	1.29	0.43
	M	3	3.3	0.70	4.50	43.41	4.31	9.00	0.51	0.37	0.08
10B	F	8	16.2	6.54	4.50	27.98	2.16	7.26	0.23	2.23	0.90
	M	8	11.3	3.46	4.50	43.41	4.31	9.00	0.51	1.26	0.39

[a]Standard errors for density estimates for sites where the number of marked animals was used as the abundance estimate were estimated based on the relationship between the average CV of $\hat{N}$ estimates for $\hat{N}$<5.0, and the CV of the area estimate (see text for formula)

Table 2.6. Density estimates for juvenile Townsend's ground squirrels at the time of their emergence from natal burrows, on the Snake River Birds of Prey National Conservation Area, Idaho, in 1992-1994 (A-C).

A. 1992 Juveniles

Site	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
1A	28	29.5	6.37	9.00	30.58	1.88	12.96	0.26	2.28	0.49
1B	9	13.3	3.33	9.00	30.58	1.88	12.96	0.26	1.03	0.26
2A[a]				9.00	30.58	1.88	12.96	0.26		
2B[a]				9.00	30.58	1.88	12.96	0.26		
3A[a]				9.00	30.58	1.88	12.96	0.26		
3B	27	41.0	19.30	9.00	30.58	1.88	12.96	0.26	3.16	1.49
4A	87	194.1	42.85	1.00	30.58	1.88	2.52	0.11	77.12	17.38
4B	122	163.6	29.36	1.00	30.58	1.88	2.52	0.11	65.00	12.02
5A	39	57.3	14.46	2.25	30.58	1.88	4.38	0.15	13.09	3.33
5B	16	40.6	30.33	2.25	30.58	1.88	4.38	0.15	9.27	6.94
6A[a]				9.00	30.58	1.88	12.96	0.26	0.00	0.02
6B	96	281.1	84.80	2.25	30.58	1.88	4.38	0.15	64.20	19.50
7A	96	128.9	18.74	1.00	30.58	1.88	2.52	0.11	51.21	7.79
7B	46	73.7	16.29	1.00	30.58	1.88	2.52	0.11	29.28	6.61
8A	45	107.0	51.78	1.00	30.58	1.88	2.52	0.11	42.51	20.68
8B	49	83.7	38.77	1.00	30.58	1.88	2.52	0.11	33.25	15.49
9A	40	58.4	10.28	1.00	30.58	1.88	2.52	0.11	23.20	4.21
9B	23	23.0		2.25	30.58	1.88	4.38	0.15	5.25	1.22
10A	106	245.9	94.58	1.00	30.58	1.88	2.52	0.11	97.70	37.86
10B	79	149.4	66.53	1.00	30.58	1.88	2.52	0.11	59.36	26.59

B. 1993 Juveniles

Site	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
1A	0	0.0		4.50	30.58	1.88	7.55	0.20	0.00	0.04[b]
1B	0	0.0		4.50	30.58	1.88	7.55	0.20	0.00	0.04[b]
2A	0	0.0		4.50	30.58	1.88	7.55	0.20	0.00	0.04[b]
2B	0	0.0		4.50	30.58	1.88	7.55	0.20	0.00	0.04[b]
3A	0	0.0		4.50	30.58	1.88	7.55	0.20	0.00	0.04[b]
3B	1	1.0		4.50	30.58	1.88	7.55	0.20	0.13	0.05[b]
4A	1	1.0		4.50	30.58	1.88	7.55	0.20	0.13	0.05[b]
4B	15	39.7	28.20	4.50	30.58	1.88	7.55	0.20	5.26	3.74
5A	1	1.0		4.50	30.58	1.88	7.55	0.20	0.13	0.05[b]
5B	4	5.9	1.89	4.50	30.58	1.88	7.55	0.20	0.78	0.25
6A	0	0.0		4.50	30.58	1.88	7.55	0.20	0.00	0.04[b]
6B	2	2.0		4.50	30.58	1.88	7.55	0.20	0.27	0.10[b]
7A	30	44.5	16.32	4.50	30.58	1.88	7.55	0.20	5.90	2.17
7B	1	3.8	4.00	4.50	30.58	1.88	7.55	0.20	0.50	0.53
8A	41	68.7	32.63	4.50	30.58	1.88	7.55	0.20	9.10	4.33
8B	9	25.4	16.40	4.50	30.58	1.88	7.55	0.20	3.37	2.18
9A	2	2.0		4.50	30.58	1.88	7.55	0.20	0.27	0.10[b]
9B	22	31.9	6.39	4.50	30.58	1.88	7.55	0.20	4.23	0.85
10A	11	44.0	42.19	4.50	30.58	1.88	7.55	0.20	5.83	5.60
10B	30	58.4	43.80	4.50	30.58	1.88	7.55	0.20	7.74	5.81

C. 1994 Juveniles

Site	Number marked	$\hat{N}$	SE($\hat{N}$)	Naive grid area (ha)	Estimated strip width, $\hat{w}$ (m)	SE($\hat{w}$)	Adjusted grid area, $\hat{A}$ (ha)	SE($\hat{A}$)	Density, $\hat{D}$ (per ha)	SE($\hat{D}$)
1A[a]				4.50	30.58	1.88	7.55	0.20		
1B[a]				4.50	30.58	1.88	7.55	0.20		
2A[a]				4.50	30.58	1.88	7.55	0.20		
2B[a]				4.50	30.58	1.88	7.55	0.20		
3A	0	0.0		4.50	30.58	1.88	7.55	0.20		
3B	3	3.0		4.50	30.58	1.88	7.55	0.20	0.40	0.26[b]
4A	5	15.8	6.79	4.50	30.58	1.88	7.55	0.20	2.09	0.90
4B	20	25.6	4.99	4.50	30.58	1.88	7.55	0.20	3.39	0.67
5A	6	6.3	0.70	4.50	30.58	1.88	7.55	0.20	0.83	0.10
5B	21	38.2	17.14	4.50	30.58	1.88	7.55	0.20	5.06	2.28
6A[a]				4.50	30.58	1.88	7.55	0.20		
6B	4	8.5	4.99	4.50	30.58	1.88	7.55	0.20	1.13	0.66
7A	42	114.9	49.52	4.50	30.58	1.88	7.55	0.20	15.23	6.58
7B	5	8.7	4.80	4.50	30.58	1.88	7.55	0.20	1.15	0.64
8A	39	150.9	105.52	4.50	30.58	1.88	7.55	0.20	20.00	14.00
8B	3	9.8	7.05	4.50	30.58	1.88	7.55	0.20	1.30	0.94
9A	4	4.0	0.25	4.50	30.58	1.88	7.55	0.20	0.53	0.04
9B	1	1.0		4.50	30.58	1.88	7.55	0.20	0.13	0.09[b]
10A	24	27.4	5.51	4.50	30.58	1.88	7.55	0.20	3.63	0.74
10B	32	105.4	52.07	4.50	30.58	1.88	7.55	0.20	13.97	6.91

[a]Sites where no trapping was conducted during the time period within which data for estimates was collected, because no adult females were captured on those sites earlier in the year.

[b]Standard errors for density estimates for sites where the number of marked animals was used as the abundance estimate were estimated based on the relationship between the average CV of $\hat{N}$ estimates for $\hat{N}<5.0$, and the CV of the area estimate (see text for formula).

Table 2.7. Results of hypothesis tests of site-specific estimates of adult Townsend's ground squirrel density in southwestern Idaho, 1992-1994, from 2 general linear models analyses: one a PROC MIXED (SAS® Institute, Inc. 1992) in which the sampling variance-covariance matrix has been specified, and the other a repeated measures model using PROC GLM (SAS® Institute, Inc. 1989). The main effects tested were habitat type (shrub or grass), location (OTA or off-OTA), and year (92,93, and 94).

		Mixed model		Repeated measures model	
Source	ndf[a]	*F*	*P*	*F*	*P*
Habitat	1	26.41	<0.001	19.53	<0.001
Location	1	68.92	<0.001	39.67	<0.001
Year	2	50.70	<0.001	54.24	<0.001
Habitat × Location	1	0.00	0.958	0.04	0.840
Year × Location	2	12.66	<0.001	11.25	<0.001
Year × Habitat	2	18.19	<0.001	20.75	<0.001
Year × Habitat × Location	2	2.25	0.118	4.87	0.026

[a]ndf = numerator degrees of freedom. For the mixed model, denominator df = 42 for all tests. For the repeated measures model, denominator df = 13 for all tests including year, and df = 14 for the others.

Table 2.8. Comparison of estimates of abundance and standard errors from: 1) the Jolly-Seber model (JS) using program JOLLY (Pollock et al. 1990), 2) the no recruitment model (NR) with no constraints on capture and/or survival probabilities (also using Program JOLLY), and 3) the no recruitment model with constraints (NRC) using our SAS program, with the best model selected according to criteria given in the text. Estimates of N given are $\hat{N}_1$ for NR and NRC models, and the maximum $\hat{N}_t$ for the JS model. Examples were chosen to represent high, moderate, and low sample sizes.

	Method	$\hat{N}$	SE($\hat{N}$)
Example 1:	JS	63.8	29.0
Site 10A, Adult females, 1992	NR	60.1	9.9
Number of individuals marked = 47	NRC	55.8	4.4
Trapping occasions = 7			
Example 2:	JS	12.0	NA[a]
Site 10B, Adult females, 1994	NR	8.0	0.0
Number of individuals marked = 8	NRC	16.2	6.5
Trapping occasions = 17			
Example 3:	JS	1.0	NA
Site 2B, Adult females, 1993	NR	3.0	NA
Number of individuals marked = 2	NRC	2.6	1.0
Trapping occasions = 3			

[a]NA = No estimate of standard error available from Program JOLLY.

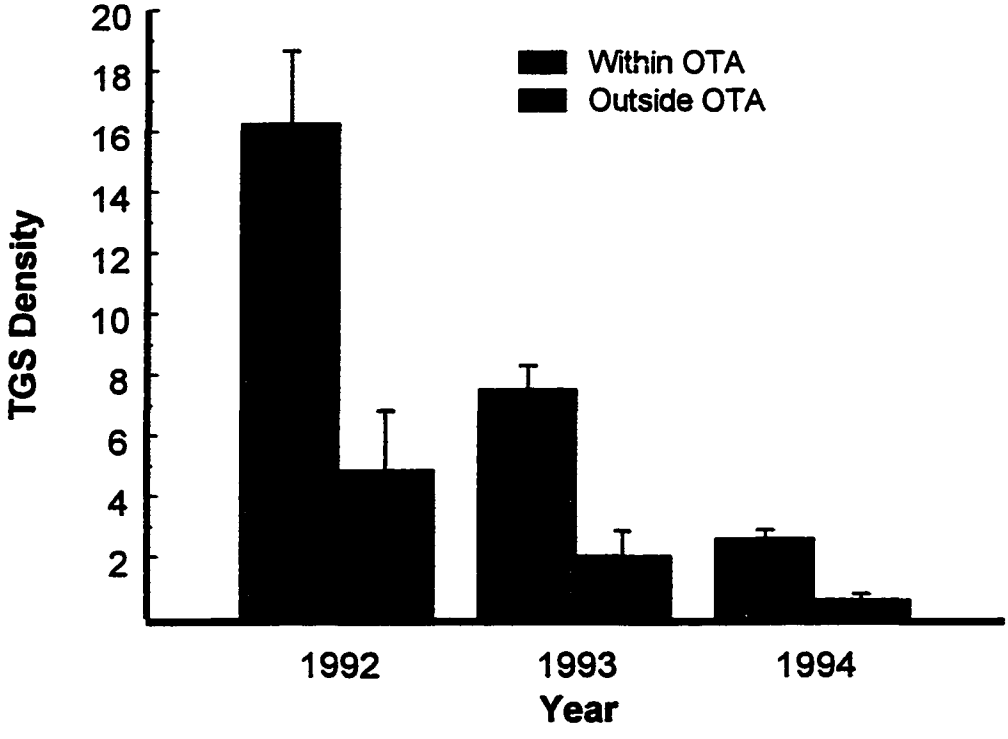

Figure 2.1. Adult Townsend's ground squirrel mean density (animals per ha), by year, for study sites on the Snake River Birds of Prey National Conservation Area, Idaho, located within the Orchard Training Area (OTA; gray bars), and outside the OTA (black bars). Error bars shown are +1 SE.

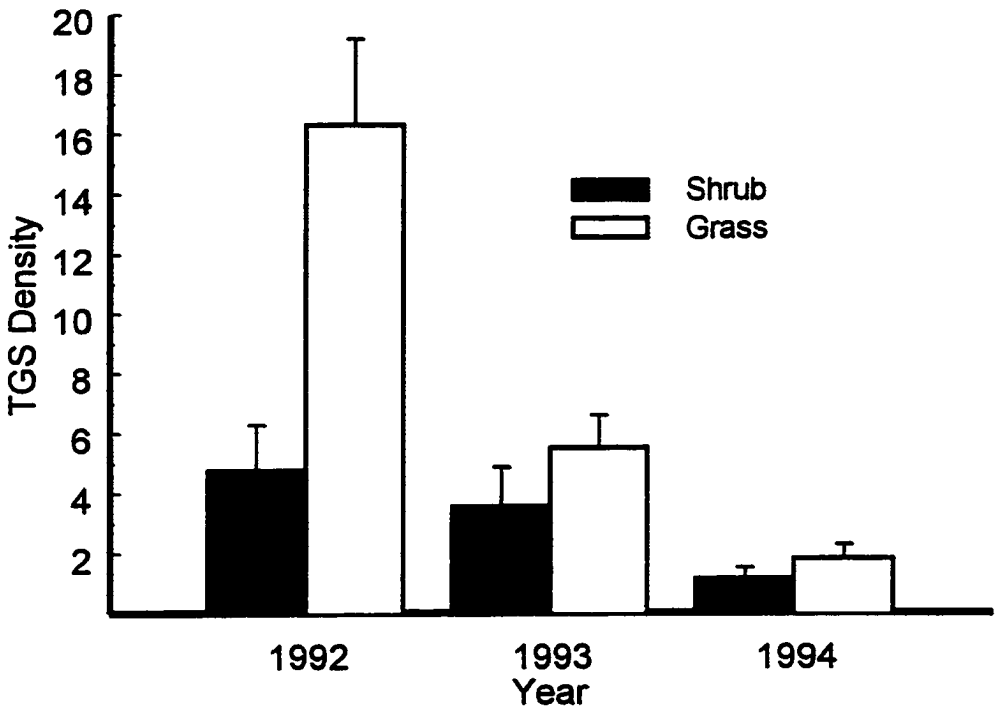

Figure 2.2. Adult Townsend's ground squirrel mean density (animals per ha), by year, for study sites on the Snake River Birds of Prey National Conservation Area, Idaho, located within shrub habitats (gray bars), and grassland (open bars). Error bars shown are +1 SE.

CHAPTER THREE

WITHIN-YEAR SURVIVAL RATES OF TOWNSEND'S GROUND SQUIRRELS

INTRODUCTION

To date, all studies of ground squirrel survival have used one of two methods: 1) capture-recapture, or 2) intensive individual observations. With the exception of the current study, all of the capture-recapture studies have computed survival estimates based on the proportion of individuals that were seen or captured in one year to the total individuals marked in a previous year (cf. Boag and Murie 1981, Smith and Johnson 1985). Most authors admit that these "disappearance rates" reflect losses due to both survival and dispersal, but when used as an index to survival, such rates also assumes that capture probabilities are the same for all categories of interest, and near 1.0, which is seldom realistic.

None of these capture-recapture studies examined within-year (seasonal) survival rates. Other studies, (notably Michener and Locklear 1990 and Michener and McLean 1996) have examined within-season survival of ground squirrels based on intensive observations of individuals. Unfortunately, such methods are rarely feasible for other animals, nor even for all species of ground squirrels. Also, because intensive observations of individuals are not practical on a broad scale, they cannot provide

information on spatial variability of survival rates, and their use to examine temporal variability is limited.

For the TGS demography study, capture-recapture data from 20 study sites over 4 years (1991-1994) were available to estimate survival probabilities using the Cormack-Jolly-Seber model (Seber 1982). Therefore, I was able to examine both temporal (among and within year) and spatial (among sites within varying habitat types) variability in survival rates.

I divided each year into 3 periods based on ground squirrel biology: early season, from emergence of adults from hibernation until juvenile emergence from natal burrows; late season, from juvenile emergence to adult immergence; and over-winter, the period of estivation and hibernation (i.e., from immergence in one year until emergence the following year). I used a biological basis rather than setting pre-determined cutoff dates because the timing of these events (emergence, reproduction, and immergence) varies both spatially (within year) and temporally (among years), and reflects environmental conditions (Van Horne et al. 1997). I estimated survival rates for each period within each year for each study site, and then tested for differences due to sex and habitat type, in addition to the temporal effects of year and period.

Prior to the analyses, I expected to see a few general patterns in ground squirrel survival:

1. *Per-day survival should be higher over-winter than for either active season periods for both sexes and habitat types, across all years. Over-winter survival of females should be lower than that of males in years with poor environmental conditions*

late in the active season, but about equal to that of males in other years. The prediction that survival rates should be highest for the over-winter period may at first seem unreasonable, but it is an elementary result of the use of per-day, rather than per-period survival rates. The over-winter period is >6 times longer than either of the active season periods (approximately 270 days compared to 40-50), and so daily rates must be high during this time if any ground squirrels at all are to survive. To illustrate this, if the estimated daily survival for Period 3 was 0.9900, the overall survival for that period would be $0.9900^{270} = 0.0663$. That same daily survival estimate, projected over a 45 day period, would result in period-specific survival estimate of $0.9900^{45} = 0.6362$.

The hypothesis regarding sex-specific differences in over-winter survival rates was based on the observation that females must delay adding fat for hibernation until later in the year than males, and thus they should be more effected by poor late-season conditions.

2. *Early season survival rates should be lower than late season survival rates for both sexes and within both habitat types, under moderate to good environmental conditions. In addition, early season survival rates of males should be lower than that of females, whereas late season survival rates of males should be equal to or higher than that of females. Male survival should be reduced by poor early season conditions, while female survival should be more affected by late season conditions.* Differences in survival between active season periods, which are of approximately equal length, may be compared directly. Early season survival rates for ground squirrels are most likely affected by their own physiological condition and the environmental conditions upon

emergence from hibernation. Therefore, in most years, I would expect early season survival to be lower than late season for both sexes, as during this time ground squirrels are exposed to generally less hospitable weather conditions, more uncertain food resources, and exposure to predation unmitigated by the presence of juveniles, all at a time when their physiological condition is at it's worst. Males, however, face additional hazards associated with breeding. During this period, they eat little, move around more searching for receptive females (presumably exposing themselves more to predation), and sometimes may fight with other males (Michener and Locklear 1990, and Michener and McLean 1996, and P.B. Sharpe, personal communication). Poor conditions during this time should have greater impact on males, as they also emerge earlier (Rickart 1987), and so are exposed to those conditions longer. However, once breeding is complete (by late February), males have at least 2 months to put on fat for hibernation. Females, conversely, are preoccupied with raising litters until weaning. The demands of reproduction, along with potential competition with juveniles for forage, mean females are also more likely than males to be sensitive to poor environmental conditions during this time.

3. *When environmental conditions are moderate or better, survival rates should be higher in grass habitats than shrub habitats. When conditions are poor, survival should be reduced in both habitats, but to a greater extent in grass than in shrub.* This hypothesis was based on evidence presented by Van Horne et al. (1997), who concluded that although grass habitats seem to be generally more favorable for ground squirrels,

they become inhospitable during drought conditions. Shrub habitats, on the other hand, are apparently less favorable under moderate to good conditions, yet seem to provide refuges to ground squirrels when environmental conditions are poor.

4. *Process variation in survival rates should be lowest during the over-winter period, and approximately the same for the active season periods. Process variance should also be smallest during years when environmental conditions are more extreme.* Here I define process variance as the variability in survival rates left unaccounted for by the global model that includes the factors: year, period, habitat, sex, and their interactions. In this global model, individual heterogeneity in survival, as well as much of the temporal variability, have been eliminated (or more correctly, smoothed over) by the use of site-, year-, period-, and sex-specific survival estimates in the analysis. Therefore, the processes that affect these components of variability are ignored. The remaining variability unaccounted for by the global model (i.e., process variance) is most likely due to spatial differences in survival among study sites, but also may include other apparently random components of variability. Theoretically, process variance might be driven to zero if enough relevant factors are included in the model. However, this is seldom possible, and the pursuit of such a model more likely leads to over-parameterization errors. It is more useful to compare estimates of process variance from models restricted to a few factors. Then, process variance should be an indicator of the importance of model factors relative to other factors not included in the model.

During the year, ground squirrels are exposed to varying sources of mortality; if they do not succumb to these, then by definition they survive. Therefore, factors that

contribute to mortality are the same factors that influence survival. The factors I examined were primarily those that might be associated either directly or indirectly with the influence of environmental conditions on ground squirrel survival. These will not account for other sources of mortality, such as predation, and deaths due to vehicles and shooting. Although some predation may occur while ground squirrels are hibernating, the majority of deaths from predation and all of the deaths from shooting and vehicles, occur during the active season. In addition, these sources are not evenly distributed throughout the study area. The net effect should be an inflation of the estimate of process variance in survival rates for the active season periods, relative to that of the over-winter period.

METHODS

For survival analyses, I included capture-recapture data from all study sites trapped for the TGS demography study in all years (1991-1994). I grouped sites by 2 major habitat classes: shrub, including all shrub dominated sites (n = 10), and grass, including all sites that had been burned previously by wildfire and were dominated by grasses (n = 10).

Environmental conditions

The mean annual precipitation (for the years 1900-1994) on the SRBPNCA is 30.6 cm. but is highly variable (range 16-47). Most precipitation occurs during the fall and winter months (Kochert and Pellant 1986). To relate temporal differences in survival rates to environmental conditions, I assigned each period within each year to 1 of 3 categories: good, moderate, or poor based on how the 3-month cumulative precipitation

for March (for Period 1 assignment) and May (for Periods 2 and 3) compared to quantiles of the long-term (1865-1994) precipitation data. I chose this measure to reflect soil moisture and vegetative conditions which appear to be the primary forces driving TGS demography (Van Horne et al. 1997). If the 3-month cumulative precipitation fell below the 10th quantile, I considered conditions to be poor, if between the 10th and 50th quantile (the median), conditions were considered moderate, and if above the 50th quantile, conditions were considered good. I chose these somewhat skewed categories as I felt that ground squirrels would be most affected by extremely poor conditions (drought), but that there was a threshold above which increased precipitation would not provide additional benefit. Using these criteria, Period 1 conditions in 1991 were considered poor (5th percentile), but Periods 2 and 3 in that year were considered good (54th percentile). All periods in 1992 were considered poor (2nd percentile for both March and May), all periods in 1993 were considered good (71st and 87th percentiles), and all periods in 1994 were considered moderate (12th and 17th percentiles).

Survival rate estimation

I used the Cormack-Jolly-Seber (CJS) model (Seber 1982) as the basis for estimating survival rates. Methods based on the CJS model can explicitly account for any variability in capture rates induced by the changes in the trapping methodology used between years. They give unbiased estimates of apparent survival (i.e., animals that have not died or permanently emigrated from the study area) provided these basic assumptions of the model are met (from Pollock et al. 1990): 1) every animal present in the population at the time of the sample has the same probability of capture, 2) every animal

present has the same probability of survival, 3) marks are not lost or overlooked, and 4) all samples are instantaneous and each release is made immediately following the sample. The general CJS model estimates capture (p_i) and survival parameters (ϕ_i) for each capture occasion (i), but these estimates can be very imprecise (i.e., have large sampling errors). Improvements to this general model, including the relaxing of assumptions 1 and 2 (above) have been made in recent years by several authors using parameter modeling techniques by which constraints or covariates are used to reduce the number of parameters to be estimated, thereby increasing their precision (cf. Lebreton et al. 1992, Schwarz and Arnason 1996). The general procedure consists of fitting several constrained models and selecting the best model for estimation based on some criteria, often using AIC (Akaike's Information Criterion; Akaike 1973, 1985, Anderson et al. 1994, Burnham and Anderson 1998). This model selection process can replace the usual hypothesis testing approach in determining whether specific factors of interest (covariates) are influential in explaining variability in survival estimates. In the TGS study, however, there were potentially 160 datasets to be analyzed (4 years × 20 sites × 2 sexes) which, along with the asynchrony of capture occasions and intervals, made it nearly impossible to construct global models using all data. Therefore, I combined model selection techniques with more conventional hypothesis testing to examine the influences of year, period within year, habitat type, and sex on survival rates.

Site- and sex-specific capture-recapture data were combined by pairs of years; year i and year i+1 were analyzed together to get period-specific estimates within year i and between year i and year i+1. Survival estimates for 1994 were not used because I

found that without recapture data from the following year, it was impossible to separate mortality from estivation. Therefore, survival rate estimates for 1994 were biased low. Each trapping date was treated as a separate capture occasion except in 1991, when several consecutive days were trapped within a cycle. Then I treated all trapping dates within a cycle as a single capture occasion that occurred on the date midway between the first and last days of the cycle. By doing so, I assumed that daily survival within a cycle was = 1.0 (i.e., population closure). I ran several preliminary analyses comparing models that assumed closure with models that did not, and found the former to be as good and sometimes better, and easier to compute estimates for.

Survival probabilities were modeled as log functions of the number of days between capture occasions, which accounted for the varying length of these intervals. Therefore, survival was estimated on a per-day basis. Using this parameter transformation, estimates of survival could be >1.0. This was not of concern, as the estimates from the CJS approach were then used in subsequent analyses for which constraining survival to be ≤ 1.0 was neither necessary nor appropriate (see below).

Capture probabilities were modeled using the logit transformation, and thus were constrained to be between 0 and 1. I fit a series of models to each data set, where per-day survival probabilities were always constrained to be constant within each time period, but capture probabilities could be constrained in one of several ways: 1) constant throughout the year, 2) constant within each time period, 3) a linear function of time elapsed since the beginning of the year, and 4) a quadratic function of time elapsed since the beginning of the year. I sometimes had to combine data from >1 site to compute estimates of

survival rates because of small sample sizes. In such cases, I included site-specific terms in the list of possible models for both survival and capture probabilities. The purpose here was primarily to reduce the number of parameters necessary for computing capture probabilities, and thereby increase precision on the estimated survival rates. I then used the period-specific survival estimates from the best model, chosen based on lowest AIC, for the hypothesis testing part of the analysis.

Although several software packages are available for CJS analyses in general (SURGE; Pradel and Lebreton 1991, POPAN-4, Arnason and Schwarz 1995, MARK, White and Burnham in review), none of these could specifically handle the asynchrony of timing and unequal numbers of capture occasions between sites, which was necessary when data were combined over sites. Therefore, I modified a SAS® program from Burnham (1989) that used Proc NLIN (SAS Institute, Inc. 1989) to compute maximum-likelihood estimates of survival and capture probabilities for the CJS model. I wrote the revised program as a series of SAS® macros (SAS® Institute 1990) that allowed me to input the capture-recapture data as capture history matrices and compute maximum likelihood estimates for the suite of models given above. I used a similar program to estimate abundance using the no recruitment special case of the Jolly-Seber model (Chapter 2), but for survival estimation, I did not make the no recruitment assumption.

Hypothesis testing

Estimates of survival from the CJS methods were used in subsequent analyses which allowed me to test for influential factors using a mixed effects general linear model, and estimate process variance, while explicitly accounting for sampling variances

and covariances. The general framework for this approach is essentially the same as that described by various authors as empirical Bayesian (Morris 1983, Johnson 1989), shrinkage methods, measurement error, or random effects models (Longford 1993). Burnham (in prep), specifically addresses the statistical theory for parameter estimation based on survival estimates ($\hat{\phi}$'s) from the CJS model. Briefly, the general model for this study was $\hat{\phi} = X\beta+\delta+\epsilon$, where $\hat{\phi}$ is the vector of survival estimates, X is the design matrix for the fixed effects, β is a vector of regression coefficients, δ is a vector of sampling errors, and ϵ is a vector of residual errors. The sampling errors (δ) are assumed to be distributed with mean = 0 and variance-covariance matrix W, which in application is the estimated sampling variance-covariance matrix from the selected CJS model. The residual errors (ϵ) are assumed to be mutually independent and to have mean = 0 and variance = σ^2, which is also the process variance. The variance-covariance matrix (VC) of $\delta + \epsilon$ (called D) is the total random error component of the $\hat{\phi}$. Assuming independence of δ and ϵ, $D = \sigma^2 I + W$, where I is the identity matrix. The $\hat{\beta}$ are used to test hypotheses regarding fixed effects and are estimated as $\hat{\beta}=(X'D^{-1}X)^{-1}X'D^{-1}\hat{\phi}$, with unconditional sampling variance-covariance matrix estimated as $VC(\hat{\beta})=(X'D^{-1}X)^{-1}$. Since the formula for $\hat{\beta}$ includes D, which is a function of both W (known) and σ^2 (unknown), an estimate for σ^2 must be found. I used the criterion:

$n-k = (\hat{\phi}-X\hat{\beta})'D^{-1}(\hat{\phi}-X\hat{\beta})$, and solved numerically for both $\hat{\sigma}^2$ and $\hat{\beta}$ (where n = the number of survival estimates in the model, and k = the number of regression coefficients -fixed effects -- in the model). The fixed effects can be tested for statistical significance

using a t-test, where $t = \frac{\hat{\beta}}{\hat{SE}(\hat{\beta})}$ for each regression coefficient and degrees of freedom are $n - k$.

For the TGS study, the fixed effects of interest were year, period within year, habitat type, sex, and the interactions between them. I used a MATLAB (The MathWorks, Inc. 1992) program specifically written for this type of analysis. Inputs to the program were the survival estimates ($\hat{\phi}$) and their variance-covariance matrix (W) from the SAS® macro program, and the design matrix (X) for the specific general linear model under consideration. Outputs from the program included $\hat{\beta}$ and its variance-covariance matrix, and the estimated process variance, $\hat{\sigma}^2$ with a 95% confidence interval (CI) on σ^2. Tests of hypotheses (t-tests) were computed by hand, as were the regression-based estimates of survival rates from the mixed model and their standard errors.

A drawback to the random effects approach is that there is no standard model selection procedure; in particular, as used here, AIC model selection is not applicable because the approach is not based on a likelihood function. Therefore, I used a somewhat subjective step-wise elimination approach to reduce the global model (which included all main effects and interactions between them) to one containing only the effects that seemed most influential. I first eliminated interaction effects for which $P > 0.10$. I then re-ran the reduced model, and subsequently eliminated any interaction effects for which $P < 0.05$, and main effects for which $P > 0.10$, unless there were interaction terms which contained the main effect still remaining in the model. Finally, main effects with $P > 0.05$ were eliminated (again, only if not contained in remaining interaction effects). This led to the final model used to determine the factors most

influential on survival rates. Process variance was always estimated from the global model, as this was the only model for which none of the process variance could be attributed to any of the factors tested.

RESULTS

A total of 5,230 animals was captured in 1,050 capture occasions over the 4 years of the TGS study. Of the 120 potential year-, site-, and sex-specific combinations for which survival rate estimates were desired, I was able to estimate survival rates for 69: 26 in 1991, 27 in 1992, and 16 in 1993. Of the remaining 51, most were eliminated because captures and/or recaptures were too few for reasonable estimates to be computed. Two sites were not included in the 1993 analyses because they had been used in the supplemental feeding experiment conducted in 1993 and 1994.

Survival sometimes could not be estimated for all periods within a year, mostly due to 0 captures or recaptures for all trapping occasions within the period. Estimates from the remaining periods were retained in the analyses even though the result was some imbalance in the number of period-specific estimates per site.

I did not estimate early season survival for 1991 because the timing of trapping on most sites was not appropriate. Therefore, I started with two separate analyses for factor effects: 1) estimates from all years (1991-1993) but for the late season and over-winter periods only, and 2) only estimates from 1992 and 1993, but for all periods. In both analyses, the presence of several higher order interaction terms with $P < 0.05$ made interpretation of results difficult. To reduce this problem, I ran separate analyses by periods to examine among-year effects, and by years to examine within-year (period)

effects. In order to make comparisons of survival rates for discussion, regression means ($\hat{y}$) were calculated as $\hat{y}=X\hat{\beta}$, where β is the vector of regression coefficients and X the design matrix from the appropriate reduced regression model.

Period-specific analyses

For the early season period (1992 and 1993 only), the reduced model consisted of habitat, year, and the year × habitat interaction. (Table 3.1; Figure 3.1). Daily survival rates for 1992 on grass sites were higher than shrub sites, whereas in 1993 they were much lower on grass sites than shrub sites. Process variance (expressed as a standard deviation) for this period was estimated as 0.0045 with 95% CI: 0.0026 - 0.0071. For the late season, the reduced model consisted of sex, year, and the sex by year interactions (Table 3.1; Figure 3.1). Survival rates in 1991 were nearly the same for both sexes, but in 1992 female survival rates were much lower than for males, and in 1993 the reverse was true. The estimated process variance for the late season was 0.0044 (95% CI: 0.0026 - 0.0070), which is not different from the early season (based on overlapping CI's). The final model for the over-winter period was more complex (Table 3.1; Figure 3.2). The year by sex interaction was significantly different between 91 and 92, and between 91 and 93, but not between 92 and 93. However, there was a year by habitat interaction between 92 and 93, which did not occur in any other year by habitat comparison. Regression means were therefore calculated separately for each year, sex, and habitat type (Figure 3.2). The estimated process variance for the over-winter period was substantially smaller than for either of the active season periods: 0.0013, with 95% CI 0.0007 - 0.0022.

Year-specific analyses

When only data from 1991 were analyzed, none of the effects tested were significant; thus the reduced model consisted only of the overall mean. For 1992, the reduced model contained sex, period, and the sex by period interaction factors (Table 3.2). While survival rates for both males and females were highest over-winter, those for females were lowest in the late season but those for males were lowest in the early season (Figure 3.3). Period was the only effect in the final model for 1993 (Table 3.3; Figure 3.3). Again, survival rates were highest over-winter, but about equal between the 2 active seasons. Process variance estimates from the full models were (with 95% CI) 1991: 0.0009 (0.0000 - 0.0020), 1992: 0.0028 (0.0015 - 0.0047), and 1993: 0.0060 (0.0035 - 0.0100). Although confidence intervals for 1991 and 1992 overlap slightly, the point estimate for 1992 is >3 times that of 1991. Likewise, confidence intervals between 1992 and 1993 overlap, although the difference in the point estimates was substantial. There was no overlap between 1991 and 1993 confidence intervals.

DISCUSSION

In general, I found survival rates for Townsend's ground squirrels on the Birds of Prey Area to be affected by a complex inter-relationship of several factors. Whereas the scope of this study was more broad than any other examining ground squirrel survival, it was still insufficient to describe how weather, habitat, and demographic features may account for observed variability in survival rates. My results are the first available for ground squirrels using these methods, however, so they provide important insights into these relationships and a basis for future hypotheses to be tested. I offer the caveat that

any conclusions that I have drawn about the relationship between environmental conditions and survival estimates are based upon the assumption that the years in which this study was conducted were representative of other years with those conditions, and that my classification of periods as poor, moderate, or good is appropriate.

My first hypothesis was mostly supported by the results. Daily survival was higher over-winter than during the active seasons, and survival rates for females in 1992, when conditions were poor late in the year, were lower than for males. Unexpectedly, they were also lower than for males in 1993, which had good conditions late in the year. This could be attributed to carry-over effects from the 1992 drought. Adult females, although having survived the 1992 drought, were in poor physiological condition (Van Horne et al. 1997) and therefore perhaps could not recover following the reproductive period. Further, there was a nearly complete reproductive year-class failure in 1992 (Van Horne et al. 1997), so the adult age class in 1993 was entirely made up of animals $\geq$ 2 years old. Thus lowered survival rates may have been a result of a disproportionate number of older individuals in the population. These same factors should have also affected males; however, they may have done so earlier in the year (see below).

Patterns of survival rates between the active seasons (my second hypothesis) were not always consistent with expectations. In all years, I expected that early season survival for males would be lower than for females, and that the reverse would be true during the late season. In years when conditions were poor, as they were in 1992, I expected this pattern to be more pronounced. Instead, I found no sex-specific differences in early season survival, and the sex-specific differences I found in late season survival were not

what I expected. Females behaved essentially as I predicted, with late season survival rates being lower in 1992 than in either 1991 or 1993 (both considered good years), and rates in 1992 being lower than for males. However, survival of males during the late season in 1993 was lower than it was in either 1991 and 1992, and was also lower than the survival rate of females for that same period in 1993. Again, either age or poor condition following the reproductive period may have contributed to these lowered survival rates. For males, the period of maximum reproductive effort occurs earlier in the year than for females; therefore, the effects of that effort should be realized earlier.

My third hypothesis was that survival during good years would be better in grass habitats than in shrub, yet during poor years the reverse would be true. This turned out to be true for over-winter survival, where survival estimates were lower in grass habitats than in shrub in 1992, but higher in grass habitats in 1991 and 1993 . But during the active season, survival rates in shrub habitats for all years were either the same or lower than survival rates in grass habitats. This seems to indicate that the interactive effects of habitat and environmental conditions involve aspects of habitat that operate primarily during the hibernation period of ground squirrels. For ground squirrels, this means the food resources they must have to build up fat reserves needed to survive during the long hibernation period. This aspect of habitat is apparently of lesser importance to survival during the active season, when other features of the habitat may have greater influence. For instance, Schooley et al. (1996), found that structural features of shrub habitat made predator detection and avoidance more difficult for ground squirrels.

My final hypothesis was that process variation should be greater during the active

season than during hibernation, and that it should be smallest during years when environmental conditions are most severe. The first part of this prediction proved to be correct. However, I expected that process variance would be smallest for 1992, and approximately equal for 1991 and 1993, and instead, it was smallest for 1991. The smaller than expected estimated process variance for 1991 could possibly be accounted for by methodological differences. Process variance, as well as the variation due to model effects, must be estimated from the variance component remaining after sampling error is removed from the total variance. If sampling error is large, relative to the total variability, there may be little residual variation left, especially after model effects are removed. This may have occurred in 1991, more so in the other years, because of the differences in trapping protocol. I did, however, get the relationship I expected for process variation between 1992 and 1993, years in which more directly comparable techniques were used.

All of the comparisons reported above were based on daily survival rates computed within each time period for each year. Period survival rates (and subsequently, annual rates) could be computed if period lengths (in number of days) were known. However, because I used a biologically-based period definition, period lengths were not easy to calculate because the timing of the events used to define these periods (emergence and immergence) was highly variable among years, study sites, and even individual ground squirrels. Furthermore, documentation of the timing of these events was limited by the trapping schedule. For instance, capturing juveniles for the first time in a year on a site indicated only that juvenile emergence had occurred at some time prior to that

trapping occasion, not the exact date of emergence. Determination of immergence dates was further complicated by the difficulty in separating immergence from emigration or death, unless an animal is recaptured the following year. While estimation of period lengths was necessary for the SEP model (see chapter 5), the lengths used are average values based on assumptions and non-rigorous analyses, and I am reluctant to apply them to the specific years of this study.

In summary, I feel the following conclusions about adult ground squirrel survival rates can be made:

1. On a daily basis, survival was highest during the hibernation period. Therefore, it is probably advantageous to ground squirrels to maximize time spent in hibernation by immerging as soon as they have achieved sufficient fat reserves.

2. The timing of environmental events relative to periods of reproductive effort affected sexes differently. This may have contributed to skewed sex ratios.

3. Habitat appeared to be an influential factor on survival among years, but not within years. Grass habitat appeared to be more favorable that shrub habitat in good years, but during a poor year it deteriorated more than shrub habitat, resulting in no differences in survival between the two habitat types.

4. Models for survival rates during the active season were less complex than those for the hibernation period. Even when global models were compared, process variance for the active season was greater than that for the hibernation period. Therefore, it seems that survival of ground squirrels during the active season was more dependent upon external factors (such as predation), whereas survival during hibernation was more

dependent upon a complex relationship between factors which affect the ground squirrels' body condition.

5. Additional factors, such as age or exposure to previous stressful environmental conditions, probably influence survival rates and so should be examined more closely.

6. Estimation of daily survival rates cannot easily be converted to period or annual rates without specific information on period lengths. The length of these time periods varies greatly, and the use of average values for period lengths would lead to inaccurate estimates of period and annual survival, and comparisons among interval survival estimates so calculated would be incorrect.

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Table 3.1. Regression coefficients (β's), their standard errors, and tests of fixed effects on Townsend's ground squirrel survival rates from period-specific random effects models, for the Snake River Birds of Prey National Conservation Area, Idaho 1991-1993. Effects listed were selected by stepwise elimination from a global model consisting of year, sex, habitat type, and all interactions between these effects (see text for details).

A. Period 1 (1992 and 1993 only)

Effect	|β|	SE(β)	|t|[a]	*P*
Year	0.0059	0.0032	1.84	0.073
Habitat	0.0015	0.0026	0.58	0.565
Year × Habitat	0.0135	0.0047	2.87	0.006

[a]Degrees of freedom for t-tests: 41.

B. Period 2

Effect	|β|	SE(β)	|t|[b]	*P*
Sex	0.0060	0.0027	2.22	0.030
Year				
91 v. 92	0.0040	0.0027	1.48	0.144
92 v. 93	0.0125	0.0049	2.55	0.013
91 v. 93	0.0165	0.0057	3.51	<0.001
Sex × Year				
91 v. 92	0.0064	0.0035	1.83	0.072
92 v. 93	0.0199	0.0063	3.16	0.002
91 v. 93	0.0135	0.0061	2.21	0.031

[b]Degrees of freedom for t-tests: 58.

C. Period 3

Effect	|β|	SE(β)	|t|[c]	*P*
Sex	0.0024	0.0012	2.00	0.050
Year				
91 v. 92	0.0005	0.0010	0.50	0.619
92 v. 93	0.0027	0.0014	1.93	0.058
91 v. 93	0.0031	0.0013	2.38	0.020
Habitat	0.0027	0.0012	2.25	0.028
Sex × Year				
91 v. 92	0.0024	0.0011	2.18	0.033
92 v. 93	0.0005	0.0015	0.33	0.742
91 v. 93	0.0029	0.0014	2.07	0.043
Habitat × Year				
91 v. 92	0.0011	0.0011	1.00	0.321
92 v. 93	0.0033	0.0015	2.20	0.032
91 v. 93	0.0022	0.0014	1.57	0.122

[c]Degrees of freedom for t-tests: 60.

Table 3.2. Regression coefficients (β's), their standard errors, and tests of fixed effects on Townsend's ground squirrel survival rates from year-specific random effects models, for the Snake River Birds of Prey National Conservation Area, Idaho 1991-1993. Effects listed were selected by stepwise elimination from a global model consisting of period, sex, habitat type, and all interactions between these effects (see text for details).

A. 1991

All effects were eliminated in the stepwise reduction for 1991, and the final model consisted of only the overall mean (intercept).

B. 1992

Effect	|β|	SE(β)	|t|[a]	*P*
Sex	0.0021	0.0020	1.05	0.297
Period				
1 v. 2	0.0020	0.0025	0.80	0.426
1 v. 3	0.0088	0.0017	5.18	<0.001
2 v. 3	0.0067	0.0021	3.19	0.002
Sex × Period				
1 v. 2	0.0078	0.0033	2.36	0.021
1 v. 3	0.0039	0.0024	1.62	0.109
2 v. 3	0.0039	0.0027	1.44	0.154

[a]Degrees of freedom for t-tests: 74.

C. 1993

Effect	|β|	SE(β)	|t|[b]	*P*
Period				
1 v. 2	0.0019	0.0041	0.46	0.648
1 v. 3	0.0100	0.0029	3.45	0.001
2 v. 3	0.0119	0.0037	3.22	0.002

[b]Degrees of freedom for t-tests: 41.

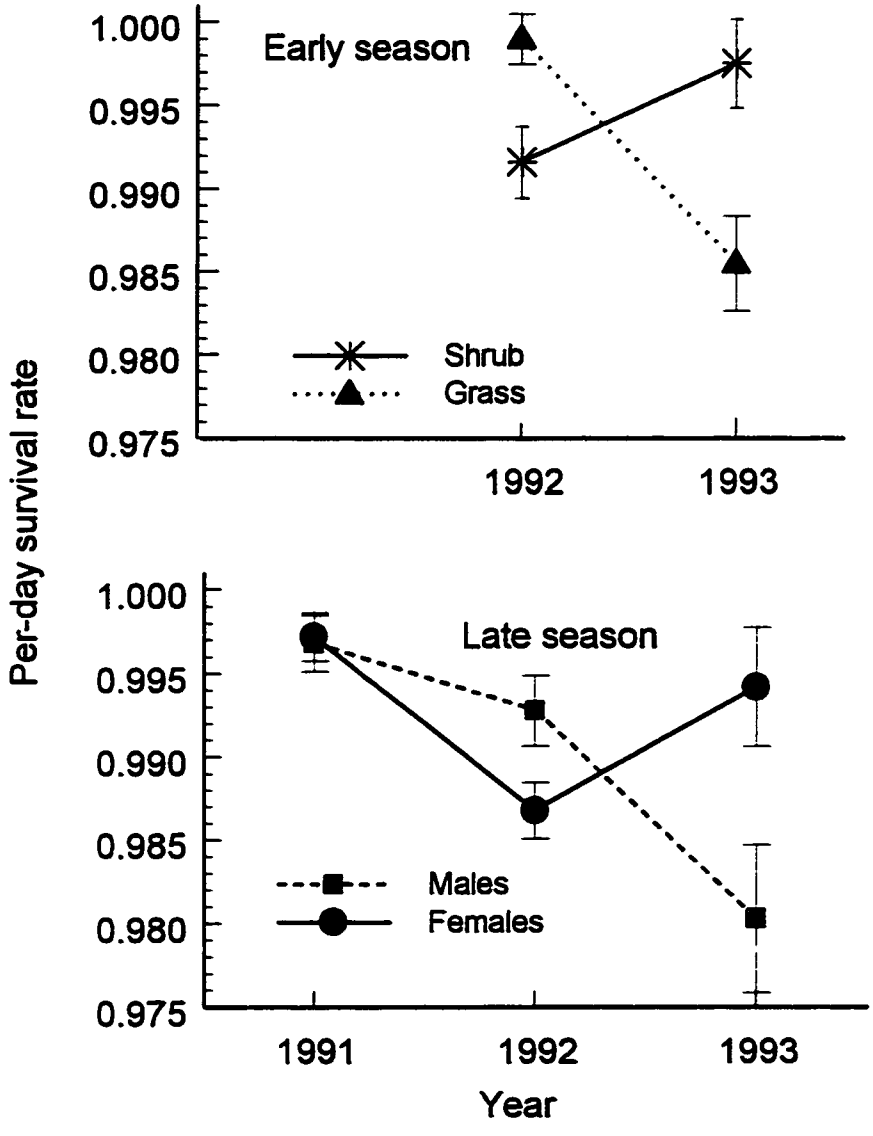

Figure 3.1. Per-day survival rates (±1 SE), estimated as regression means, of adult Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, Idaho, during seasons of above ground activity. For the early season (emergence to juvenile emergence), top graph, estimates were available only for 1992 and 1993, and the regression model consisted of habitat (shrub or grass), year, and the interaction, habitat × year. For the late season (juvenile emergence to immergence), bottom graph, estimates are from 1991-1993, and the regression model consisted of year, sex, and the interaction, sex × year.

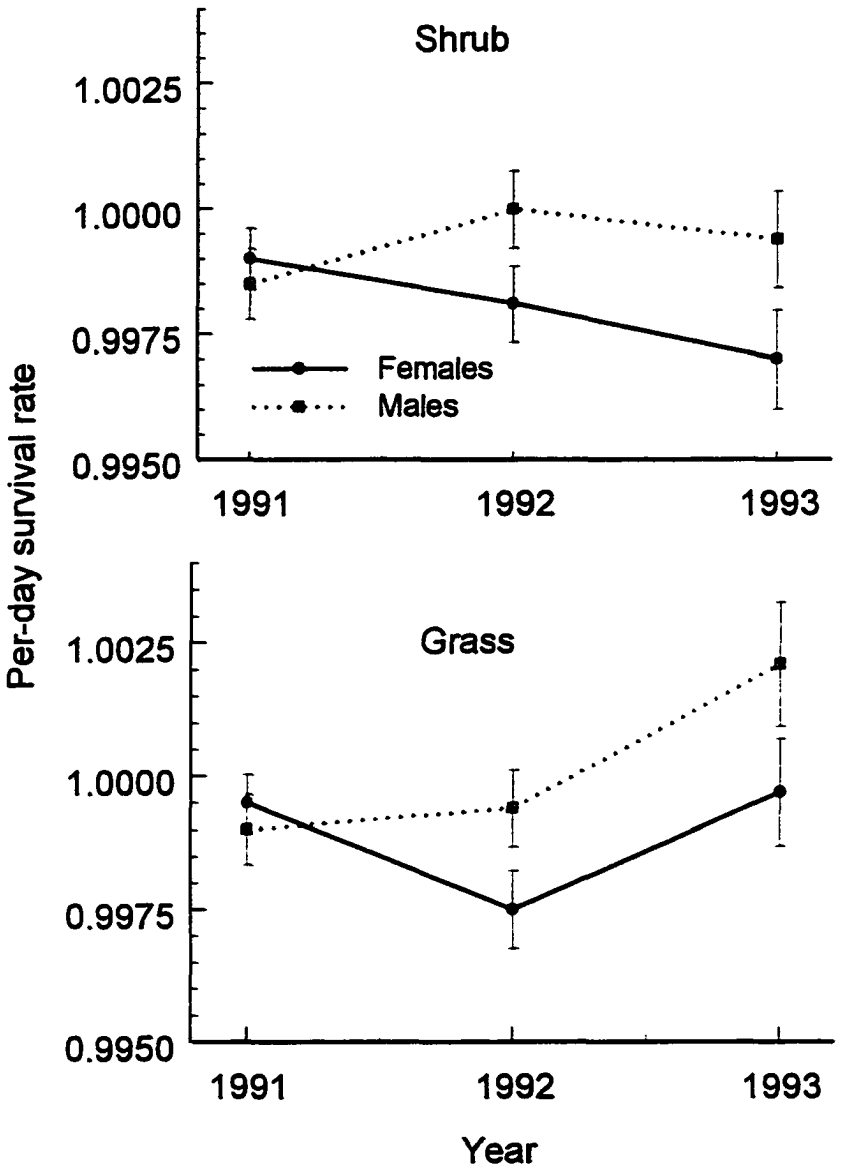

Figure 3.2. Over-winter per-day survival rates (±1 SE) of adult Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, Idaho, in 1991-1993, estimated as regression means from a model containing the factors year, sex, habitat type (shrub or grass), and the interactions sex × year and habitat × year (see text for details). The top graph displays estimates for shrub habitat, and the bottom graph for grass habitat.

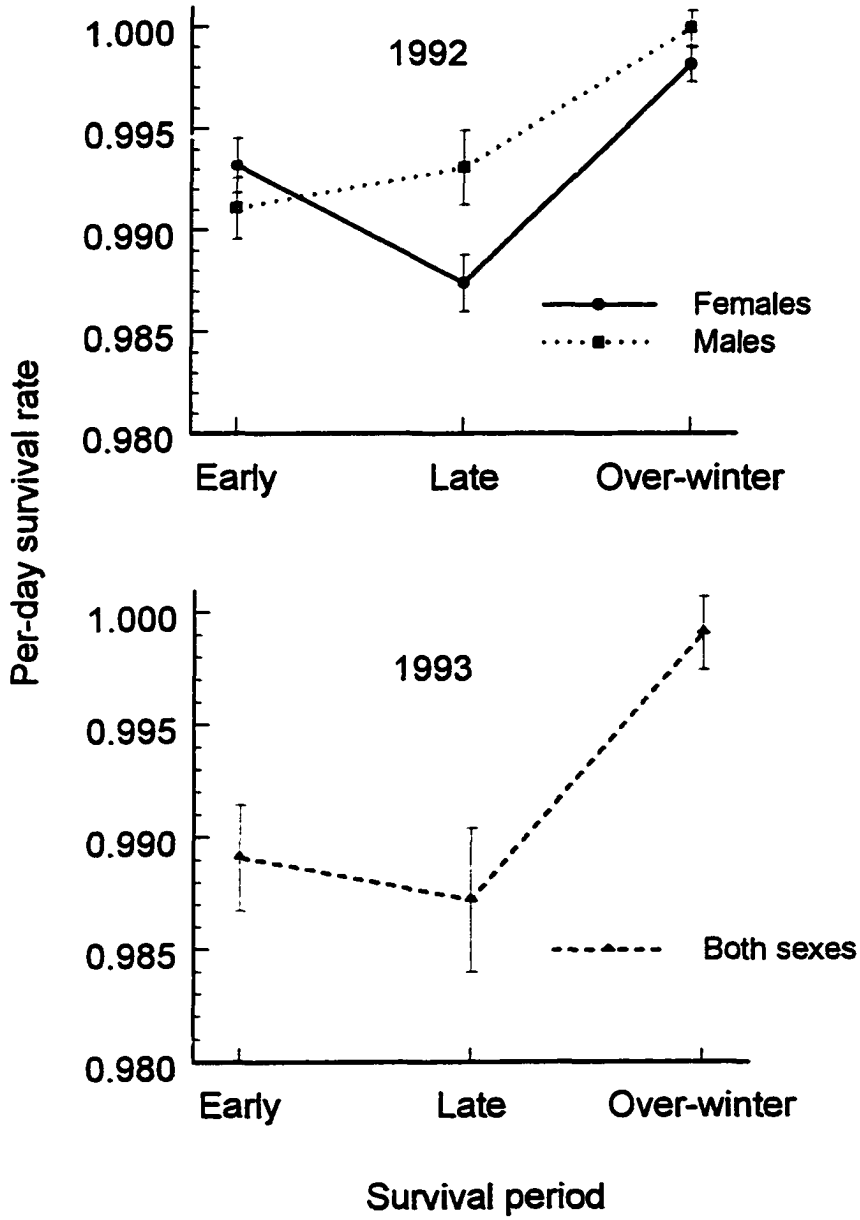

Figure 3.3. Per-day survival rates (±1 SE) of adult Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, Idaho for 3 periods (early active season, late active season, and over-winter) in 1992 and 1993, estimated as regression means from reduced models resulting from a stepwise selection procedure (see text for details). The top graph shows estimates for 1992, where the reduced model consisted of the factors sex, period, and a sex × period interaction. The bottom graph shows estimates for 1993, where the reduced model contained only a period effect.

CHAPTER FOUR

DISPERSAL PATTERNS OF JUVENILE TOWNSEND'S GROUND SQUIRRELS

Long ignored by most population biologists, dispersal (i.e., immigration and emigration) is now being specifically incorporated into many population models, and is a primary focus of some. Two general classes of such models have emerged: metapopulation models (Hanski and Gilpin 1991), where only dispersal rates are of interest, and spatially explicit population (SEP) models (Dunning et al. 1995) which also require information on the specific patterns of dispersal movements. To develop a SEP model for Townsend's ground squirrels (TGS), I required information about both their rate of dispersal, and the pattern of their dispersal movements.

Although there have been several studies of dispersal of other ground squirrel species (see Holekamp 1984, Hackett 1987, Wiggett et al. 1989, and Weddell 1991), no information was available on dispersal characteristics of TGS. Whereas some assumptions might be made about dispersal patterns of TGS based on other ground squirrel species (such as the predominance of natal, or pre-breeding, dispersal), the habitat within which TGS were studied was sufficiently different from that of the other species studied to warrant a specific study of TGS dispersal. In addition, I required information patterns of dispersal movements that had not been studied in ground squirrels previously.

As pointed out by McShea and Madison (1992), radio-telemetry is superior to live-trapping techniques for verification of the occurrence of dispersal, description of dispersal movements, and establishment of the fate of dispersers. Although some ground squirrel researchers (cf. Michener and Michener 1977, Holekamp 1986) have been able to observe directly the dispersal movements of the species they studied, this was not practical for TGS on the SRBPNCA because of their small size (juveniles are approximately 100-120 g at time of dispersal) and because the habitat precludes continuous observation. Therefore, I used radio-telemetry methods to investigate dispersal of juvenile TGS collared in 1993 and 1994. My specific objectives were:

1. to confirm sex-specific differences in dispersal rates;
2. to compare dispersal patterns between juveniles born in the two habitat types, shrub and grass;
3. to quantify aspects of Townsend's ground squirrel dispersal patterns, such as direction and distance; and
4. to compare fates of dispersers to those of non-dispersers.

METHODS

This study was conducted in April-June 1993 and 1994. Four sites were selected from among the 20 sites being trapped as part of the TGS demography study to represent 2 habitat types (2 sites in each habitat type): shrub, dominated by big sagebrush, and grass, formerly sagebrush areas that had burned and are now dominated by Sandberg's bluegrass (Figure 4.1). Sites of the same habitat type were within 2 km of each other, with approximately 10 km between the sites in differing habitat types. Although sites

were originally selected for the demography study because of the homogeneity of habitat type at the scale of the site (10 ha), all sites had patches of at least 2500 m^2 of the other habitat type within <500 m. All sites were within the Orchard Training Area, but no training took place on these sites while this research was conducted. Only 2 sites (designated as 9B and 10B by the demography study) were used in 1993 because captures of juvenile squirrels were too few on the other 2 sites (5B and 10A) to justify the additional effort required to monitor radio-collared animals on those sites. All 4 sites were used in 1994.

Collaring and radio-tracking

The radio transmitter package used in this study (constructed by Advanced Telemetry Systems, Isanti, MN) was attached via a neck collar made of synthetic webbing, perforated with a series of holes that allowed adjustment to fit individuals, and using a threaded bolt (permanently glued to the package) and nut to fasten the collar. This attachment system enabled us to adjust collars as juveniles grew. This was the smallest (4.4-5.4 g) package available at the time of the study that had sufficient signal strength (detectable at up to 400 m when animals were below ground and up to 800 m above ground), and duration (guaranteed up to 30 days) for this study to be feasible, as determined by a pilot study I conducted in 1992.

All animals in this study were captured during the course of normal trapping operations for the demography study, although the sites selected for this study were trapped more frequently to increase the number of capture opportunities. All eligible juvenile ground squirrels (up to the target sample sizes, n = 30: 10 males, 5 females in

each of the 2 habitat types) on each of the 4 study sites were radio-collared, with the eligibility criteria that 1) they be of sufficient weight (generally, >90 g), so that transmitter packages would be no more that 5% of body weight, 2) that no animal >115 g was collared unless it was known to have been captured previously on the site at <100 g, and 3) no animal was collared at >135 g. The minimum weight criterion was imposed by the size of the transmitter package. The maximum weight criteria were used conservatively as an approximation of age to minimize the likelihood of collaring animals that were born elsewhere and immigrated into the trapping area, or that were beyond the age at which they would disperse. Initially, juveniles were not collared at the same time they received PIT tag injections (their first capture). In 1993 recaptures of juveniles were rare, so juveniles >100 g were collared at first capture if they appeared to be unaffected by the PIT tagging procedure.

Because the guaranteed duration time of batteries powering transmitters (30 days) was shorter than the time interval during which I thought dispersal would take place, all functioning radios were replaced with new transmitters 30 days after initial collaring, or earlier if the signal started to fail prematurely. Collars were also periodically checked and loosened as necessary to accommodate growth.

Whenever possible, all collared animals were located at least once daily using a hand-held 3-element folding Yagi antennae (Model ASA10H3, Advanced Telemetry Systems, Isanti, MN) and 1 of 2 16 channel receivers (Fieldmaster Model RSA161N, Advanced Telemetry Systems, Isanti, MN) . At the minimum, signals were recorded as within or outside of the trapping grids. About 60% of the time, however, exact locations

of animals were determined by walking them up (White and Garrott 1990: 42). When animals were tracked to burrows below ground, the entrance (or the point of the strongest signal when no associated entrance was evident) was marked with an aluminum tag bearing a unique code, and the azimuth and distance to a nearby reference point was recorded. Burrows used as temporary refugia (for <10 minutes) were not marked unless they were found in an area in which the animal had not been located previously. The UTM (Universal Transverse Mercator) coordinates of the reference points were determined with a Global Positioning System unit (manufacturer unknown) that had a 2.5 m circular error probable (i.e. 50% of recorded points would fall within that radius). The UTM coordinates of all marked locations were calculated by trigonometry. The error of each such determined location was assumed to be negligible, and was ignored in subsequent calculations.

Daily monitoring continued until the signal was lost, the collar was found (either on a dead animal or alone), or the signal was tracked to the same location underground for more than 5 consecutive days. When a signal was lost, an area up to 4 km in radius from the point where the signal was last recorded was searched on foot and by vehicle, in an attempt to relocate the animal. All tracking was concluded by 30 June in both years.

Dispersal measures

A major difficulty in studies of dispersal is recognizing dispersal when it occurs. For this study, I defined dispersal as a 1-way, permanent movement away from the natal area, such that the area used by an animal after dispersal no longer overlapped with the area it used before. Therefore, I mapped the sequential locations for each animal and

classified as dispersers those which showed a bi-modal distribution pattern, with the cluster of locations taken later no longer overlapping the cluster of earlier locations. This method appeared to be sufficient to distinguish dispersers from non-dispersers even for animals with broad daily movement patterns.

Distance of dispersal was measured as the straight-line distance from the natal burrow (if known), or from the point of first capture, to the last hole known to be used by the animal. I tested the distance data for fit to a truncated exponential distribution. Although geometric distributions are more commonly considered for dispersal distance models (Waser 1985, Buechner 1987), they require knowledge of some appropriate interval size to group the distance data. Often these intervals are home range or territory size. Townsend's ground squirrels are not territorial, nor was an appropriate home range size known. As noted by Rees (1993), the geometric distribution is a discrete case of the exponential distribution, which only requires the actual distance data and not some arbitrary interval size. The exponential distribution assumes that there is a "stopping rate" (β) that is the same for each unit of distance >0 (meters, in this study). Although β remains constant regardless of how far the animal has moved (and so is considered a "memoryless" distribution), the probability of moving any particular distance, *d*, declines rapidly as *d* becomes large. I used a truncated version of the exponential distribution to re-scale the range of the exponential and account for the fact that, by definition, dispersers must have moved some minimum distance, *c*, in order to be considered a disperser. The truncated exponential distribution function may be given as:

$$f(d) = \beta e^{-\beta(d-c)} \quad , c > 0, d > c .$$

The estimate of β and it's standard error, for the truncated exponential distribution with *c* unknown, are:

$$\hat{\beta} = \frac{n-1}{n}\frac{1}{\bar{d} - d_{\min}}, \qquad SE(\hat{\beta}) = \frac{\beta}{\sqrt{n-1}},$$

where d_{min} is the smallest dispersal distance recorded. A (1-α)100% confidence interval for β is based on the χ^2 distribution:

$$\frac{\hat{\beta}\chi^2_{2(n-1),\frac{\alpha}{2}}}{2(n-1)} \le \beta \le \frac{\hat{\beta}\chi^2_{2(n-1),1-\frac{\alpha}{2}}}{2(n-1)}.$$

The truncation factor, c, is estimated as:

$$\hat{c} = d_{\min} - \frac{\bar{d} - d_{\min}}{n-1},$$

with standard error:

$$SE(\hat{c}) = \frac{n}{n-1}\frac{\bar{d} - d_{\min}}{n-1}.$$

A (1-α)100% confidence interval for c is (Epstein and Sobel, 1954):

$$d_{\min} - a(\bar{d} - d_{\min}) \le c \le d_{\min}, \text{ where } \quad a = \alpha^{-\frac{1}{(n-1)}} - 1.$$

More specific details on the use of the truncated exponential distribution function for

modeling dispersal can be found in Olson and Burnham (in review).

The direction of dispersal was computed as the azimuth, in degrees, from the starting to ending point, defined as for distance. The distribution of dispersal directions was tested for deviation from a uniform distribution ranging from 1 to 360°.

Animal fates

I categorized the fates of radio-collared animals as died, survived to estivation, or unknown. In 1994, I was able to establish specific fates for transmitters tracked to stationary locations by digging them up; either immediately if they were outside the trapping grid boundaries, or after trapping had concluded if they were within the grid areas (and transmitters were still functioning at this time). No transmitters were dug up in 1993 because in all cases, stationary signals occurred on or very near trapping sites, and I did not wish to influence the results of the demography study by undue disturbance to the area.

I classified as died animals that were either found dead, or for which death was a nearly certain outcome based on the circumstances in which the collar was found. I assumed animals had survived to estivation if they were known to be alive up to the period immergence generally took place (as indicated by live-trapping data and personal observation), showed localization of movements prior to estivation, and were tracked to undisturbed holes for several consecutive days following localization. In 1994, I attempted to establish the post-hibernation fates of animals that survived to estivation in 1993 by target trapping in areas near hibernation burrows immediately after animals in general began to emerge. By that time, however, transmitters were no longer functioning,

so if animals were not trapped I did not know what their ultimate fate was.

Statistical tests

I tested for differences in the proportion of dispersers by sex, habitat type, and year using logistic regression (SAS® Proc Genmod, SAS® Institute, Inc.1993). I also used logistic regression to test for differences in the proportion of collared squirrels surviving to estivation due to habitat type, year, and dispersal status. Comparison of means were calculated with parametric t-tests if data were either normally distributed or could be transformed to make them so; otherwise Wilcoxon rank sum tests were used. The distribution of dispersal direction was tested for deviation from a uniform distribution using Kuiper's test (Batschelet 1981: 76) for circular data. Program TRANSECT (Burnham et al. 1980) was used to test for goodness-of-fit of the adjusted ($d - \hat{c}$) distance data to the exponential distribution (Epstein and Sobal 1954). Exact probability levels (P-values) are given when available; when tables were used the range within which the P-value falls is given. In general, results of tests for which P-values were ≤ 0.05 were considered statistically significant.

RESULTS

Collaring and radio-tracking

A total of 59 juvenile Townsend's ground squirrels were radio-collared: 28 (17 males, 11 females) in 1993, and 31 (20 males, 11 females) in 1994. Although collaring began on all sites as soon as eligible animals were trapped, the initial collaring dates differed between years (for grass sites, with 1994 nearly 2 weeks earlier than 1993) and between habitat types within years (1 week earlier on grass sites in 1993 and 3 weeks

earlier on grass sites in 1994). I initially had problems with ground squirrels apparently slipping collars; in just 2 cases in 1993 this was established with certainty by subsequent recaptures of animals that had been collared. Additionally, 8 animals in 1993 and 5 animals in 1994 were thought to have slipped their collars, because collars were found lying on the ground with no sign of predation, or were tracked to a single location underground for several consecutive days within 5 days after the collar was placed on the animal. For stationary collars that were dug up in 1994, slips were thought to have occurred if the collar was found in a burrow system with no sign of disturbance.

With 1 exception, collars appeared to have no effect on either movements or survival. This was supported by observations made by P. Sharpe (personal communication) during a concurrent behavioral observation study. The exception was 1 animal in 1993 that was found dead with a foreleg slipped inside the collar.

Five transmitters were replaced using target trapping in 1993, and 15 in 1994. I removed, without replacement, the collar from one animal that had dispersed when abrasions were discovered on its neck. No other injuries of collared squirrels were noted.

In 1993, 860 radio checks (mean per animal: 30.7) were recorded, with signals found 797 (28.5) times, and animals tracked to exact locations 526 (18.8) times. Those numbers increased in 1994 to 1199 (38.7) checks, 1147 (37.0) finds, and 613 (19.8) exact locations. In 1993, a mean of 6.4 unique locations (primarily burrow entrances) per individual were marked (180 total), with a range of 0-24. About double these numbers of locations were marked in 1994 (11.7 locations per individual, 363 total), but the range was similar (2-24). Signals were lost from 4 animals (3 in 1993 and 1 in 1994); 1 of

these (in 1993) had dispersed prior to signal loss, but for the remaining 3 no information on dispersal was available.

Dispersal measures

In 1993, I identified 5 dispersers, all males, from 14 animals (9 males, 5 females) whose dispersal status was known. In 1994 there were 11 dispersers (10 males and 1 female) from a total of 24 (17 males and 7 females). Of the main effects (and their interactions) tested in the logistic regression model, the proportion of dispersers (p) differed only by sex ($\chi_1^2 = 8.98$, $P = 0.003$), with males ($\hat{p} = 0.58$, SE = 0.097) much higher than females ($\hat{p} = 0.08$, SE = 0.078).

Dispersal distances averaged 505.0 m in 1993 (range: 204-1005 m), and 520.8 m in 1994 (range: 146-1076 m), and were not significantly different between years ($t = 0.14$, $P = 0.89$, test performed on log of distance in meters). Pooled over both years, the mean dispersal distance was 515.5 m. There also were no differences between habitat types (means: grass, 495.0 m; shrub, 542.7 m; $t = 0.08$, $P = 0.94$). Therefore, distance data were pooled.

A total of 15 dispersers (males only) were included in the test of the distance distribution. The stopping rate, β, was estimated as 0.0024, with standard error 0.00064 and 95% confidence interval 0.0013 - 0.0038. The estimated correction factor, $\hat{c}$, was 118.5 (SE: 29.5) with 95% confidence interval 90-146. The exponential distribution was not rejected as fitting the distance data ($P = 0.053$). A plot of the distance data, and the fit of the estimated exponential distribution, are given in Figure 4.2.

The distribution of the direction of dispersal, for all data pooled, was not

significantly different from uniform ($K = 1.43$, $0.10 < P < 0.20$), using Kuiper's test.

In all cases, an individual's dispersal occurred over a span of ≤ 3 days, regardless of the distance moved. In fact, it is likely that most movements were made in a single day because searches for lost signals were not initiated unless they could not be located for 2 consecutive days. Only 1 animal was known to have dispersed over a 3-day period.

The timing of dispersal proved to be highly variable within and between sites (Figure 4.3). Neither habitat ($Z = 1.71$; $P = 0.09$) nor year ($Z = 0.23$; $P = 0.82$) were significantly related to timing of dispersal (Wilcoxon rank sum test).

Animal fates

I was able to determine fates (survived or died) for 29 radio-collared animals (11 in 1993, 18 in 1994; see Table 2). For the 26 animals that survived through the dispersal period, there were no significant differences in subsequent fates (survival to estivation or death) for dispersers vs. non-dispersers , nor were there differences in fates between years, habitat types, or any interactions. Twelve animals were known to have survived to estivation, 6 in each of the 2 years. Of those that survived in 1993, only 2 were recaptured in 1994. Both of these were non-dispersers captured during trapping conducted for the demography study. Target trapping for dispersers was unsuccessful. For the 4 animals not recaptured in 1994, an examination of their hibernation burrow entrances early in that year indicated that 1 disperser may have survived (fresh sign was seen at the entrance), while holes for 1 disperser and 1 non-disperser had been dug up by badgers at some time during the hibernation period and thus those animals were thought to have died. The fate of the 4th could not be determined.

DISCUSSION

Sex-specific dispersal patterns

The finding of male-biased juvenile dispersal rates was not surprising, as this has been the case for virtually all other species of *Spermophilus* (Holekamp 1984). Although the intentionally skewed sample sizes (37 males, 22 females) might have biased the results somewhat, finding only 1 female disperser over both years lends strong support to the conclusion that dispersal by females is rare, at least under the conditions which occurred during this study. The latter caveat may be important as Dobson (1979) has suggested that female dispersal may be triggered by food shortages. The 2 years of this study followed a substantial decline of TGS populations (Van Horne et al. 1997) and food resources were evidently abundant in both years. Dispersal by male juvenile ground squirrels is thought to be less influenced by resource availability (Dobson 1979, Holecamp 1984, Wiggett and Boag 1992), occurring at higher rates even when resources are abundant. This conclusion was supported by my study.

As only 1 female dispersed, I could not examine sex-specific differences in dispersal patterns. Although Michener and Michener (1977) found that females disperse shorter distances than males, most studies concluded that there were no differences in dispersal distances between sexes (Holekamp 1986, Hackett 1987, Weddell 1991). In my study the single female disperser traveled 283 m, which was the second shortest distance of any disperser.

Habitat-specific differences in dispersal patterns

To date, no other study has examined habitat-specific characteristics of dispersal in ground squirrels, and few have examined these differences for other small mammals. Although I did not detect differences in dispersal patterns between the two habitat types examined (see below), this does not diminish the importance of further investigating possible habitat influences on dispersal movements. However, caution should be exercised to remove possible confounding between habitat and density. I did not have this problem as densities were similar between the 2 habitat types during the years of this study (Chapter 2).

In general, I am satisfied with the conclusion that dispersal rates do not differ by habitat type. However, despite the fact that the number of animals collared (59) was more than that of many small mammal studies, small samples sizes may have inhibited my ability to detect habitat-specific differences in dispersal rates. For instance, the difference in the estimated proportion of male dispersers between the 2 habitat types in 1993 (0.75 for grass vs. 0.40 for shrub), while apparently substantial, is not statistically significant ($n = 9$; $\chi^2 = 1.14$, $P = 0.29$). At least double my sample size, equally balanced, would be required to detect a difference of this magnitude with a χ^2 test ($\alpha = 0.05$) with power = 0.80. However, when years were pooled, with larger sample sizes and between site variation ignored, the estimated difference between habitat-specific rates is only 0.06, which may not be biologically significant either.

The similarity of dispersal rates between habitat types seems to indicate that there may be no habitat-specific differences in what prompts juvenile ground squirrels to

disperse. Likewise, finding no differences in average dispersal distance between habitat types suggests that the process of dispersal is not influenced by habitat. However, during the course of this study, I noticed a tendency for dispersers to immigrate to locations in the same habitat type as that from which they emigrated. In 1993, all dispersers ended dispersal movements in the same habitat type as that in which they began; in 1994, all but 3 did. Although the study sites on which the animals were trapped were of a single habitat type, all were surrounded by numerous patches of the opposite habitat type of varying size, well within the range of dispersing ground squirrels. Although actual dispersal paths are unknown, it is highly likely that in many cases, and especially for the longer-distanced dispersers, they must have encountered patches of the other habitat type. In many cases, the end point of the disperser's movement was located at the edge of a habitat patch. Unfortunately, I did not design this study to examine this phenomenon and therefore do not have specific habitat information at a scale relevant to dispersing squirrels. However, these observations are worth noting as they indicate an important area for future research. Animals dispersing preferentially to similar habitat types may view the landscape as having an island structure, even in an area such as the SRBPNCA which appear to be composed of relatively contiguous, if variable, ground squirrel habitat. Habitat dispersal preferences will have implications for gene flow models as well. According to Barton (1992), it is just this pattern of differential dispersal that is required to maintain polymorphism in population, such as ground squirrels, with high dispersal rates.

Estimation of dispersal movement patterns

Small sample sizes may also have prevented detection of differences in dispersal distance and direction distributions from the relatively simplistic distribution functions I examined (exponential and uniform, respectively). Probability values for both tests were somewhat low, offering the possibility that differences might have been detected with more power, i.e., larger sample sizes. Although it may be difficult to determine what sample size would be adequate, Buckland et al. (1993) advocate 60-80 as a minimum sample size for estimating the detection function in line transect sampling; this is at least 4 times greater than my sample size of 15. Therefore, my inability to reject the exponential distribution (at $\alpha = 0.05$) as a model for dispersal distances is not surprising. With such small samples, it would be also be inadvisable to draw definitive conclusions based on the low P-value associated with the test for the fit of the exponential distribution. From Figure 4.2, it appears that more dispersers travel distances moderate distances (near the mean), and fewer traveling short and long distances, than would be expected under the exponential null model. Such a pattern could arise from variation in the stopping rate, β, either as a function of distance from the originating area, or due to some habitat characteristic that may be correlated with distance. Miller and Carroll (1989) proposed alternatives to the geometric distribution that incorporate variability in the discrete analog to β. Such models may also be appropriate for modeling TGS dispersal distances, but I have insufficient data to test that theory.

Although I did not reject a uniform distribution for dispersal direction, when dispersal endpoints are plotted with a common origin (0,0), there appears to be a distinct

trend toward dispersal to the northwest (Figure 4.4). A χ^2 test for whether endpoints were evenly distributed in each of the 4 map quadrants (1-90°, 91-180°, 181-270°, 271-360°) is highly significant ($P < 0.001$). At this time, I can offer no plausible explanation for why this may be so, especially given the relatively wide geographic range over which these data were pooled (Figure 4.1). It may simply be an artifact of the data.

Comparison of fates

Low sample sizes also may have precluded detection of differences in fates between dispersers and non-dispersers, although the estimated difference (0.10) in the proportion of survivors between the two groups was small. This seems to support observations by others (Hackett 1987 and Wiggett et al. 1989) that dispersal is not an especially risky event for ground squirrels.

In summary, I found dispersal characteristics of Townsend's ground squirrels to be similar to those of other ground squirrels, as far as they are known. This study, however, examined additional aspects of dispersal patterns of ground squirrels that had not been studied previously, and demonstrated that more information is needed on the details of dispersal movements to adequately assess what determines these patterns, as well as how such patterns might be modeled. Whereas several authors (cf. Holecamp 1986, Wiggett and Boag 1992) have examined the stimulus for dispersal, much remains to be studied about the process of dispersal once it has been initiated.

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Table 4.1. Proportions of dispersers (sample size) by sex, and for sexes combined for 1993, 1994, and years combined, within and across habitat types.

	1993			1994			Years Combined		
	Grass	Shrub	Overall	Grass	Shrub	Overall	Grass	Shrub	Overall
Males	0.75 (4)	0.40 (5)	0.56 (9)	0.55 (11)	0.67 (6)	0.59 (17)	0.60 (15)	0.54 (11)	0.58 (26)
Females	0.00 (1)	0.00 (4)	0.00 (5)	0.00 (3)	0.25 (4)	0.14 (7)	0.00 (4)	0.12 (8)	0.08 (12)
Combined	0.60 (5)	0.22 (9)	0.36 (14)	0.43 (14)	0.50 (10)	0.46 (24)	0.47 (19)	0.37 (19)	0.42 (38)

Table 4.2. Proportion of survivors (sample size) among dispersers and non-dispersers (sexes pooled) for each year, years combined, and within habitat type with years combined.

	Year			Habitat	
	1993	1994	Combined	Grass	Shrub
Dispersers	0.50 (4)	0.33 (6)	0.40 (10)	0.43 (7)	0.33 (3)
Non-dispersers	0.67 (6)	0.40 (10)	0.50 (16)	0.40 (10)	0.67 (6)

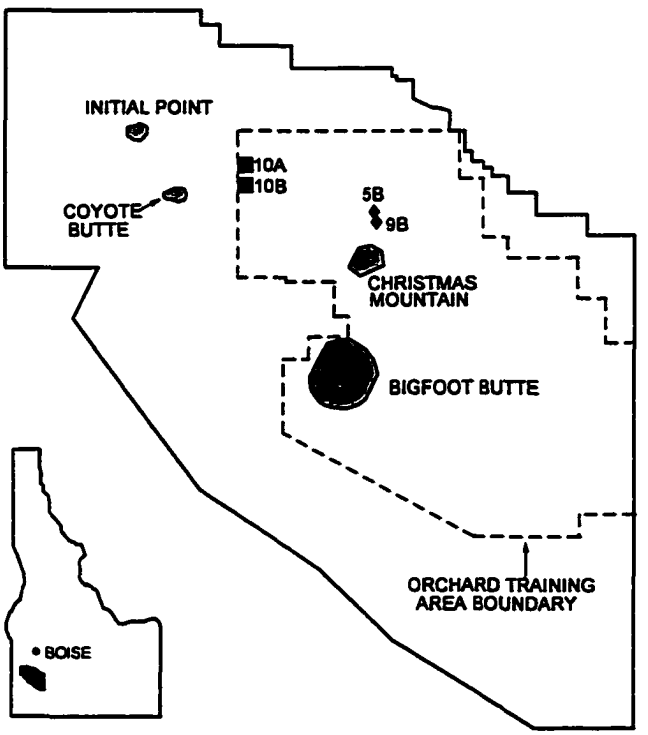

Figure 4.1. Location of the Snake River Birds of Prey National Conservation Area in southwestern Idaho (inset) and radio-telemetry sites used in the dispersal study (larger map). Grass sites are shown as solid squares (sites 10A and 10B) and shrub sites are shown as solid diamonds (sites 5B and 9B). The distance between sites within a habitat type is ≤ 2 km., and 10 km. between sites in differing habitat types. (Modified from Van Horne et al. 1992).

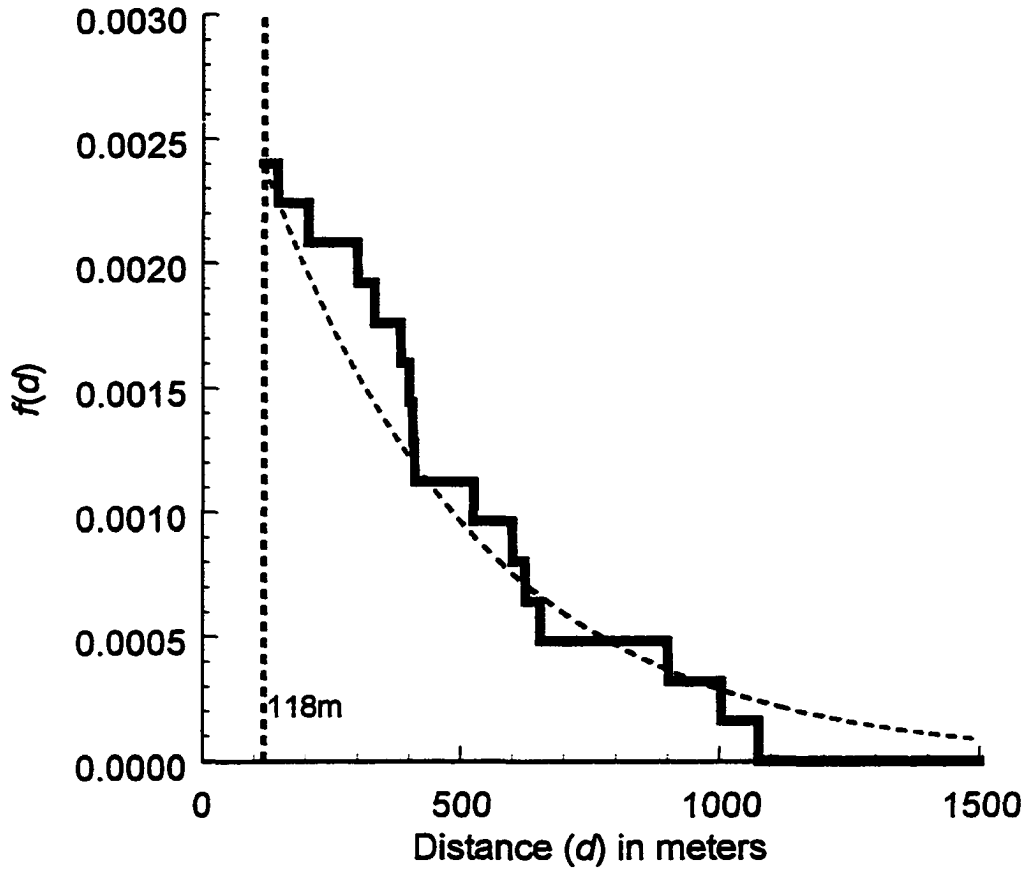

Figure 4.2. Plot of the exponential probability function (dashed line): $f(d) = \beta e^{-\beta(d-c)}$, where $\hat{\beta} = 0.0024$. Actual distance data are shown by a Kaplan-Meier type hazard function (solid line), where the distance each disperser stops at is represented as a "loss" and the axis is scaled to match the exponential function. The vertical dashed line is the truncation distance ($\hat{c} = 118$) as estimated for these data; the formula is given in the text.

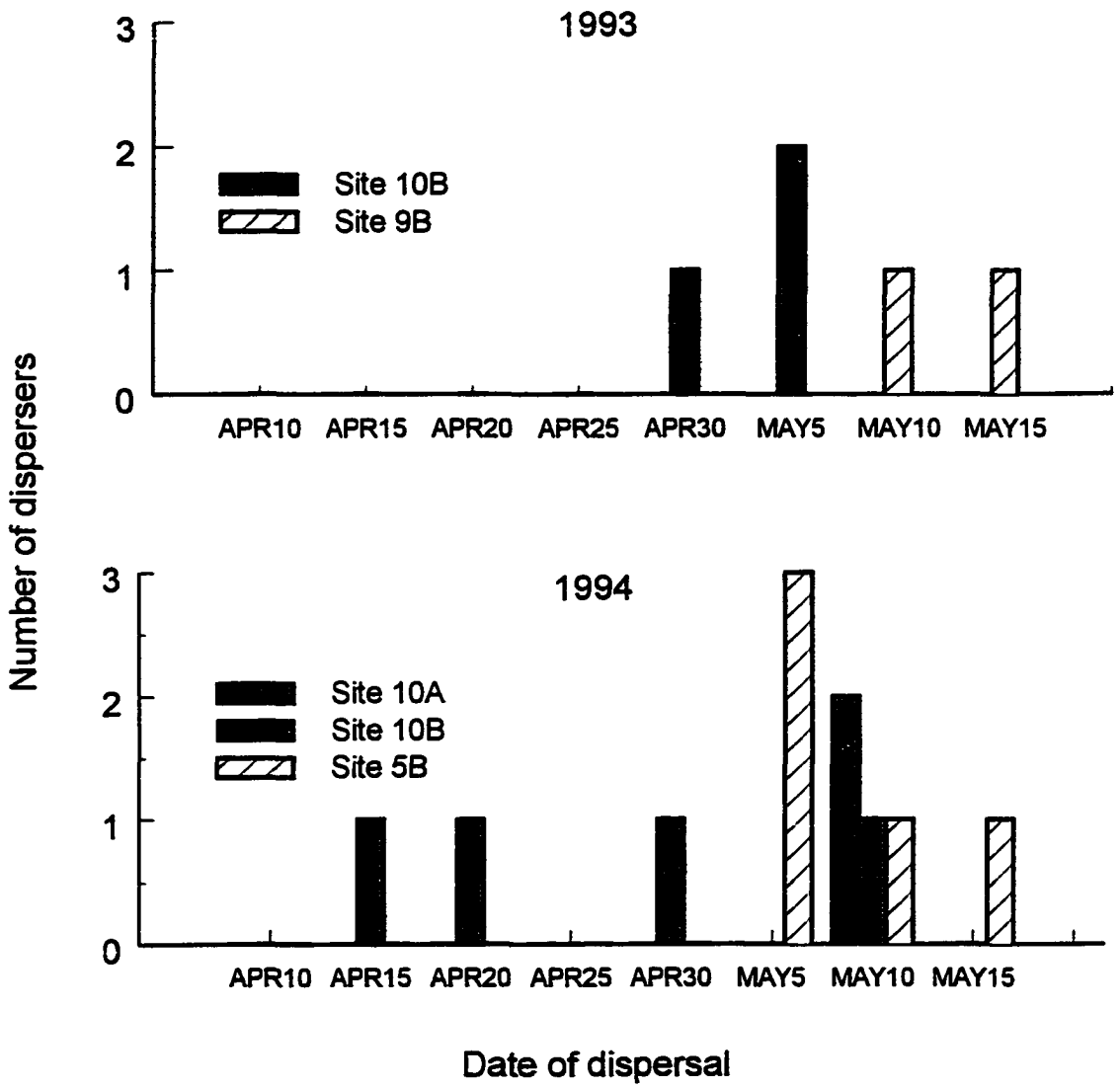

Figure 4.3. Dates of dispersal for sites 9B and 10B in 1993, and sites 5B, 10A, and 10B in 1994. Sites 5B and 9B are shrub sites (open bars), and sites 10A and 10B are grass sites (shaded bars).

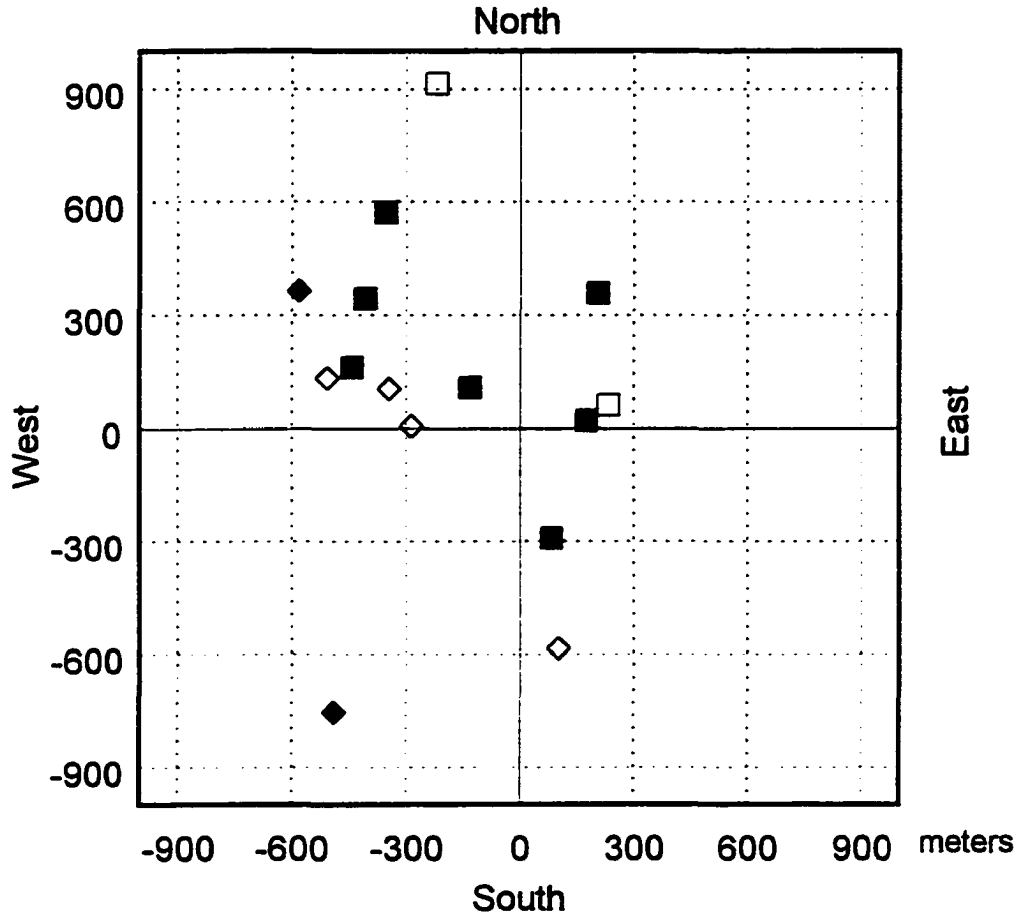

Figure 4.4. Endpoints of dispersal movements for all radio-collared juvenile Townsend's ground squirrels from 1993 and 1994 on the Snake River Birds of Prey National Conservation Area, standardized to a common starting point (0,0). Squares represent dispersers from grass sites and diamonds dispersers from shrub sites, with differing sites within habitat type distinguished by filled or open markers.

CHAPTER FIVE

A SPATIALLY EXPLICIT POPULATION MODEL FOR TOWNSEND'S GROUND SQUIRRELS ON THE SNAKE RIVER BIRDS OF PREY NATIONAL CONSERVATION AREA

In previous chapters, I described how I estimated parameters and examined factors that may explain variability in those parameters. While useful in expanding our knowledge of Townsend's ground squirrel (TGS) population biology, those results only provide random snapshots of the their population dynamics on the Snake River Birds of Prey National Conservation Area (SRBPNCA). Much as a Hollywood screenwriter develops a script from a handful of historical facts, my development of a population model for TGS was an attempt to connect the snapshots, and fill in the gaps in a comprehensive manner. Unlike the movie-makers, however, my aim was to create as realistic a model as possible, straying from the facts only when absolutely necessary, and keeping "artistic license" to a minimum. Developing a spatially explicit population (SEP) model was in keeping with that realist theme.

Most spatial models have focused on species which either are naturally occurring metapopulations (sensu McCullough 1996, i.e. spatially divided populations), or have experienced fragmentation of their primary habitat and are theorized as exhibiting metapopulation behavior (but see Harrison 1994). Very little work has been done on populations of species that are contiguously, yet patchily, distributed across the

landscape. Perhaps it is assumed that such populations are panmictic, and their spatial distribution is not important. Yet all species are affected by spatial heterogeneity to some degree; even a contiguously distributed population will exhibit variability in density consistent with habitat variability. Further, connectivity among individuals or sub-populations may be fallacious, especially if unapparent dispersal barriers exist. Therefore it is prudent that population modelers consider spatial features in a manner, and at the relevant scale, appropriate for the modeled population, even if the metapopulation model does not seem applicable.

I believed that TGS fit in the realm of species that do not exhibit metapopulation characteristics, yet are affected by spatial heterogeneity. From my own (Chapters 2-4), and other research (Smith and Johnson 1985, Yensen et al. 1992, Van Horne et al. 1997), TGS were found to be patchily distributed over the SRBPNCA landscape, and to exhibit variable population dynamics among differing habitat types that are intermingled. The relative quantity of theses habitats, as well as habitat patch characteristics (size, shape, and juxtaposition), should impact the dynamics of the TGS population at large. Furthermore, habitat patches themselves are dynamic; shrub habitats may be converted to grass habitats via wildfires, and grass habitats may become shrub habitats by succession or by re-seeding of shrubs by area managers. It was my reasoning that a model of TGS population dynamics should be capable of accounting for both the existing (static) pattern of habitat on the SRBPNCA, and the projected pattern due to these dynamic processes. The issue then became determining the appropriate means to incorporate spatial processes into a population dynamics model of TGS.

Dunning et al. (1995; p. 3) defined a SEP model as one that "... combines(s) a population simulator with a landscape map that describes the spatial distribution of landscape features." Several authors (Walters 1992, Pulliam et al. 1992, Dunning et al. 1995, Turner et al. 1995) have claimed that SEP models are superior to other types of models when predictions of the effects of landscape alterations on population dynamics are desired. Therefore, it seemed to me that it was important to explore the utility of a SEP approach for modeling TGS population dynamics.

Spatially explicit population models are a subset of ecological models incorporating spatial features, which have been the focus of much attention since the late 1980s. Generally, these models require simulation approaches, because inclusion of spatial heterogeneity renders analytical models intractable (Fahrig 1991). Simulation methods also are more realistic and easier to apply to field situations (Onstad 1988). Although analytical models may be useful to test specific theories, they often lead to different results than simulation methods (cf. Wennergren et al. 1995). Therefore, it was clear that a simulation approach was necessary for modeling TGS, as is the case for nearly all SEP models.

Within the realm of spatial models, SEP models may be distinguished by their target of investigation (the population) and the explicit nature of the space (landscape) incorporated into the model. Although the population may be further subdivided into smaller units (individuals, or local populations within a metapopulation, for instance), the results from these modeled units are usually aggregated to draw conclusions about the

population status as a whole.

Not all spatial population models are spatially explicit. Some, especially those that are extensions of the Levins (1969, 1970) metapopulation model (cf., Hanski 1991, Bascompte and Sole 1996), may be considered spatially implicit. That is, there is a presumption that populations (or patches) are separated in space, but the actual locations of patches are not important. These models may be adequate for situations where the inter-patch matrix is unimportant, between-patch population processes (dispersal) are not directly related to spatial attributes (such as distance between patches, existence of corridors), and within-patch processes are unrelated to patch geometry. Yet few of these models have been developed for wildlife populations, perhaps because such restraints are too unrealistic.

Spatially explicit population models may be further divided into those that are spatially realistic, and those that are not (Travis and Dytham 1998). The difference between them is the former are based on spatial features and arrangements that actually exist and include spatial heterogeneity, whereas the latter are hypothetical. While spatial realism (usually in the form of a GIS-based landscape map) is frequently presumed to be part of the definition of a SEP model (cf. Doak and Mills 1994, Ruckelshaus et al. 1997), many published SEP models are not spatially realistic. Both types of models are useful, but spatially realistic models are the only ones that can be used to predict the dynamics of particular populations (Hanski 1994). Spatially "unrealistic" models may be highly useful (if not critical), however, in evaluating the outcomes of spatially realistic models (Dytham 1995, Tilman et al. 1997, With and King 1997, Fahrig 1998) as they may

distinguish results that are dictated by the spatial reality from those that are not.

Spatially realistic models have been developed for a number of species in recent years. These may be divided into three types based on the population unit or sub-unit being modeled: individual-based, patch-based, and cell-based. (Gilpin, 1996, used similarly named categories in his review of metapopulation models, but his classifications were based on how space is structured in each type of model). The choice of model types to use is usually dictated by life history characteristics of the species, but may also be based on data limitations.

Individual-based models (IBMs) are usually developed for species that occur in low densities, are territorial (or at least can be linked to a distinct point in space, such as a nest or den site) (DeAngelis and Rose 1992, Murdoch et al. 1992). Most often, IBMs model space as discrete units. Usually these units are identical in geometry, as in a regular grid or lattice, but they may also be irregular units such as habitat patches (Tischendorf 1997). The size of the spatial units are usually equal to territory size. Dispersal among units is usually modeled by a stepping-stone approach, with decision rules to regulate whether settlement occurs at each step. The best-known example of these models is one developed for the northern spotted owl (McKelvey et al. 1993), but other examples exist (Bachman's sparrow (Pulliam et al. 1992; red-cockaded woodpecker, Letcher et al. 1998; salmon, Jager et al. 1997;)

Patch-based models are most often used for metapopulations. The emphasis is placed on between-patch dynamics, and patch occupancy is usually the state variable of interest. These models are most appropriate for species which inhabit disjunct habitat

patches located within a matrix of non-habitat, such as the Glanville fritillary butterfly (Moilanen and Hanski 1998), the California gnatcatcher (Akçakaya and Atwood 1997), and the American pika (Moilanen et al. 1998). Metapopulation models are often the simplest to develop, as they do not always require stochastic approaches, and within-patch population dynamics (births, deaths) may be ignored or reduced in complexity (Hanski 1998).

In cell-based models, the geographic model space is divided into equal units or cells, each of which contains a number of individuals. Generally within-unit dynamics (primarily birth and death processes) are modeled independently, but they may also be influenced by or interact with the surrounding cells (especially via dispersal). Cell-based models are especially useful for modeling species that are not restricted to isolated habitat patches, have large number of individuals, or have dispersal movements within a small geographic range relative to the area modeled. The use of cells thus is a convenient mechanism for dividing the area of interest into more workable units, the size of which depend upon the scale of the habitat map, dispersal distances, and computer capacity. Price and Gilpin's (1996) model of Stephens' kangaroo rat is one of the few examples of this type of SEP models that is spatially realistic, but others exist that use hypothetical space (cf. Lee and DeAngelis 1997 for unionid mussels).

Some SEP models combine several of the approaches given above, especially when more than one species (or trophic level) is being modeled. For instance, Rushton et al.'s (1997) model of red and grey squirrel dynamics is basically patch-based, yet model outcomes are assessed on a larger cell-based scale. Wilber and Shapiro (1997) modeled

host-parasite interactions between TGS and 2 of its parasites using an individual-based model of the host (TGS) with parasites modeled in a patch-based manner. Lamberson et al. (unpublished) combined the individual- and cell-based approaches in a model of black-footed ferrets. Thus, it appears that population modelers are choosing from among a variety of spatial approaches to suit the species and systems being modeled, rather than attempting to force them into a single approach, which has been more commonly the case previously in population modeling. One drawback to this flexibility has been the need for case-by-case, custom development of computer models, but a newly-developed software package called PATCH (Schumaker 1998) may have resolved this dilemma. The PATCH model, despite its name, allows a number of options that are individual- or cell-based, as well as patch-based. Unfortunately, this software was not available at the time I developed a SEP for TGS.

The major drawback to SEP models is that they are data-hungry, i.e., they require more information about population processes than are generally available from wildlife studies. Some have questioned the use of SEP models either because the empirical data used to construct the models are unreliable (Ruckelshaus et al. 1997), or the complex structure of such models renders them impractical for realistic application because of the considerable data requirements (Wennergren et al. 1995). The first point may be answered by using improved methods for parameter estimation (Conroy et al. 1995), whereas the latter can only be addressed by conducting more comprehensive studies. Unfortunately, very few wildlife studies have been sufficiently broad-scaled to meet the data requirements of SEP models: reasonable estimates of essential population parameters

(density, survival, reproductive rates, and dispersal processes), information on the variability of these parameters through time and space, and explicit geographic information on the area under study. This study of TGS was an exception, which led me to believe development of a SEP model was feasible. Based on the population ecology of TGS, and supported by the review of SEP models given above, I believed the best general type of model for TGS was the cell-based approach, but with dispersal modeled on an individual basis. This would also be a spatially realistic model because of the availability of a GIS-based landscape map for the SRBPNCA (see below).

MODEL OBJECTIVES

McCullagh and Nelder (1989: p.8) stated "... all models are wrong; some, though, are more useful than others." My aim was to develop one of the more useful models. With that in mind, the specific questions of interest to be answered by the SEP model were:

1) Are TGS populations likely to persist given the current habitat configurations (spatial arrangement of habitat types) and expected population parameter values ?

2) What population parameters appear to be most important in maintaining populations under current conditions?

3) What are the effects of uncertainty in parameter values on model outcomes?

4) What are the most important needs for better information?

During the late stages of model development, it became obvious that I could not adequately answer the above questions within the time frame of a normal dissertation project; that it would take years, not months, to fully investigate results that can be

obtained from simulation runs of the model. Therefore, I developed a set of intermediate objectives, and results for these are reported in this chapter. These objectives were to:

1) develop a data-driven population model for TGS,

2) investigate the results from this model using a sub-area of the SRBPNCA,

3) draw preliminary conclusions in answer to the questions above, and

4) determine the priority needs for further development of the TGS model.

Although the TGS model was developed as a single entity, it was also intended to fit into a more comprehensive SEP model of habitat, prey, and predator dynamics called EcoChange (Knick et al. in prep). The main objective underlying this master model of the SRBPNCA was to examine the effects of habitat changes on the entire system. Meeting this objective was beyond the scope of my research, and the results of that larger effort will be reported elsewhere.

MODEL OVERVIEW

The computer code for EcoChange, including the TGS module, was written by Brett Hoover (while at the Patuxent Wildlife Research Center, MD, then part of the National Biological Service, U.S. Dept. of Interior) in C++ to run on either a UNIX or an OS/2 platform. Although Brett is responsible for the actual program code, I specified to him the features I thought necessary for modeling ground squirrels. In addition, I wrote the majority of the code for the specific ground squirrel parameter algorithms, including setting their values.

Habitat information for EcoChange is stored as a map layer manipulated by an ARC/INFO Geographic Information System (GIS). The TGS module can be run

separately from other components of EcoChange, and all simulations reported in this chapter were done on the TGS module only. Further, all references herein to "the SEP model" are for the TGS portion only.

A critical aspect of constructing the SEP model was determining which features of the landscape, and what components of TGS population biology should be included. I strove for a balance between simplicity and realism, using empirical sources and analytical results whenever possible to determine appropriate model structure and to set parameter values. Although the main sources of data for the model were the TGS capture-recapture and radio-telemetry studies (Chapters 2,3, and 4), I had access to limited raw data from Smith and Johnson's (1985) study, and from Knick's (1991) study of broad scale pattern of TGS. Other information came from published sources cited as used.

From the sources cited above, it was clear that environmental factors, specifically weather and habitat, play key roles in TGS population dynamics. Both major population studies of TGS on the SRBPNCA (Smith and Johnson 1985, and this study) identified significant population responses to drought and winter conditions. Van Horne et al. (1997a), and analyses I conducted reported in Chapters 2-3, found that habitat also plays a key role in the dynamics of TGS populations. Therefore, these environmental factors certainly needed to be accounted for in the model.

Although environmental factors influence TGS population dynamics (births, deaths, and possibly, dispersal) directly, they also affect the timing of key events in TGS phenology. Delays in emergence from hibernation, or a shortening of the time available

to put on fat reserves, may in turn affect population vital rates. Therefore, the ability to allow flexibility in the timing of events was also programmed into the model.

Demographic factors, such as age and sex, were also found to account for significant variability in population parameters. Adults clearly differ from juveniles in all aspects of population dynamics, and within age class, I found differences between sexes in survival (for adults; Chapter 3), and dispersal (for juveniles; Chapter 4).

In building the SEP model for TGS, I incorporated all of the key factors cited above. Figure 5.1 summarizes the relationships between environmental and demographic factors, the timing of TGS events, and the basic population parameters in the SEP model.

The population model is stochastic with discrete time intervals. Both temporal and spatial variability are generated by random number generating (RNG) functions. There are 4 statistical distributions used to model random variables, the values of which are generated using corresponding RNG functions: uniform, binomial, gamma and beta. For the uniform distribution, the RNG function (which I refer to as the random uniform function) generates a random value between 0 and 1. Generally, the random uniform function is used in the model to generate a discrete random variable from a set of specified probabilities (p_j) where $\sum_j p_j = 1$ (Ross 1994). For the binomial distribution, the RNG function (referred to as a random binomial function) generates x, the number of "successes", given n, the number of "trials", and p, the probability of a success in a single trial. The random binomial function is used in the model with population parameters that are actually probabilities, such as survival rates and dispersal rates. For the gamma and beta distributions, the RNG functions (random gamma function and random beta

functions, respectively), as used by the model, generate a random variate, x, given 2 parameters, α and β, which define the shape and location of the gamma or beta distribution function. The specific usage of the gamma and beta distribution functions is described in the Survival rate and Litter size sections, below.

Time in the model is based on a model year, which is made up of 365 days, numbered 1 to 365, i.e., Julian dates in a non-leap year. Days are discrete (i.e., they cannot be sub-divided) and therefore they form the basic time units of the model. Days can be aggregated to form periods within a year, but the length of all periods must sum to 1 complete model year (i.e., partial years are not allowed).

MODEL STRUCTURE

A flow diagram of the overall model structure is given in Figure 5.2. It consists of 4 basic components: model inputs, the cell population model, a dispersal sub-model, and model outputs. Each of these components is explained in detail below.

Model inputs

Model inputs include the global model parameter file, the TGS prey parameter file, and a habitat map. The global parameter file is used to control the execution of the main modules associated with the master EcoChange model, and to set attributes of the simulation run that apply to all modules executed. These include a title, the number of years in the simulation, the log file name (to which are written statements about the simulation run) and the level of output desired (primarily used for debugging the program).

The TGS prey parameter file consists of 4 sections that are specific to the TGS

module: 1) model area attributes, 2) model habitats, 3) time period definitions, and 4) probability functions to generate environmental condition values. The period and environmental condition variable definitions are discussed in separate sections, below.

The model area attributes are used to set the population cell units, model area and habitat map which define the spatial dimensions of the model. These are discussed in separate sections, below. Other options in this section include the specification of output file names, whether to include a gradient map overlay and whether the fire module (another module in EcoChange) is to operate, which allows updating of cell habitat values as a result of fire or succession. Finally, the model area is where the population base and time base for the model are set. Currently, the population base is set as group-based (as opposed to individual-based), and the time base is set to period (as opposed to day or year). Other population and time base options are not currently available, but could be programmed into the model in the future if warranted.

The model habitats section is where the vegetation map categories are aggregated into model habitat types (see map area and habitat section, below). This section also contains the function statements which identifies the life history functions (survival, reproduction, dispersal, etc.) to be run by the population cell model for each habitat type.

Population cell units

TGS are distributed throughout the SRBPNCA, occurring in a variety of habitat types. Armitage (1981) placed them among the group of ground squirrels that aggregate in favorable habitat. Therefore, their distribution can be best described as loosely clumped, with some areas having relatively high densities of TGS, others having

somewhat lower densities, and still other areas being completely devoid of ground squirrels. This generally contiguous distribution of ground squirrels does not readily fit into the patch structure most often assumed by metapopulation and some other spatially structured population models. Therefore, I divided the model area into 2.25 ha (150 × 150 m) population cell units. Cell shape was dictated by the use of square pixels in the GIS habitat map. The choice of cell size was arbitrary, but fits well with the study site areas (trapping grids varying from 1.0- 9.0 ha.) for which population parameters were estimated and has dimensions which are a multiple of the pixel size (25 × 25 m) used for the GIS map. Cells are large enough to encompass average adult movements within the cell, yet small enough so that minimum dispersal movements by juveniles would result in a change of cell residency. Finally, given the potential range of ground squirrel densities (0 to >200 animals/ha), the 2.25 ha cell size offers a compromise between many smaller cells that would have very small ground squirrel populations, and fewer larger cells that would often contain very high population sizes.

The exact positioning of grid lines is dependent on the habitat map being used for the simulation run and the UTM coordinates set in the model area section of the prey parameter program. The lowest left corner cell (the southwestern corner of the map) is given the address (0,0), and all other cells are assigned an address in terms of columns and rows relative to that position (i.e., cell 2,25 would be located 2 cells east and 25 cells north of cell 0,0). Selection of a different cell size is relatively straight-forward, as long as there is a corresponding habitat map of the same scale. I did not explore the effects of different choice of cell size in the model simulations, although the choice of the scale of

investigation may affect results and conclusions (Wiens 1989).

Map area and habitat

The model may be run using any raster-based map in either ARCINFO or GRASS format. However, it is not intended for use outside the SRBPNCA. The entire SRBPNCA is 196,225 ha, but only a portion of it was sampled during the Idaho Army National Guard / Bureau of Land Management study. The area within which the TGS demography study sites were located (a polygon of 34,450 ha) was in the northwest portion of the SRBPNCA. The map area for the model, however, must be rectangular, although portions of the map may be essentially left out of the simulation by being given the code -9999, or no data. The total rectangular map area that the SEP model will eventually be run with is 390,298 ha, but of that, only 138,051 ha will be actually modeled. The test runs reported in this chapter were conducted using a 22,500 ha portion of the model map. Figure 5.3 shows the relationship between the TGS study sites, the total map and model areas, and the test model portion.

Rotenberry and Knick (1996) identified 30 vegetation classes for the SRBPNCA based on satellite imagery. Those classes were grouped into 7 vegetation categories used by the EcoChange model. Because I did not have sufficiently detailed data for ground squirrels in each of those categories, I further aggregated them into 3 main categories for the TGS SEP model: shrub, grass, and non-habitat (Table 5.1).

Environmental conditions

The stochastic effects of weather are programmed into the model via 2 variables that reflect environmental conditions during 2 times of the year, February and April. In

the model, these variables are called GREENUP and GREENNESS, respectively, because they represent the condition of green vegetation at those times of year. Although these variables were initially developed for use in the habitat module, I felt they also contained the essential elements of the effects of environmental conditions on TGS. Early season environmental conditions definitely affect TGS reproduction (Smith and Johnson 1985) and timing of emergence (Van Horne et al. 1997a), and probably affect TGS survival (Chapter 3). Late season conditions definitely affect survival and timing of immergence (Van Horne et al. 1997a, Chapter 3). Therefore, these variables were used to adjust the appropriate parameter values. However, I did not feel I had sufficient information on the relationships between environmental conditions and population parameters to model them on a continuous basis, and therefore chose to create categories of conditions, within which I adjusted the parameter values (see individual algorithm descriptions, below).

I created 4 categories of environmental conditions for the GREENUP variable: very poor, poor, moderate, and good; and 3 categories for GREENNESS (poor, moderate, and good). The difference in number of categories was primarily to enable separate modeling of 2 types of poor conditions encountered by ground squirrels early in the season: 1) poor conditions due to drought, as encountered by Smith and Johnson (1985), and 2) poor conditions due to cold and snow, as encountered by Van Horne et al. (1997a). The first type of condition is modeled as very poor, and the second as poor. These conditions had very different impacts on ground squirrel populations.

Using a random uniform function, each of the two variables is assigned a condition category based on probability of occurrence. These probabilities were based on

the frequency of occurrence of those conditions over 55 years (1940-1994) as determined from daily weather records taken at the Boise Airport recording station (NOAA, National Climate Center data). (Although there are some differences between Boise airport weather records and the SRBPNCA, Steenhof et al. 1996, found those records to be highly correlated. Records for the SRBPNCA were only available for 1991-1994).

To determine frequency of occurrence, I defined weather conditions for each category. For GREENUP, these definitions were based on average daily February temperatures (computed as the mean of the minimum and maximum temperatures) and soil moisture, which was estimated based on the 3-month cumulative precipitation totals for December-February. Very poor conditions were assumed to occur if precipitation was < 4 cm, regardless of what the temperature was. Poor conditions were assumed to occur if precipitation was ≥4 cm, yet average daily temperatures were below freezing (≤0° C). Moderate conditions were assumed to occur when precipitation was between 4-9 cm and temperatures were > 0° C but ≤ 2.8 ° C, and good conditions were assumed if precipitation was >9 cm or temperatures were > 2.8° C. These definitions are based on a few key assumptions: 1) when precipitation is very low, there will be little food available upon emergence, regardless of temperature, 2) when temperatures average below freezing, most precipitation will be snow, and vegetation growth will be minimal no matter how much precipitation occurs, 3) warmer temperatures speed vegetation growth, and 4) there is some threshold of precipitation, above which good conditions do not get better. The 9 cm precipitation cut-point is the median value for 3-month cumulative precipitation for the 55 years; the 4 cm cut-point was chosen to distinguish extreme drought conditions

such as those that occurred in 1977, a year in which TGS did not reproduce at all (Smith and Johnson 1985), from winter conditions such as occurred in 1993. That year also had the lowest recorded cumulative precipitation value of any year (3.2 cm); therefore I considered those conditions to be relatively rare. Similar precipitation (3.5 cm) fell in 1985, but I do not know if there was a similar response in TGS reproduction. The 2.8 ° C cut-off for temperature range was based on the median mean daily temperature.

The frequencies of occurrence for the 4 categories defined above were: very poor, 2 of 55 years (3.6%); poor, 10 of 55 (18.2%); moderate, 7 of 55 (12.7%); good, 36 of 55 (65.5%). Based on these, I set the selection probabilities in the model for GREENUP to be: very poor, 0.04; poor, 0.18; moderate, 0.13; good, 0.65. Table 5.2 shows the classification of years during which research was conducted on TGS. Even with the unbalanced categories I designated, all 4 categories occurred during at least 1 year of study.

As temperatures later in the year were assumed not to be a factor, I considered vegetation conditions later in the year to be strictly a function of moisture and based the categories for GREENNESS on precipitation alone. Using a 3-month cumulative total (for May), I considered conditions to be very poor if precipitation was <4 cm, moderate if 4-9 cm, and good if precipitation was ≥ 9 cm. Again, 9 cm was the median value for the 55 years of data. The lower cut-point (4 cm) was chosen because there was a distinct break in the distribution of years at this point. The frequencies of occurrence of these conditions were: poor, 4 of 55 years (7.3%); moderate, 24 of 55 (43.6%); and good, 27 of 55 (49.1%). Based on these frequencies, I set the probabilities for GREENNESS to be:

poor, 0.06; moderate, 0.44; and good, 0.50. The classification of ground squirrel study years is given in Table 5.2.

It is worth noting that the definitions for environmental condition categories I used for the model do not exactly coincide with the categories used in Chapter 3, and the difference in definitions in turn led to some differences in assignment of the TGS study years to condition categories. The reason for this difference in definitions is that in Chapter 3, I was only interested in how survival rates related to environmental conditions, whereas in the model, the condition categories had to serve a more general purpose because I used the same categories to model variability in several model parameters. Because I did not want (nor was it possible) to develop condition variables to correspond to each model parameter affected by weather, the categories described here are a compromise. Finally, the condition variables also are used by other portions of the EcoChange model.

Time periods

Currently, the model year is divided into 3 time periods, which are defined differently for each age class. Within age class, the timing and duration of periods may be adjusted by sex, habitat type, and environmental conditions. The ability to break up the year into biological relevant periods is an important feature in the model, for the following reasons: 1) estimated survival rates of adults (Chapter 3) are daily rates per period; 2) the timing of mortality relative to reproduction and dispersal can be directly controlled; and 3) it allows the flexibility of relating parameter values to environmental conditions at different times of the year. Droughts, especially, appear to have differing

influences depending upon when they occur relative to the ground squirrel active period (Smith and Johnson 1985, Van Horne et. al 1997a).

For adults, period definitions are the same as defined in Chapter 3 for survival rate estimation: Period 1 is from emergence from hibernation until emergence of juveniles from natal burrows; Period 2 is from the end of Period 1 until immergence into estivation; and Period 3 is from the immergence until re-emergence the following year. Juvenile time periods (for both sexes) are: Period 1, from emergence from natal burrows until the onset of dispersal; Period 2, from the end of Period 2 until immergence into estivation; and Period 3, from the end of Period 2 until re-emergence the following year.

The timing and length of the periods can be set in several ways, with the only restriction being they must total to 365 days (one model year). Three parameters control period specifications: start day, period length, and end day; specification of any 2 of these will determine the third. Both start and end days are given as the number of days from January 1 (Julian date), and period length is simply end day - start day. The start day must be specified for Period 1, and the start days for Periods 2 and 3 are always the day after the end day for Periods 1 and 2, respectively. The end day for Period 3 is always specified as 365, but the actual length of Period 3 depends upon the start day of Period 1 for the following model year, as the number of days between day 1 and the start day of Period 1, year $i+1$, is added to the length of Period 3, year i.

The period definitions used in the model are quite complex. In the analyses of factors which affected the timing and length of periods (see below), I found differences attributable to sex, habitat, and year, and to the interactions between these factors.

Unfortunately, the SEP model was designed such that adjustments in period definitions by habitat type could not be easily made. The main reason for this is that when the TGS model is integrated with the other modules in EcoChange, then habitat becomes a dynamic variable, with changes due to fire and succession possible during the model year. So even though the TGS model as reported here uses a static (unchanging) habitat map, there are limits to how habitat can be used to adjust parameter values. Time period definitions are the only part of the model that are so affected. The importance of this apparent flaw in the model is unknown. However, I created 2 sets of period definitions, 1 where period definitions are variable by habitat type, and 1 where they are not (Tables 5.3, 5.4; Figures 5.4, 5.5). I then used a SAS® program (SAS® Institute, Inc.) to compute the effect the difference in definitions had on annual survival rates, which are the only parameters affected by period definitions directly. The results of those analysis are reported later in this chapter (see Results), along with further discussion of the potential effects of inclusion or exclusion of habitat as a factor in period definitions. First, however, I report the analyses that led to the identification of the factors that apparently affect period timing and length, and the values I used based on those analyses.

The key to defining periods is establishing the timing of the biological events that the periods are based upon. Unable to observe these events directly, I relied mostly on the live-trapping capture records from the demography study. However, there are several problems with using capture data to track the timing of events, which may be grouped into 2 categories: 1) capture probabilities are < 1.0, meaning that not capturing animals does not indicate they are not present, and 2) dates of capture are restricted to dates

trapping was conducted, which may not encompass the date(s) the event took place. The radio-telemetry data do not have these problems, but those data are sparse and restricted to juveniles.

In all years examined (1975-82, 1991-1994), the earliest date trapped was January 27, in 1993, which is the only year any trapping was conducted in January. Trapping in all other years (and on most sites in 1993) was initiated in early to mid-February. Usually, ground squirrels were captured immediately, supporting observations that some ground squirrels had emerged prior to when trapping began in all years. For those years when trapping began within the first 10 days of February (1992, 1993, and 2 sites in 1994), females were captured from the start in 1992 and 1994, but not until 2-3 weeks later in 1993. The latter delay in capturing females (presumably caused by their later emergence), follows the pattern found by other TGS studies, which reported that females emerge 2-3 weeks later than males (Rickart 1987). While the data from 1992 and 1994 suggest that there may be some conditions in which females emerge earlier, there was not sufficient information to determine what those conditions are. My conclusions from this review were that males, at least, generally emerge before the end of January, and that females emerge 2-3 weeks later. However, I could not establish the actual timing of emergence for years other than 1993, and so I had to rely on other data to determine when to set these dates.

The start day of Period 2 for adults and the start day for the juvenile Period 1 coincide. Therefore, one way to determine the start day for the adult Period 1 was to determine the emergence date for juveniles and the interval length for Period 1, and back-

calculate to get emergence dates for adults. Emergence dates of juveniles (estimated by the first date a juvenile was captured on a site) were quite variable, and differed between habitat types ($F_{1,14} = 12.61$, $P = 0.003$) and among years ($F_{2,25} = 38.86$, $P < 0.001$). There was no interaction between habitat and year, leading me to believe these relationships are consistent. Juveniles emerged earlier on grass sites (mean Julian date = 97.2, SE = 2.01) than on shrub sites (mean = 104.4, SE = 2.29), and earlier in 1992 (mean = 90.8, SE = 1.69) than in 1993 (mean = 107.5, SE = 2.05) or 1994 (mean = 103.2, SE = 2.43).

From capture data from 1993, the only year for which I was reasonably certain that initial capture dates (for females at least) reflected emergence dates, I computed the difference between the first day an adult male was captured and the first day a juvenile was captured, and did likewise for the difference between adult females and juveniles. This difference was found to vary by sex, as expected, ($F_{1,13} = 138.04$, $P < 0.001$) but also by habitat type ($F_{1,12} = 6.99$, $P = 0.022$). Sites within habitat were also significantly different ($F_{12,13} = 3.65$, $P = 0.014$), but I attributed that result to disparities in trapping dates.

The difference between adult (for both sexes) and juvenile emergence was about 8 days greater on shrub sites than grass sites. This difference in interval length is approximately the same as the habitat-specific differences in juvenile emergence, indicating that adult emergence occurred at about the same time in both habitat types in 1993, yet for some reason juveniles in shrub habitats emerged later. The difference in interval length between males and females reflects their presumed differences in emergence. Although these analyses are based on data from a single year, I assumed the

results should be relatively consistent among years. Ground squirrels breed almost immediately upon female emergence, and the timing of juvenile emergence depends upon gestation time and time to weaning, which are relatively inflexible. According to Rickart (1987) the gestation period for TGS is 24 days, and the age at which juveniles begin eating solid food is 26-28 days, thus juveniles would not be expected to emerge in < 50 days following female emergence. To support the rationality of these figures, I used them to back-calculate emergence dates for adults for 1992 and 1994, based on dates of juvenile emergence in those years. The results were consistent with my personal observations of TGS (sex undetermined, but presumably male) activity as early as January 20 in 1992, and during the first week of February in 1994.

Since the calculated dates of adult emergence varied among years (as they are based on the juvenile emergence dates), I assumed that this variability was due to environmental conditions at that time. Since 1992 was classified as a good year early in the season, 1993 a poor year, and 1994 a moderate year (Table 5.2), I used the dates from those years to set the start day for Period 1, adults (Table 5.3). The very poor category of environmental conditions was included with the moderate category in this case because I had no reason to think that emergence would be delayed in years when precipitation was reduced.

Period 1 for juveniles ends when dispersal takes place. Dates of dispersal from the radio-telemetry study were quite variable, even among individuals from the same site in the same year. For the model, however, the exact date of dispersal (and therefore the time boundary between juveniles Periods 1 and 2) is probably not important, as there was

no evidence to suggest that survival was different for juveniles pre- and post-dispersal (whether dispersers or not). Therefore, I set the start day for Period 2 (juveniles) to be 126, which is approximately the average date of dispersal during the 2 years (1993 and 1994) of the telemetry study.

The boundary between Periods 2 and 3 for both adults and juveniles is their immergence date. Accurate selection of this date is important because per-day survival of TGS was lower during the active season (Periods 1 and 2) than during the period of torpor (Period 3) (Chapter 3). The problems with using capture records to determine emergence dates were magnified when they were used to determine immergence dates. Whereas individuals captured early in the trapping season are known to have emerged (although there is uncertainty as to exactly when), there are several possible reasons, aside from immergence, why an animal may stop being caught toward the end of the trapping season: the animal may have died, emigrated, or simply did not enter traps while remaining active. There also appeared to be much variability among individuals, with some animals disappearing in early May and others remaining active until late June. Altogether, these problems made exact determination of immergence dates impossible. However, some end point for Period 2 had to be set. In addition, it was important to determine if these end dates varied by year, sex, or habitat. I assumed, without analysis, that immergence dates varied by age, and that adults immerged prior to juveniles. This has been well-documented elsewhere (Rickart 1987, Van Horne et al. 1997a). Subsequent analyses were therefore conducted separately for each age group.

For both age groups, I limited the data to individuals that were captured late in the

trapping season (details below) to increase the likelihood that individuals remained within trapping grid areas and survived to immergence. I chose to use the 75th percentile date of last capture as an estimated average immergence date. My rationale was that, given all of the reasons why an animal might still be active past its last date of capture, then using the mean (or median) last capture date of a group of individuals would almost certainly underestimate their average immergence date. I hoped to balance that bias by using the 75th percentile date. Sample sizes were too small in 1993 and 1994 to compute site-specific estimates, so sites were pooled within habitat type, and dates were computed separately for each year and sex.

For adults, I limited analyses to individuals that were captured at least once after 15 April. Other criteria were considered, but this seemed to be the best compromise between attributing immergence to animals that either died or emigrated and not accounting for early immergers. Because I was concerned about the potential effects of supplemental feeding (as was conducted on 2 sites in 1993 and 1994), I conducted 2 analyses: 1) of all 3 years (92-94) with supplemental feeding sites dropped, and 2) of 1993 and 1994 only where the supplemental sites were considered a third habitat type. Surprisingly, none of the analyses I conducted found differences in immergence dates attributed to sex (Table 5.5). Despite having more time in which they can put on fat for torpor, males do not appear to immerge earlier than females, on average. In the first analysis, I did find differences in immergence dates due to year and habitat, and based on the second analysis, the supplemental feeding apparently also had an effect (Table 5.5). A means test for habitat types in the second analysis showed the grass habitat to have

earlier immergence dates (mean = 132.5; SE = 2.87) than either the shrub (mean = 139; SE = 2.10) or the supplemental feeding sites (mean = 142; SE = 1.58), which were not different than each other. Since both supplemental feeding sites were considered grass sites prior to experimental manipulation, then these differences should be attributable to the feeding treatment.

Based on the results of these analyses, I assigned varying end dates for Period 2, adults, to differing environmental conditions and habitat types (Table 5.3). The environmental condition assignments were based on the late season (GREENNESS) condition categories for the study years (Table 5.2). Because of the interaction between habitat and year found in the first analysis, the relationships among conditions were slightly different within habitat type. For shrub habitats, animals immerged earliest under poor conditions, and progressively later as conditions improved. In grass habitats, animals immerged earliest when conditions were moderate, and later when poor or good.

For juveniles, actual immergence dates were available from the radio-telemetry study for 12 animals in 1993 and 1994. Although data were sparse, a significant interaction between year and habitat was found ($F_{1,7} = 18.75$, $P = 0.003$). (Data from 1 animal was deleted from the grass habitat in 1994, as its immergence date was >10 days from the next closest immergence date. With this assumed outlier included in the analysis, the year × habitat interaction had $F_{1,8} = 4.77$, $P = 0.061$). Mean immergence dates for both habitats were nearly identical in 1994, a moderate year (mean = 162.5; SE = 1.50 for shrub, and mean = 163.2, SE = 1.25 for grass), therefore I set the end day for juveniles, Period 2 to be 165 under those conditions for both habitat types. In 1993, a

year with good late conditions, the mean immergence date for shrub habitat was much later (mean = 178.3; SE = 0.67) than for the grass habitat (mean = 168.5; SE = 0.50). This is a similar effect as was seen for adults, but more pronounced. Based on this, I set the end day for Period 2, juveniles, to be day 180 for shrub habitat, and day 170 for grass.

Radio-telemetry data from 1992 came from a single collared juvenile that was tracked as part of a pilot study on the feasibility of radio-tracking ground squirrels. That animal, located on a grass site, immerged on day 157. While tracking that animal (and 2 adult females that were also collared as part of the pilot study), I observed very few other animals to be active at that time. Early disappearance of juveniles from study sites in 1992 was likely due primarily to mortality caused by the drought, and possibly to increased rates of dispersal. Therefore, it was extremely difficult to establish an immergence date for juveniles in 1992. Analyses of capture records, in a manner similar to those done for adults, were not helpful as they indicated that last capture dates were the same in 1992 as in 1993 (and that both occurred earlier than in 1994, which for the 1993-1994 comparison directly contradicts the radio-telemetery results). Based on the single animal collared in 1992, I set the end date for Period 2 juveniles in poor conditions to be day 155 for both shrub and grass habitats.

Cell population model

A flow diagram depicting actions occurring within each population cell is given in Figure 5.6. Each cell operates as an independent population for most of the year, with the only interactions between cells occurring during juvenile dispersal (discussed below). Each cell is initialized with an adult population, and from then on its dynamics are

determined by the survival, reproductive, and dispersal parameter values selected for that cell. The values for these sets of parameters are generated within the model by a series of algorithms (described below) that are contained within a prey function file in the EcoChange model. These functions are not easily changed; if modifications are made, then EcoChange must be recompiled.

Initial population size

The initial population sizes were allocated to cells using probability distribution functions specific for each habitat type, shrub and grass; all non-habitat cells were given an initial population of 0. Population sizes and probabilities were based on estimates of adult population density in 1991 (Van Horne et al. 1997a). I used total densities of adults (the sum of male and female estimates) from the first trapping cycle for each site (in all but 2 cases, this was the maximum density for the year), grouped by habitat type. Within each habitat type, I used empirical Bayes methods (as described in Chapter 3) to compute shrinkage estimates of density, i.e. with sampling variance removed (Table 5.6). Population numbers, computed as density times the cell size of 2.25 ha, were grouped into 4-5 categories for each of the 2 habitat types (Table 5.6), with probabilities assigned based on the frequency of occurrence (i.e., number of sites in each population class). The classes and probabilities were verified as having nearly the same expected values for means and variances as the shrinkage estimates.

Although study sites were not selected randomly, selection was thought not to be biased towards higher density sites, with the exception that areas with 0 ground squirrels might be under-represented. To explore this potential bias, I compared the expected

proportion of cells with 0 ground squirrels in the model area with TGS burrow counts conducted during 1991. Although Van Horne et al. (1997b) have shown such counts to be unreliable indices to population density, I felt that they could still be used to provide insight into the frequency of locations that were apparently devoid of ground squirrels. In 1991, Knick (1991) sampled 115 5 × 400 m transects placed at randomly selected locations over a large portion of the SRBPNCA, with an additional 53 transects located in areas that had been previously sampled by other TGS researchers (Peterson and Yensen 1986, Wheeler et al. 1989). Within each strip transect, observers counted apparent ground squirrel burrow entrances, and further, classified them as active or inactive. For my analyses, I excluded samples taken from outside of the model area, resulting in a sample size of 68. As I was interested in the proportion of the area with 0 ground squirrels, I used 3 increasing liberal criteria to classify the transects as to whether ground squirrels were likely to be absent: 1) if total burrows counted were = 0; 2) if active burrows were = 0, and inactive burrows < 20; and 3) if total burrows was < 20. Even using the most liberal criteria (3), only 19 of the 68 transects (27.9%) were classified as having 0 ground squirrels. In the model, using the initial population assignments described above, 20% of all shrub cells, 10% of all grass cells, and 100% of all non-habitat cells are initialized with populations of 0. For the current habitat pattern of the model area, the expected percentage of cells with population size 0 is 38.6%. Therefore, it is unlikely that the proportion of areas with 0 ground squirrels is under-represented in the model. I was not concerned that the proportion of 0 initial population sizes was greater than that found in the burrow counts, because the latter generally over-estimate

the presence of ground squirrels (Van Horne et al. 1997b). Also, given the timing of the counts (late spring through summer), individuals may have been detected that had dispersed into unsuitable areas and did not survive or remain until the following year.

I did not consider spatial correlation among densities in the initial population size assignments because a more general analysis of density data from all years (1992-1994) found no evidence for spatial correlation, based on proximity, at the scale at which density data were collected. Using years as replicates, I computed a correlation coefficient among densities for all site pairs (the 2 supplemental feeding sites were dropped) and then used simple linear regression to determine if correlations declined as distances between pairs of sites increased. For all habitats combined, no relationship with distance was detected ($t = 1.02$, $P = 0.311$, $n = 153$), nor was there a relationship within habitat type (shrub only: $t = 0.31$, $P = 0.756$, $n = 45$; nonshrub only: $t = 0.61$, $P = 0.545$, $n = 28$).

Following assignment of initial population sizes to individual cells by a random uniform function, the number of females is determined for each cell from a random binomial function and the expected proportion of females. The latter was determined based on analyses of sex ratios calculated from 1991 density estimates. In general, sex ratios were skewed towards females (female:male ratio was 2.1:1). I used the random effects model approach to test for the potential effects of habitat and population density on sex ratios, and found neither to be significant (habitat: $t_{15} = -1.03$, $P = 0.319$; density: $t_{15} = 0.06$, $P = 0.953$). Therefore, I computed the average proportion of females for all sites combined, which was 0.59, and rounding slightly, used 0.60 in the model as the

expected proportion of females in the initial cell populations.

Survival rates

Deaths are computed in the model based on survival rate functions. Survival rate functions vary according to period, habitat, age, sex, and environmental conditions (Chapter 3). For adults, a cell-specific daily survival rate is selected by a random beta function for the appropriate category, and converted to a period rate based on the number of days in that particular period. A period mortality rate (1-survival rate) is then computed and applied to the appropriate cell population group using a random binomial function to determine the number of deaths in the interval, and these are subtracted from the cell population size.

The beta distribution function was used in the model to simulate spatial variability of survival rates among cells of the same habitat type. Although it was chosen primarily because it yields values between 0 and 1 and has a reasonable and flexible shape, there is precedence for the use of the beta distribution for modeling variability in survival and other probabilities. Some authors (Boswell et al. 1979, Burnham and Rexstad 1993) have used the beta distribution similarly, i.e., to model heterogeneity of "success" in a binomial process. More commonly, the reverse process is employed whereby the beta-binomial distribution is used as a model for analyzing data that are binomial, but are found to be over-dispersed (c.f. Holgate 1966, Griffiths 1973, Danaher 1988, Link and Hahn 1996).

If the probability density function for a beta distribution is written as:

$$f(x) = \frac{\Gamma(\alpha+\beta)}{\Gamma(\alpha)\Gamma(\beta)} x^{\alpha-1}(1-x)^{\beta-1}, \; 0 \le x \le 1,$$

then the parameters α and β may be computed from a mean (μ), and variance (σ^2) as:

$$\alpha = \frac{\mu^2(1-\mu)-\mu\sigma^2}{\sigma^2} \qquad (5.1)$$

and

$$\beta = \alpha\left(\frac{1}{\mu}-1\right). \qquad (5.2)$$

Survival means and variances were based on analyses of survival rates estimates from capture-recapture data. For adults, those results were reported in Chapter 3. Generally, I assigned period-specific estimated daily survival rates for 1991-1993 to environmental conditions categories based on the assignment of periods within study years to the categories given in Table 5.2. Early season conditions were assumed to affect Period 1 survival, and late season conditions were assumed to affect survival during Periods 2 and 3. This gave me at least 1 survival estimate for each of the 3 periods under good and poor conditions. Although 1994 was considered a moderate year throughout, survival estimates for that year were not available (see Chapter 4). Therefore, I used a simple average of the period-specific good and poor estimates as an estimate of survival rates for moderate years.

The resulting assigned survival rates (Table 5.7) were used as means for the

survival rate functions. Variances for those functions were taken from the corresponding estimated process variances. The parameters α and β were then calculated from Eqs. 5.1 and 5.2 (Table 5.8).

I was unable to estimate juvenile survival rates from capture-recapture data. I assumed that juvenile survival was less than adult survival under all environmental conditions. This is supported by all studies of ground squirrel survival. In addition, I felt that juvenile survival is more variable, with survival rates in poor conditions, particularly, much lower than adult survival than in good conditions. With no data upon which to base juvenile survival estimates, I set daily survival rates such that annual rates of survival would approximate the proportions of marked juvenile females that were recaptured the following year (Van Horne et al. 1997a). I used results only for females, because the relatively high male dispersal rates would result in reduced recapture rates. Even so, use of recapture rates as a measure of survival are known to have several problems. Two of the most important are: 1) the assumption that capture probabilities are high (near 1.0) and equal among groups being compared, and 2) that the time period associated with the recapture rates is uncertain. Although Van Horne et al. (1997a) and others have used recapture rates as indices to over-winter survival, they actually reflect losses occurring both before and after the hibernation period. The effect of both of the problems stated above would be to underestimate true survival rates. Therefore, recapture rates were used only as guidelines to set minimum survival rates for juveniles.

A test of habitat and year effects by logistic regression found them both to be influential on explaining differences in recapture rates. In this analysis, data from sites

7A and 8A (the supplemental feeding sites) was eliminated. Results from the analysis found differences due to years ($\chi^2_2 = 351.76$, $P < 0.001$), habitat types ($\chi^2_1 = 10.63$, $P = 0.001$), and the interaction between years and habitat ($\chi^2_2 = 8.41$, $P = 0.015$). Therefore, mean recapture rates were computed for each year and habitat type (Table 5.9). In all years, recapture rates were higher in shrub habitat than nonshrub, yet the magnitude of that difference was greatest from 1993 to 1994.

As recapture rates are known to under-estimate true survival, I set daily survival rates for each period for juveniles such that recapture rates would be 80-90% of the product of the survival rates over the 3 time periods. Further, I assumed that daily rates did not differ for juveniles between Periods 1 and 2, and their relationship to Period 3 rates was approximately the same as for adults. For adults, the percent differences between Period 2 and Period 3 rates for each condition category were: Good, 0.24%; Moderate, 0.58%, and Poor, 0.90%. These percentages were used to set the differences between Period 3 and active period rates for juveniles. Using a SAS® (SAS Institute, Inc.) program that included the time period definitions for juveniles for each habitat and condition category, I changed period-specific daily rates under the conditions stated, until I achieved annual survival rates that were approximately 1.25× the respective recapture rates (Table 5.9). These were the daily rates used in the model (Table 5.10). For poor years in grass habitats, where the recapture rate was 0.00, I assumed most losses occurred during the over-winter period; therefore I set low, but non-zero survival rates for Periods 1 and 2, and 0.00 as the survival in Period 3.

I did not incorporate spatial variability in survival rates for juveniles into the

model, as I could think of no sound basis from which to estimate it. Although I could compute spatial variability in the recapture rates, it would be extremely difficult to translate these estimates into spatial variances corresponding to the survival estimates constructed as above. This is unfortunate, as I believe that spatial variability in survival rates among juveniles is probably greater than that for adults, not less.

Reproduction

Reproduction takes place in the model at the end of Period 1 for adults, and after survival functions for the period have been applied. There are two functions that can be used to control reproduction: reproductive rate and average litter size. Reproductive rate (the proportion of individuals that reproduce) applies only to females, although the model does check for whether there are adult males in the cell population and reproduction only occurs if at least 1 adult male is present. TGS are polygynous, so this is probably not an unreasonable assumption, unless the ratios of females to males becomes very high. Currently, the reproductive rate for females in all habitats under all environmental conditions is set to 1.0, except when early season conditions are very poor, in which case the reproductive rate is 0.0. The latter emulates the suspension of reproduction noted by Smith and Johnson (1985). Although reproductive rates (measured as the proportion of females captured that were found to be pregnant or lactating) in both the current TGS study and Smith and Johnson's study were very high, they were usually < 1.0. However, I calculated litter sizes based on the number of total females, not reproductive ones, so a reproductive rate of 1.0 is more appropriate (see below). The model can be run with reproductive rates between 0 and 1, in which case the number of reproductive females is

determined from a random binomial function, and litter sizes are only applied to those reproductive females.

Litter sizes in the model refers to the average number of juveniles per female that emerge from natal burrows. Therefore, they do not reflect births per se, but are the final result of a series of several opportunities for ground squirrels to adjust their reproductive output in response to degrading conditions. Ground squirrels, like other small mammals, are thought to adjust numbers of embryos by reabsorption or abortion, and also may aggressively (via cannibalism) or passively (through neglect) induce mortality of juveniles postpartum. As a result, the number of juveniles that emerge from natal burrows probably is more closely tied with environmental conditions than litter sizes at birth. In any case, it would be nearly impossible to measure birth numbers or pre-emergence mortality.

The average litter size for each cell is randomly selected from a gamma distribution function with parameter values determined by habitat type and the environmental conditions at the time of emergence of adult ground squirrels (early season conditions). The gamma distribution has been used by others as a distribution for modeling over-dispersion in Poisson processes either explicitly (Braner and Hairston 1989, Houggard et al. 1997), or implicitly by use of the negative binomial distribution (cf. Tempelman and Gianola 1996, White and Bennetts 1996). If the litter size of individual female ground squirrels (X) are considered a Poisson random variate, then each cell has a Poisson distribution with parameter λ. If the expected value of X (the average litter size for the cell) varies across cells, this extra variability is what is modeled by the gamma

distribution, and the resulting mixture of Poisson distributions follows a negative binomial distribution (Boswell et al. 1979, Johnson et al. 1992).

If the probability density function of the gamma distribution is given as:

$$f(z) = \frac{\beta^{\alpha} z^{\alpha-1} e^{-\beta z}}{\Gamma(\alpha)}, z > 0,$$

then the parameters of the gamma function, α and β, can be computed from a mean (μ) and variance (σ^2) as:

$$\alpha = \mu\beta \tag{5.3}$$

and

$$\beta = \frac{\mu}{\sigma^2}. \tag{5.4}$$

Litter size means and variances were computed from the TGS density estimates. Only 1992-1994 data were used, as estimates of juvenile density in 1991 often included immigrants to the site, and thus were not considered measures of local production. Litter size means (LS) for each site in each year (Table 5.11) were estimated as: $\hat{LS} = \frac{\hat{D}_J}{\hat{D}_F}$, where $\hat{D}_J$ is the site-specific estimated juvenile density and $\hat{D}_F$ is the estimated site-specific adult total female density. For these analyses, I did not attempt to distinguish reproductive females from non-reproductive ones, nor did I account for differences in litter size between yearling females (born the previous year) and adults (>1 years old), although Smith and Johnson (1985) found yearlings to have a lower reproductive rate and have smaller average litter sizes. Thus litter sizes in the model are on the basis of total

females in the population, and may be more variable than if I had computed age-class specific reproductive rates and litter sizes.

The variance for LS was estimated as:

$$\hat{\mathrm{Var}}(\hat{\mathrm{LS}}) = \hat{D}_J^2\left[\frac{1}{\hat{D}_F^4}\hat{\mathrm{Var}}(\hat{D}_F)\right] + \frac{1}{\hat{D}_F^2}\hat{\mathrm{Var}}(\hat{D}_J) - \hat{\mathrm{Var}}(\hat{D}_J)\left[\frac{1}{\hat{D}_F^4}\hat{\mathrm{Var}}(\hat{D}_F)\right].$$

I then computed per-year habitat-specific mean litter sizes (LS_S and LS_G, for shrub and grass, respectively) based on the simple average of litter size estimates from all sites within each habitat type (Table 5.11). (Note that I included LS values of 0.0 in analyses only for sites where $\hat{D}_F > 0$, and $\hat{D}_J = 0$). These estimates served as the basis for the means of the random gamma distributions.

Process (i.e., spatial) variance (σ^2) for the gamma distribution function, was estimated based on the following formulae (from Burnham et al. 1989: 263-264):

$$\frac{1}{n-1}\sum_{i=1}^{n}\hat{w}_i(\hat{\mathrm{LS}}_i - \hat{\mathrm{LS}}_\cdot)^2 = 1,$$

where $$\hat{\mathrm{LS}}_\cdot = \frac{\sum_{i=1}^{n}\hat{w}_i\hat{\mathrm{LS}}_i}{\sum_{i=1}^{n}\hat{w}_i}, \qquad \hat{w}_i = \frac{1}{\hat{\sigma}^2 + \hat{\mathrm{Var}}(\hat{\mathrm{LS}}_i|\mathrm{LS}_i)},$$

and $\hat{\mathrm{Var}}(\hat{\mathrm{LS}}_i|\mathrm{LS}_i)$ is the estimated sampling variance for the site-specific estimated mean litter size.

Because some estimates of σ^2 were <0, I used a bootstrap procedure to generate positive, but possibly biased, estimates. The bootstrap consisted of computing $\hat{\sigma}^2$ repeatedly ≥ 1000 times, from a data set consisting of samples of size *n* drawn at random with replacement from the available data, where *n* was the year-specific number of sites within each habitat type. The final estimate of σ^2 was then the mean of the bootstrapped sample estimates. For groups where this estimate was <0, I ran 2 additional bootstraps using the following conditions: 1) if any sample estimate was <0, the estimate was set to 0, and 2) if any sample estimate was <0, then the sample was ignored. These conditions established a minimum value (condition 1) and maximum value (condition 2), between which the true value of σ^2 was likely to fall. I then used the midpoint between these values as my estimate of process variance. Parameters α and β of the gamma distribution were then computed from the year- and habitat- specific means and variances (Table 5.11).

The final step of determining the litter size algorithm for the model consisted of assigning year-specific litter size means and variances to appropriate environmental condition categories, and providing values for conditions not encountered during any of the study years. I used early season (GREENUP) conditions as the basis for assignment, and as a result, I used the 1992 estimates for good conditions, 1994 for moderate conditions, and 1993 for poor conditions.

The number of juveniles produced in a cell is calculated as the number of reproductive females times the average litter size, rounded to the nearest integer value. Juveniles are then assigned to sex classes based on a random binomial function that

assumes a 1:1 sex ratio. Although Smith and Johnson (1985) reported that male:female ratios of juveniles were biased towards males (1.26:1), Rickart (1982) found them to be nearly equal (0.95:1), and the ratio for the demography study averaged 0.85:1 for all years. There may be some circumstances under which juvenile sex ratios are not biased, but I did not further explore this possibility.

Dispersal sub-model

All population processes operate within the cell with the exception of dispersal. The dispersal sub-model currently applies only to juveniles, although it could be modified to model adult dispersal as well. A flow diagram is given in Figure 5.7. The numbers of male and female dispersers in each cell are determined by applying a sex-specific dispersal proportion to the number of male and female juveniles surviving the first juvenile period, using a random binomial function. For males, that dispersal proportion remains constant ($p = 0.60$) throughout all years and for both habitat types. This is based upon the results given in Chapter 4, and supported by dispersal studies of other ground squirrels. For females, the dispersal proportion is set to 0.10, but this rate increases to 0.40 when environmental conditions are poor or if the number of adult females in a cell exceeds 100 (approximate 44 per ha). The increase in rates for females is purely speculative, but consistent with findings by others, such as Dobson and Kjelgard (1985) that female ground squirrels may increase dispersal in response to dwindling food resources.

After the number of dispersers of each sex is determined, the model structure

changes from a population based model to an individual based approach. An animal, once identified as a disperser, is moved from its cell of origin to its destination cell based on a direction chosen at random (i.e., 1 degree of 360 possible), and a distance (in meters) chosen at random from a 2 parameter exponential distribution. The values for the parameters were based on those estimated in the radio-telemetry dispersal study (Chapter 4), and is the same for each habitat type ($\hat{\beta} = 0.0024$ and $\hat{c} = 118.5$ m). The same parameter values for dispersal distance were used for both sexes, since evidence from other studies of ground squirrels found no sex-specific differences in dispersal distance (Holekamp 1986, Michener and Michener 1977, Hackett 1987).

Dispersal movement starts at the center of the originating cell, the x,y coordinates of which are calculated in meters from the lower, left-most corner of the map area. The location of the dispersal endpoint is calculated by trigonometry, and the receiving cell address (in rows and columns) is determined. The disperser is then added to the population number in the receiving cell, and deleted from the population of the originating cell. The disperser is thereafter considered indistinguishable from receiving cell non-dispersers, and therefore has the same survival rate, and other attributes, as they do.

The habitat type of the receiver cell is disregarded, thus dispersal is strictly random. If a disperser "lands" in a cell that is non-habitat, it remains in the cell until the end of the model year, but does not "survive" to emerge the following year (i.e., it is lost to the system). If the location of the receiving cell is computed to be beyond the boundaries of the model area, the disperser is also lost to the system. I felt this was

appropriate because I was using a large model area (thereby reducing the edge to area ratio), and the fact that much of the area beyond the model area is unsuitable for TGS.

Post-dispersal, the model returns to the population cell mode, and completes the model year. Juveniles "grow up" to become adults before the start of the next model year. Therefore, the initial population for each cell in the subsequent year is the total number of animals surviving Period 3 (over-winter) with sex ratio determined by the numbers of males and females (both adult and juvenile) that are in the population.

Model outputs

There are 2 types of data files that are normally output from the model, output files and grid files (other files may be output when debugging options are set). One of each type of file is generated at the beginning of the first model year (initial values) and at the end of each year in the simulation. The output data file is an ASCII file that lists, for each cell in the model, the cell address (in row number, column number format), the habitat type, and the number of ground squirrels of each age and sex, as well as the total number of grounds squirrels. These files are suitable for import into SAS® (SAS® Institute, Inc.) or other data analysis software packages. The grid data file is a map file in ARC/INFO format, the values of which are the total number of ground squirrels in each cell. This file can be displayed or used in further analyses using ARC/INFO, or could be converted to another GIS such as GRASS.

MODEL SIMULATIONS

Programming verification and test runs

When developing any complex model, programming errors are inevitable. Aside

from outright errors, many other things can occur in the modeling process that can lead to a model that does not perform as expected. Therefore, at every stage during model building, I ran extensive test simulations to verify that the program itself was correct. I did so by isolating the portion of the model to be tested as much as possible (i.e., eliminating many steps), setting the remaining model parameters to standard values, and generally controlling as much variability as possible. I then analyzed the output from the test runs, and compared the results to the expected values. In some cases, I wrote SAS® (SAS® Institute, Inc.) programs that performed the same functions, and compared the results from those programs to the model output.

Following the program verification runs, I programmed the model with the parameter values as estimated and described above. Using the test map area (Figure 5.3) I first ran several simulations of just 10 years in length, where I set the environmental conditions to be always good, always moderate, or always poor, to determine what the apparent response of ground squirrel populations would be to those conditions.

Finally, I ran 2 sets of simulations, 1 set 10 years in length, and the other 25 years, with the random assignment of environmental conditions. Simulation runs of longer duration are not recommended at this time, because the model lacks a mechanism to stop the simulation run when populations grow to unrealistic levels. Most of the results I report are from the 10-year simulation runs, because population trends were mostly evident by that time. The longer simulations were used to confirm these trends.

For simulation runs under both controlled and random sets of environmental conditions, I computed the year-specific mean cell population growth rates, λ_t

(as N_{t+1} / N_t) within each repetition. For each repetition, I computed the mean λ over the 10 year interval as a geometric mean: $\left(\prod \lambda_i\right)^{1/y}$ where the λ_i are the year specific λ, and y is the number of years in the simulation. I used λ as the primary statistic to evaluate model results, but I also looked at the variability in λ, the absolute cell population size, the relative variability among cell population sizes, and the distribution of cell population abundance. In most cases, I examined both overall and habitat-specific results.

RESULTS

Effect of habitat adjustments to periods

Using a SAS® (SAS® Institute, Inc.) program I wrote to compute annual survival rates (ASR) from period-specific per-day survival rates (Tables 5.3 and 5.4), I compared "cumulative survival rates" (CSR) using period specifications with and without habitat adjustments. CSR was computed as ASR^n, where n = 1,2,3,...10, and was intended to show both the immediate and long-term effects of the differences in period definitions on survival. The results are displayed in Figure 5.8.

For adult females and juveniles, the pattern of the effects were similar, with moderate differences in the first few years under some conditions, but with those differences declining as time passes. The magnitude of the differences, while low, could affect model outcomes under the conditions for which those differences are greatest. However, the conditions under which the impact of habitat specific period definitions is more likely to be noticed are not the same for adult females and juveniles.

The pattern for adult males is complete different than for the other groups. All sets of conditions show some effect, and the effects remain even after 10 years. The

differences in CSR actually increase after the first year, and begin to decline slowly after year 3. Although the magnitude of the differences again remain low (< |0.05|), the persistence of these differences, and their somewhat unpredictable pattern, may lead to appreciable effects on model outcomes.

Model verification runs

In the model verification runs, I confirmed that the achieved parameter values were as I expected, with one exception: juvenile survival. I discovered that the survival algorithm for Period 3, juveniles only, was being ignored; as a result too many juveniles survived to adulthood. This flaw did not exist in an earlier version of the TGS model, and I believe it is the result of additional coding intended to integrate the TGS model into EcoChange. Although I was unable to correct this flaw, I was able to compensate for it by changing Period 2 survival to account for mortalities occurring in both Periods 2 and 3. This was possible because no significant population events take place between these periods. I computed what the new combination Period 2 and 3 survival rates using the same methods I used to calculate the period-specific rates. Using these rates, the achieved annual survival rates were approximately what I expected using the correct period-specific rates (Table 5.9).

Computing limitations (time constraints)

In constructing the SEP model, I gave little consideration to potential limitations in computer time and space. Yet my ability to fully explore model results was certainly affected by these limitations, which became evident while doing the simulation runs under the controlled environmental conditions. I quickly discovered that the addition of

the random beta functions to the survival algorithms increased the time for each model run (of 10 years) significantly, as compared to a model run where spatial variability (cell-to-cell, with habitat type) in survival was eliminated. For example, under poor conditions year-round, the average 10-year simulation took 11 minutes; with the spatial variability added, it took over 2 hours. This increase in time would severely hamper my ability to conduct a number of simulation replications. I therefore investigated what the impact of eliminating the spatial variability component from the model would have on model results.

Figure 5.9 shows the results of comparisons of model results with and without the random beta function component, under the controlled conditions. From these graphs it is apparent that for most situations, the differences are insignificant. However, there are exceptions. For conditions that are good early, and moderate late, the population trend with spatial variance added increased to a point and leveled off, whereas without the spatial variance component, it declined slowly after 4 years. Under moderate conditions throughout the year, and to a lesser extent for poor early, and good late conditions, the effect of the added spatial variance appeared to be a slight moderation of the population decline after 3 years. These difference due to added spatial variance are of some concern, as time limits prevented me from adequately testing their effects in model simulations under the randomly assigned conditions. Good/moderate conditions are expected to occur 28.5% of the time, whereas moderate/moderate and poor/good conditions occur an additional 14.7% of the time. Therefore, the potential for significant effects of ignoring spatial variance on model outcomes may be appreciable.

I also looked for differences in variability among cells, expressed as a coefficient of variation (CV), between the 2 model versions. Surprisingly, there were none (Figure 5.10). Although it would seem obvious that CVs should increase when spatial variance is added, this was not the case. I attributed this lack of difference to the relatively small magnitude of the spatial variance in survival rates when compared to other stochastic elements in the model.

Controlled conditions

Aside from the differences due to the spatial variance in survival discussed above, the results of the simulation runs with conditions held constant were somewhat as expected (Figure 5.9). Late season conditions have a greater impact on the population growth or decline, but except when conditions are poor late, early season conditions also have an effect. None of the sets of conditions led to a stable population, although the λ for both good/moderate and poor/good conditions was near 1.0. Therefore, population stability through time, under this model, could only be achieved by a mixture of environmental conditions. Whereas most conditions led to a declining population, both the good/good and moderate/good conditions led to rapid population growth. As these conditions are expected to occur 39% of the time, they probably occur frequently enough to rescue TGS populations from declines which occur the rest of the time (see random condition runs, below).

Although population growth was highly affected by environmental conditions, the relative variability among cell populations was less affected. Under initial population assignments, CVs were slightly < 1.0, and under both moderate and good conditions, they

remained approximately 1.0 throughout the 10 years of the simulation (Figure 5.10). Only when conditions were poor late in the season was there an appreciable trend, with CVs increasing to > 2.0 through time.

I also examined population responses to constant environmental conditions within each habitat type (Figure 5.11; Table 5.12). In all cases, the population trends were similar in both habitat types; however, when conditions were poor throughout the year, λ was consistently higher in shrub cells than in grass cells.

Based on the results from the simulations under controlled conditions, I grouped environmental condition combinations into 3 categories to make evaluations of subsequent simulations easier. The categories were based on the population trends that resulted from the condition combinations: 1) increasing, consisting of good/good and moderate/good condition combinations; 2) stable, including the poor/good, moderate/moderate, and moderate/good conditions, and 3) declining, with all the remaining condition combinations.

Random conditions

In the set of 40 repetitions of 10 years in length, the mean λ over all repetitions was 1.14 (SE = 0.02), indicating net population growth. In fact, in only 4 of the 40 reps did populations show a net loss. Figure 5.12 shows the frequency distribution of λ, which ranged from 0.90 - 1.40. Results from the 25-year simulation runs (Figure 5.12) were similar, indicating that the 10-year runs were probably sufficient to determine trends in population growth rates. Figure 5.13 shows the trends in mean cell populations for the 40 10-year simulation runs, grouped by categories of λ.

To investigate the effects that environmental conditions had on model outcomes, I also tabulated the frequency of occurrence of each condition combination categories (increasing, stable, and declining), for the 10-year simulation runs grouped by levels of population growth rate (Table 5.13).

The variability about λ was relatively large, with CVs averaging 30.6% (CVs were calculated based on arithmetic means and standard deviations), and ranging from 18.8 - 42.4%. There was no apparent relationship between population stability over the 10 years (indicated by a λ near 1.0) and its consistency over the 10 years (indicated by a low CV). The mean CV for the 9 reps for which λ was between 0.95 and 1.05 was 32.9%, but ranged from 25.8 - 42.4%. There was also no relationship between the reps with the highest net growth rates and CV; for the 9 reps with λ>1.25, mean CV was 28.6% and ranged from 18.8-39.8%.

Comparing habitats, mean population growth over the 10 years was lower in shrub habitat than in grass, although it was still >1.0. Over all 40 repetitions, mean λ in shrub habitats was 1.06 (95% CI: 1.01 - 1.10) and in grass habitat, mean λ was 1.15 (95% CI: 1.11 - 1.19). In none of the 40 reps was the mean growth rate higher in shrub than in grass habitats. However, in 30.3% of all years in the 40 simulations, mean growth rates were higher in shrub cells than in grass cells, and in all but 1 simulation, at least 1 year had a higher mean growth rates in shrub habitat than in grass habitat.

Although it might be expected that population growth rates would be greater in shrub habitats when conditions were poor late in the season (when juvenile survival in grass habitats is 0), shrub cell population growth rates exceeded grass rates under other

conditions as well. Of the 109 years when growth rates were higher in shrub habitats, 83.5% were years with good early conditions, which greatly exceeds the rate of 65.0% which would be expected by chance alone (the expected rate of occurrence for good early season conditions). Years with moderate early conditions were under-represented (7.3% vs. 13.0% expected), as were years with poor early conditions (9.2 vs 18.0%). Years that were very poor early never had higher shrub population growth rates. Years with good late conditions were under-represented (39.4% vs. 50.0% expected), but years with moderate late conditions occurred exactly as expected (44.0%). As anticipated, years with poor late season conditions more often had higher population growth rates in shrub habitats (16.5%) than would be expected by chance (6.0%).

Although population growth rates convey important information about population trends, they may not indicate when populations have grown to unrealistic levels. For example, a population may grow to very high levels within the 10 years, then decline to near the initial population size, resulting in a λ near 1.0. Thus the overall growth rate may seem reasonable, but the interim dynamics may be unrealistic. Therefore, I also examined the maximum mean cell population levels achieved in each simulation run. Creating 6 categories of population classes (Figure 5.14), I found that in 16 of the 40 reps (40.0%) mean cell populations grew to >100 total animals (>44/ha) at some time during the 10-year runs. Although densities of > 100 ground squirrels/ha were recorded during the demography study, the model values are means over all cells (not including non-habitat), and even in 1992, when TGS populations were at their greatest, the mean density over all TGS study sites was considerably less than that. Only under the most favorable

habitat conditions might such high population levels be sustained, but even that is unlikely.

Most of the high population levels occurred in grass habitats, as in only 1 rep was the mean population in shrub habitat cells >250. In grass habitats, however, mean cell populations exceeded 250 at least once in 22.5% of the repetitions, and reached 100-249 in an additional 42.5% of simulation runs (Figure 5.14).

I also looked for changes in the spatial distribution of TGS population abundance by computing the variance/mean ratio: $s^2/\bar{x}$, where s^2 was the variance among cell populations for a given year, and $\bar{x}$ was the mean cell population. This ratio should be near 1.0 if cell populations are distributed randomly (i.e., distributed as Poisson where $E[s^2] = E[\bar{x}]$), and >1.0 if populations are clumped. Because of the relative patchiness of the habitat map (Figure 5.15), some clumping was evident under the initial population assignment (Figures 5.16-19), even though those assignments were random within habitat type. Following initial assignment, populations became increasingly aggregated through time, whether populations were growing or declining (Figures 5.16-5.19). There also was no point at which spatial aggregation leveled off, as shown by the graph of the variance/mean ratio from the 25-year simulation runs (Figure 5.20), although there is certainly a theoretical limit. Populations in shrub habitats were initially more clumped, but did not aggregate as much as did populations in grass habitats through time.

DISCUSSION

Townsend's ground squirrel populations appear to be doing well under the current habitat conditions, at least within the area of the test map. In the majority of simulation runs, populations grew through time. For the set of simulation runs where the frequency of environmental conditions most closely matched their expected frequencies, population growth rates were in the 1.05-1.15 range (Table 5.13). When good environmental conditions occurred more often than expected, populations grew much faster, and populations remained stable only when poor environmental conditions occurred more frequently than expected (Table 5.13). The latter indicates that if the relationships between model parameters and environmental conditions in the model are accurate, then population stability is unlikely to occur under the assumptions noted above. That is, poor conditions do not occur often enough to keep TGS populations in check, and therefore stable populations could only be maintained by other means.

Population growth rates over a 10-year period were higher in grass habitats than in shrub habitats, which is consistent with the results from the simulation runs under constant conditions. Yet the yearly comparison between habitat-specific growth rates indicated that good early conditions were frequently more favorable to ground squirrels in the shrub habitat, while poor late conditions were less detrimental to ground squirrels in shrub habitat than in grass. The latter result supports the conclusions of Van Horne et al. (1997a), whereas the former result was somewhat unexpected.

In tabulating the results for the yearly comparison of habitat-specific growth rates, I noted that the results were not always consistent. That is, in some years with poor late

conditions, growth rates were higher in grass habitats than in shrub habitats. Likewise, growth rates in shrub habitats were sometimes higher than in grass habitats, even when the conditions favored higher grass growth rates. This is due to the stochastic nature of the model, but it serves as a reminder that conclusions based on a single year may be completely erroneous. Undoubtably, real ground squirrels respond to environmental conditions in ways that are not well simulated by the random components in the model, but until we know the nature of those responses, care should be taken in making generalizations based on results from a single year.

Under the dynamics modeled, TGS populations became increasingly concentrated in grass habitat cells, especially in areas with large expanses of this habitat type. On the other hand, populations in large areas of shrub remained low, even when populations elsewhere were increasing rapidly (Figures 5.17-19). Intermediate population levels appeared to be maintained only in areas where the two habitat types were intermingled, especially when shrub cells were the predominant habitat type.

Although the model I've presented here is somewhat preliminary, I believe that much can be learned from its construction and implementation. However, I make no claims that model results reflect the reality of TGS population dynamics, UNLESS model assumptions are correct. Aside from the assumption that parameter estimates are accurate, these assumptions include:

1. Study sites are representative of habitat types.
2. Study years are representative of years with similar environmental conditions;

3. There are no carry-over effects, i.e., population parameters are not affected by prior conditions;
4. There are no density dependent feedback mechanisms;
5. There are no effects of predators on prey, or on habitat by prey;
6. Dispersal movements are random with respect to spatial attributes, including habitat.
7. The habitat map used is accurate.
8. The test map is representative of the entire model area.

The first 2 of these assumptions are unavoidable. I had no choice but to assume that study sites and years were representative of spatial and temporal patterns in population parameters on the SRBPNCA. Twenty study sites is a large sample by almost any standards for a field study of this type, and although random selection of sites was not possible due to the logistics of carrying out this research project, the sites were not chosen based on the likelihood of capturing ground squirrels. Several sites were intentionally chosen to be close together, but they did not appear to show more correlation in population dynamics than sites located further apart within the same habitat type.

The 4 year duration of the study is more troublesome. At least 2 years of data collection under each environmental condition category would be necessary to verify the representativeness of the years studied, thereby requiring study over several more years. Even Smith and Johnson's (1985) study, of 7 years in duration, encountered only 3 of the 12 possible combinations of condition categories as I defined them. As it was, I was fortunate to have data collected under a wide range of conditions (4 combinations

represented) within the 4 years of the study reported here. However, the caution noted earlier about extrapolating results collected from a single year certainly applies here.

Replication of years with similar environmental conditions would also help to measure the effects of the fourth assumption: that there are no carry-over effects within or between years. I'm fairly certain that this assumption was violated in reality. Van Horne et al. (1997a) and my own conclusions about the factors influencing survival rates (Chapter 3) assumed that carry-over effects did occur. Animals that had survived the 1992 drought surely were not in as good physiological condition in 1993 as they would have been following a year with less harsh conditions. Although I considered including prior conditions in the model (and it is possible to include them), I felt that I did not know enough about their effects under conditions other than the ones encountered. When I was aware that prior conditions may have affected parameter estimates (such as survival rates for adults estimated in some cases in 1993), I did not use those estimates in the model. The net result of ignoring carry-over effects, in situations such as the one encountered in 1993, is that populations would rebound unrealistically after experiencing harsh conditions. This may be one of the mechanisms by which populations are naturally regulated that prevent the kind of growth rates that occurred in the model simulations.

Also ignored in the model is virtually any kind of regulating mechanism that may occur in response to population density. Whether that mechanism is intrinsic (i.e., a physiological or behavioral change initiated by TGS individuals) or extrinsic (imposed by an external influence, such as a deteriorating food source or predation), there must be something that generally prevents TGS populations from achieving the unrealistically

high numbers which occurred in model simulations. Surprisingly, few studies of ground squirrels have examined population regulation mechanisms. Dobson (1995), in an experimental study, concluded that Columbian ground squirrels (*Spermophilus combianus*) regulated populations mainly through decreases in reproductive success and juvenile survival, and that adult survival remained largely unaffected. This is probably also true for TGS, as indicated by their response to drought conditions. When drought occurred early, they suspended reproduction entirely (Smith and Johnson 1985), and when drought occurred late, juvenile survival was near 0 (this study). Although adult survival declined also, this was probably due to the severity and timing of the 1992 drought. The 1992 conditions were more likely a catastrophe for ground squirrels of a magnitude that could not be compensated for by normal regulatory mechanisms.

Another potentially catastrophic event, not included in the model, would be the occurrence of an epizootic such as plague (*Yersinia pestis* infection). Plague is known to decimate prairie dog (*Cynomys* spp.) colonies (Rayor 1985, Barnes 1993), yet little information seems to be available on its effects on *Spermophilus spp.* Messick et al. (1983) documented the presence of plague in TGS individuals found dead on the SRBPNCA, yet they also noted that they did not observe high mortality in the TGS population at large. Therefore, whether plague or another type of disease could play a roll in controlling TGS populations remains unknown. Even less known are possible effects of parasitic infection. Wilbur et al. (1994) studied eimerian prevalence in TGS, but they did not find any effect of infection on survival or reproduction, nor did I find any other published studies that did so for other ground squirrels species.

As currently constructed, the model does not allow TGS to affect their habitat, or for predators to affect TGS populations. Even when the TGS model is linked with the other components of EcoChange, the assumption is that the SRBPNCA ecosystem is "bottom-up" regulated. That is, habitat affects prey, which in turn affect predators, but neither prey nor predators affect habitat, and predators do not affect prey. The assumption that TGS do not affect their habitat is probably reasonable. Although high densities of ground squirrels probably affect a single year's vegetation crop, they probably do not causes longer-term changes in habitat composition, except under the most severe circumstances. During the 1992 drought, TGS were observed digging and eating the regenerative portion (crowns) of bunch grasses (personal observation), but it is not known if this led to a decline in the occurrence of bunch grasses in subsequent years.

The assumption that predators do not affect prey is weaker. Although it is unlikely that predators can control TGS populations when growth is high, they probably do affect TGS population numbers in some cases. However, the EcoChange model does not even include the predator that likely has the most influence: badgers. Badgers are plentiful on the SRBPNCA; Messick and Hornocker (1981) found densities in that area to be among the highest recorded. They also tend to key in on population "hot spots", and can reduce local numbers considerably. During the current study, badgers seemed to be most abundant in 1993, the year following TGS population highs but a year during which ground squirrels were scarce. In that year, badgers appeared to be keying in on areas where TGS were relatively abundant, thereby reducing TGS populations to even lower levels (personal observations, partially based on radio-telemetry results). Although

reduction of population numbers by badgers on a broad scale may be rare, the general pattern of badger predation may serve to reduce population hot spots, thereby reducing the clumping that occurred during the simulation runs.

The assumption that dispersal movements are random with respect to habitat and other spatial attributes (such as topography) is probably a poor one, but I lacked sufficient evidence to model dispersal otherwise. It is difficult to assess what effects non-random dispersal patterns would have on population growth or distribution. Habitat imprinting, which I suggested as a possibility in Chapter 4, would increase the degree of aggregation within the grass habitat, and make any "rescue" effect between populations residing in differing habitat cells unlikely. On the other hand, dispersers would probably avoid highly populated areas in favor of areas with lower densities, which would have the effect of evening out the population distribution through space. At this time, such non-random dispersal scenarios would be difficult to include in the model, but the linkage of the model to a GIS layer incorporating dispersal probabilities might be possible.

The final model assumptions listed concern habitat patterns. The habitat map is what makes the model spatially explicit, and it is presumed that results would be different if the habitat map used with the population dynamics simulator was different. However, the potential for error in model results associated with the habitat map may be large. Although Rotenberry and Knick (1996) have confidence in the validity of the vegetation classification based on satellite imagery (they report a residual misclassification rate of 1.5%) , there is no doubt that mis-classification of habitat exists. This might be partially offset by the grouping of categories into the 3 broad classifications I used here, but

certainly not eliminated. In some respects, the map is too "detailed"; i.e., it appears to pick up habitat differences at a scale that may be inappropriate. This point is best illustrated by a detailed look at the habitat map in the area around some of the TGS study sites (Figure 5.21). These sites were selected based because they appeared to be homogeneous with respect to a specific habitat type, both within the 10 ha site and in the immediate surrounding area. Yet the habitat map used with the model makes those areas appear to be much more heterogeneous. This is probably a result of the criteria used to classify areas as shrub habitat; because shrubs are more detectible by satellite imagery than the surrounding grassland, more cells may be classified as shrub than occur in reality.

The effect of these probable classification errors in the habitat map are: 1) over-estimation of shrub habitat, and 2) the appearance of many isolated habitat cells (i.e., single cells of one habitat type surrounded by another). In the first case, results may be somewhat biased toward TGS dynamics based on shrub habitat population parameters. In the second case, parameter values are assigned to cells unrealistically; it is more likely that a population residing in an isolated cell has dynamics more like that of the surrounding cells, even if they are of the differing habitat type, than it does of like habitat cells that are further away. To account for these problems I recommend that some "fuzzing" (i.e., reduction of resolution) of the habitat map be used to smooth out these apparent anomalies.

Since all model results are based on a subset of the intended model area (Figure 5.3), caution should be exercised in extrapolating those results to the larger area. The test

map area used in the simulations reported here contained about half of the TGS study sites, although it was only 16.3% of the model area. Therefore, the estimates obtained from data collected on TGS study sites may more accurately reflect dynamics of TGS populations located within the test area than within the model area as a whole. Large areas of the latter were excluded from intensive study, so projection of results to this area based on the smaller area is probably unwarranted.

CONCLUSIONS

Of the objectives listed for the SEP model, the first 2 were certainly met. The model exists, and I constructed it almost entirely based on empirical results. Simulation runs using the habitat map were successful, and yielded results that should offer insight into the questions the SEP model is intended to answer. My answers to those questions, based on these preliminary results, are as follows:

1) Are TGS populations likely to persist given the current habitat configurations (spatial arrangement of habitat types) and expected population parameter values?

Yes, probably, if model results mimic reality. Population growth rates are >1.0 for almost all scenarios where environmental conditions vary randomly. However, the tendency for populations to build to high levels in grass cells is troubling. Since these levels cannot be maintained, population crashes similar to that experienced in 1992 are inevitable. On the other hand, TGS seem to fare poorly in large expanses of shrub habitat. From the limited vision of this model, it appears that TGS populations would be more stable if shrub and grass habitats were intermingled.

2) What population parameters appear to be most important in maintaining populations under current conditions?

3) What are the effects of uncertainty in parameter values on model outcomes?

These questions are related, and would be best answered by a detailed sensitivity analysis. Although I was unable to conduct such an analysis, close examination of model behavior does provide preliminary insight into the relative importance of model parameters. The model simulations run under controlled conditions show an initial increase, followed by a later decline, when conditions are either good or moderate early, and moderate late. This must be due to high adult survival rates, but reproduction is too low to replace adults as they die over time. Although populations may be able to sustain themselves through a year or two with low reproduction, they will decline unless there is an increase in reproductive output in the long term. Reproductive effects may also be seen in the habitat-specific results; litter sizes estimated for shrub habitats were less than replacement levels for most conditions, whereas grass litter sizes were probably much higher than necessary, under most conditions, to simply replace adult losses (Table 5.11).

The model results from the controlled condition simulations also show the relative importance of adult female survival vs. adult male survival. There were several cases in which male survival rates did not appear to match the environmental condition categories to which they were assigned (Table 5.6). Adult male survival was often estimated as higher during poor late season conditions than during good late season conditions. I had been concerned about not "fixing" that anomaly somehow, until I saw that they appeared to have little impact on model results. This is not very surprising, as adult males exert

little influence on reproduction in this model; as long as at least 1 male survives, regardless of conditions, females will reproduce. Therefore adult male survival is one area where uncertainty in the parameter estimates probably has little effect on model outcomes. As model results seem to follow adult female survival patterns more closely, then those parameters may be assumed to have more effect on TGS population dynamics. It follows that uncertainty in those parameters will have a greater impact on model results.

It is not so obvious what the effect of the uncertainty in juvenile survival parameters is. Certainly periodic failures of the juvenile age class have little impact on longer-term population dynamics, as long as those conditions do not occur often. This is one area that should be explored further. I would guess, however, based on the results from other population studies of relatively long-lived mammals, that juvenile survival is less important in dictating population trends then adult female survival.

4) What are the most important needs for better information?

Unfortunately, the most important needs may be those that are the most difficult to obtain: parameter estimates under a wider variety of environmental conditions and information on density regulating mechanisms. Lacking the ability to control when those conditions occur, closer investigation of the links between the condition of the habitat (presumably controlled by environmental conditions, but potentially also by ground squirrels) and ground squirrel survival and reproduction may be possible through experimentation. The food supplementation experiment conducted in conjunction with this study may provide further insights when complete results are available. Field

experiments such as those conducted by Dobson (1995) and Hubbs and Boonstra (1997) on Columbian and Arctic ground squirrels, respectively, may also provide insight into population regulation mechanisms. It may be difficult to be optimistic about actually finding such mechanisms, however, in light of Chitty's (1996) review of the subject. His conclusion regarding the more than 60 years of study of the topic, is that we don't know what regulates populations. Still, the effort seems worth pursuing.

If production and survival of juveniles is a significant regulatory mechanism , as Dobson (1995) found for Columbian ground squirrels, then reliable estimates of juvenile survival may be important. Such estimates may also be difficult to obtain because of the very short period between juvenile emergence from natal burrows and dispersal. Fortunately, the need for information about juvenile survival is probably greatest when levels of production, and therefore sample sizes, are high.

Adult survival rates were much easier to estimate, yet the importance of adult female survival to TGS population dynamics demands that this area receive more attention. In fact, it would probably be worthwhile to focus on the mechanisms that determine adult survival. The simulation model I developed loosely linked survival with environmental conditions; a better approach would be to directly model survival (and probably other parameters, especially litter size) as a function of the condition of the vegetation, especially the grasses upon which TGS are most dependent (Van Horne et al. 1998). This should be possible to implement with the current model structure.

Finally, the spatial aspects of TGS population dynamics remain largely unknown. Dispersal should be examined more intensely through studies designed specifically to

address hypotheses about non-random movement patterns. The effects of habitat patch size and juxtaposition on population dynamics should also be examined, at least to determine the influence of surrounding habitat areas on isolated habitat patches.

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Table 5.1. Assignment of vegetation map classification categories to habitat types for a spatially explicit population model of Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, Idaho. The original categories were classified from satellite images by Rotenberry and Knick (1996) and are available to the model as a single GIS map layer.

Vegetation map category		TGS model habitat type	
Number	Description	Number	Description
0	Non-vegetation	3	Non-habitat
1	Sagebrush	1	Shrub
2	Shadscale	3	Non-habitat
3	Winterfat	1	Shrub
4	Russian thistle	3	Non-habitat
5	Native grassland	2	Grass
6	Exotic grassland	2	Grass
7	Agriculture	3	Non-habitat

Table 5.2. Environmental condition classifications for Townsend's ground squirrel study years (1975-1981: Smith and Johnson 1985; 1991-1994: Van Horne et al. 1997) on the Snake River Birds of Prey National Conservation Area in southwestern Idaho. Early season conditions (GREENUP) are based on average daily temperatures in February and 3-month cumulative precipitation totals (December - February). Late season conditions (GREENNESS) are based on 3-month cummulative precipitation totals (March-May) only. (See text for complete definitions of categories).

Year	GREENUP	GREENNESS
1975	GOOD	GOOD
1976	GOOD	MODERATE
1977	VERY POOR	MODERATE
1978	GOOD	GOOD
1979	GOOD	MODERATE
1980	GOOD	GOOD
1981	GOOD	GOOD
1991	GOOD	GOOD
1992	GOOD	POOR
1993	POOR	GOOD
1994	MODERATE	MODERATE

Table 5.3. Parameter values used to define the timing and duration of periods within years for a population model of Townsend's ground squirrels. For adults, Period 1 lasts from emergence from hibernation to the appearance of juveniles, Period 2 from then until immergence into estivation, and Period 3 is the entire period of torpor. For juveniles, Period 1 is from emergence from natal burrows until onset of dispersal, Period 2 is from then until immergence into estivation, and Period 3 is the entire period of torpor. Environmental condition categories are based on temperature and precipitation at 2 times of the year, February and May (see text for definitions). Entries marked with a V vary depending upon the preceding or following period definitions. End days and interval length for Period 3, both age groups, are determined by the start day for Period 1, adults, the following model year.

Age	Period	Sex	Habitat	Conditions[a]	Start	End	Length
Adult	1	M	Shrub	Good	21	95	75
				Moderate	36	110	75
				Poor	41	115	75
				Very poor	36	110	75
			Grass	Good	21	85	65
				Moderate	36	100	65
				Poor	41	105	65
				Very poor	36	100	65
		F	Shrub	Good	36	95	60
				Moderate	46	110	60
				Poor	51	115	60
				Very poor	46	110	60
			Grass	Good	36	85	50
				Moderate	51	100	50
				Poor	56	105	50
				Very poor	51	100	50
	2	M	Shrub	Good	V	140	V
				Moderate	V	135	V
				Poor	V	130	V
			Grass	Good	V	135	V
				Moderate	V	130	V
				Poor	V	135	V
		F	Shrub	Good	V	140	V
				Moderate	V	135	V
				Poor	V	130	V
			Grass	Good	V	135	V
				Moderate	V	130	V
				Poor	V	135	V

Age	Period	Sex	Habitat	Conditions[a]	Start	End	Length
Adult	3	M	Shrub	Good	141	V	V
				Moderate	136	V	V
				Poor	131	V	V
			Grass	Good	136	V	V
				Moderate	131	V	V
				Poor	136	V	V
		F	Shrub	Good	141	V	V
				Moderate	136	V	V
				Poor	131	V	V
			Grass	Good	136	V	V
				Moderate	131	V	V
				Poor	136	V	V
Juveniles	1	Both	Shrub	Good	96	125	V
				Moderate	111	125	V
				Poor	116	125	V
			Grass	Good	86	125	V
				Moderate	101	125	V
				Poor	106	125	V
	2	Both	Shrub	Good	126	180	55
				Moderate	126	165	40
				Poor	126	155	30
			Grass	Good	126	170	45
				Moderate	126	165	40
				Poor	126	155	30
	3	Both	Shrub	Good	181	V	V
				Moderate	166	V	V
				Poor	156	V	V
			Grass	Good	171	V	V
				Moderate	166	V	V
				Poor	156	V	V

[a]Period 1 values are for early season conditions, Period 2 and 3 values are for late season conditions.

Table 5.4. Parameter values used to define the timing and duration of periods within years for a population model of Townsend's ground squirrels, ignoring habitat effects on period timing and length. See Table 5.3 for complete definitions of periods, and table format

Age	Period	Sex	Conditions[a]	Start	End	Length
Adult	1	M	Good	21	90	70
			Moderate	36	105	70
			Poor	41	110	70
			Very poor	36	105	70
		F	Good	36	90	55
			Moderate	46	105	55
			Poor	51	110	55
			Very poor	46	105	55
	2	M	Good	V	140	V
			Moderate	V	130	V
			Poor	V	130	V
		F	Good	V	140	V
			Moderate	V	130	V
			Poor	V	130	V
	3	M	Good	141	V	V
			Moderate	131	V	V
			Poor	131	V	V
		F	Good	141	V	V
			Moderate	131	V	V
			Poor	131	V	V
Juveniles	1	Both	Good	91	125	V
			Moderate	106	125	V
			Poor	111	125	V
	2	Both	Good	126	175	50
			Moderate	126	165	40
			Poor	126	155	30
	3	Both	Good	181	V	V
			Moderate	166	V	V
			Poor	156	V	V

[a]Period 1 values are for early season conditions, Period 2 and 3 values are for late season conditions.

Table 5.5. Analysis of variance of factors effecting estimated average immergence dates for adult Townsend's ground squirrels on the Snake River Birds of Prey Area, Idaho, in 1992-1994. Immergence dates are estimated as the 75th percentile last capture date for individuals captured after 15April, computed by year, sex, and habitat type. For analysis A, 2 sites receiving supplemental feed during 1993 and 1994 were dropped from the analysis in those years. In analysis B, those sites were treated as a separate habitat type.

A. 1992-1993, supplemental feeding sites dropped.

Source	DF	MS	*F*	*P*
Sex	1	10.08	0.88	0.392
Year	2	60.75	5.29	0.058[a]
Habitat type	1	18.75	1.63	0.257[a]
Year × Habitat	2	59.25	5.16	0.061[a]
Error	5	11.48		

[a] In a reduced model, with Sex dropped from the effects, the P-values for Year and Year × Habitat were $P = 0.046$ and $P = 0.048$, respectively (error df = 6, and MSE = 11.25). The *P*-value for Habitat in this model was $P = 0.244$.

B. 1993-1994, supplemental feeding sites as separate habitat types.

Source	DF	MS	*F*	*P*
Sex	1	2.08	0.13	0.734
Year	1	52.08	3.24	0.132[a]
Habitat type	2	87.75	5.46	0.055[a]
Year × Habitat	2	25.08	1.56	0.298[a]
Error	5	16.08		

[a] In a reduced model, with Sex dropped from the effects, the P-values for Year and Year × Habitat were $P = 0.100$ and $P = 0.240$, respectively (error df = 6, and MSE = 13.75). The *P*-value for Habitat in this model was $P = 0.033$.

Table 5.6. Estimates used to determine population classes and probabilities for initial population sizes in the spatially explicit population model of Townsend's ground squirrels. Study site-specific density estimates for 1991 were computed from mark-recapture data, with corresponding "shrunk" estimates calculated from shrinkage methods (see text and Chapter 3 for details) conducted for each habitat type. Population estimates for 2.25 ha cell sizes were computed as shrunk estimates × 2.25, and population classes were assigned to produce a mean and variance similar to those calculated for the population estimates. The frequency of sites within each population class were used to set the probabilities of assignment for initial population sizes for the model.

Habitat = Shrub

	Density estimates		Population size	
Site	Original	Shrunk	Estimates	Class
1A	2.12	2.12	4.77	4
1B	0.88	0.88	1.98	2
2A	0.58	0.58	1.31	2
2B	0.27	0.27	0.61	0
3A	0.00	0.00	0.00	0
3B	1.15	1.15	2.59	2
5A	5.57	5.52	12.42	14
5B	8.82	6.91	17.60	16
9A	7.98	7.82	15.55	16
9B	6.74	6.65	14.96	14
mean	3.79	3.19	7.18	7.10
variance		9.87	49.98	48.54

Grass

	Density estimates		Population size	
	Original	Shrunk	Estimates	Class
4A	19.2	14.52	32.67	32
4B	14.56	13.13	29.54	32
6A	0.24	0.24	0.54	0
6B	6.95	7.24	16.29	18
7A	11.57	11.33	25.49	24
7B	11.67	11.28	25.38	24
8A	10.25	10.16	22.86	24
8B	10.36	10.27	23.11	24
10A	8.49	8.57	19.28	18
10B	16.59	14.95	33.64	32
mean	10.99	10.17	22.88	22.80
variance		18.06	91.62	91.73

Table 5.7. Assignment of period-specific per-day survival rates to environmental condition categories (and year associated with value). Values in italics are speculative and were obtained by computing the simple average of the good and poor category estimates.

Table A. Adults

Sex	Habitat	Period	Good	Moderate	Poor
M	Shrub	1	0.9916 (92)	*0.9945*	0.9975 (93)
		2	0.9968 (91) 0.9803 (93)[a]	*0.9948*	0.9928 (92)
		3	0.9985 (91) 0.9994 (93)[b]	*0.9995*	1.0000 (92)
	Nonshrub	1	0.9990 (92)	*0.9988*	0.9985 (93)
		2	0.9968 (91) 0.9803 (93)[a]	*0.9948*	0.9928 (92)
		3	0.9990 (91) 1.0021 (93)[b]	*0.99998*	0.9994 (92)
F	Shrub	1	0.9916 (92)	*0.9945*	0.9975 (93)
		2	0.9972 (91) 0.9942 (93)[a]	*0.9920*	0.9868 (92)
		3	0.9990 (91) 0.9970 (93)[a]	*0.9985*	0.9981 (92)
	Nonshrub	1	0.9990 (92)	*0.9988*	0.9985 (93)
		2	0.9972 (91) 0.9942 (93)[a]	*0.9920*	0.9868 (92)
		3	0.9995 (91) 0.9997 (93)[b]	*0.9986*	0.9975 (92)

[a]1993 estimates were assumed to be influenced by poor conditions the previous year. Only 1991 estimates were used as the estimated mean survival rate under good conditions.
[b]1991 and 1993 estimates were averaged to obtain a single estimate of mean survival rates.

Table 5.8. Parameter estimates used in the adult survival rate algorithms in the spatially explicit population model of Townsend's ground squirrels. Given are the mean daily survival rate (μ) and process variance (σ^2) for each sex, habitat, period and environmental condition category (as assigned in Table 5.6), and the computed parameters (α and β) of the beta distribution function used to generate expected cell survival rates for each sex.

Sex	Habitat	Perio	Conditions	μ	σ^2	α	β^a
Male	Shrub	1	Good	0.9916	.0000202	407.893	3.455
			Moderate	0.9946	.0000202	263.453	1.430
			Poor	0.9975	.0000202	399.000	1
		2	Good	0.9968	.0000196	311.500	1
			Moderate	0.9948	.0000196	261.559	1.367
			Poor	0.9928	.0000196	361.083	2.619
		3	Good	0.99895	.00000176	951.381	1
			Moderate	0.99948	.00000176	1922.08	1
			Poor	0.99999	.00000176	99999.0	1
	Nonshrub	1	Good	0.9990	.0000202	999.000	1
			Moderate	0.9988	.0000202	832.333	1
			Poor	0.9985	.0000202	665.667	1
		2	Good	0.9968	.0000196	311.500	1
			Moderate	0.9948	.0000196	261.559	1.367
			Poor	0.9928	.0000196	361.083	2.619
		3	Good	0.99999	.00000176	99999.0	1
			Moderate	0.99998	.00000176	49999.0	1
			Poor	0.9994	.00000176	1665.67	1
Female	Shrub	1	Good	0.9916	.0000202	407.893	3.455
			Moderate	0.9946	.0000202	263.453	1.430
			Poor	0.9975	.0000202	399.000	1
		2	Good	0.9972	.0000196	356.143	1
			Moderate	0.9920	.0000196	400.667	3.231
			Poor	0.9868	.0000196	654.820	8.759
		3	Good	0.9990	.00000176	999.000	1
			Moderate	0.99855	.00000176	820.478	1.191
			Poor	0.9981	.00000176	1074.45	2.045
	Nonshrub	1	Good	0.9990	.0000202	999.000	1
			Moderate	0.9988	.0000202	832.333	1
			Poor	0.9985	.0000202	665.667	1

Sex	Habitat	Perio	Conditions	μ	σ^2	α	β^a
		2	Good	0.9972	.0000196	356.143	1
			Moderate	0.9920	.0000196	400.667	3.231
			Poor	0.9868	.0000196	654.820	8.759
		3	Good	0.9996	.00000176	2499.00	1
			Moderate	0.9986	.00000176	792.230	1.111
			Poor	0.9975	.00000176	1412.36	3.540

[a]The algorithm used to solve for the parameters of the beta distributions sets $\beta = 1$ if $\beta < 1$, and then solves for α.

Table 5.9. Recapture rates (means of sites within habitat type) for female juvenile Townsend's ground squirrels (TGS) on the Snake River Birds of Prey National Conservation Area, 1991-1994. Recapture rates (defined as the proportion of animals tagged in year *i* that were recaptured in year *i*+1) were used as the basis for approximation of annual survival rate for juveniles of both sexes in a spatially explicit population model. Recapture rates were assumed to under-estimate survival by approximately 80%; therefore target annual survival is 1.25 times the recapture rate. 1991 recapture rates were assumed to represent survival under good conditions, and 1992 rates were assumed to represent poor conditions. Rates from 1993 were thought to be affected by factors other than environmental conditions, and so were not used in further analyses. Target rates for moderate conditions were based on the average of good and poor values. Achieved rates are the estimates of annual survival obtained by iteration from a SAS® program that optimized the criteria for period-specific survival rate used in the model. More information on the criteria is given in the text, and the period-specific survival rates are given in Table 5.10.

Year (Conditions)	Habitat	Recapture rate	Target rate	Achieved rate
1991 (Good)	Shrub	0.4571	0.5714	0.5467
	Grass	0.4060	0.5076	0.4899
1992 (Poor)	Shrub	0.0179	0.0223	0.0201
	Grass	0.0000	0.0000	0.0000
1993 (Good)	Shrub	0.1538		
	Grass	0.0652		
(Moderate)	Shrub	0.2375	0.2969	0.2822
	Grass	0.2030	0.2538	0.2490

Table 5.10. Period-specific daily survival rates used for juvenile Townsend's ground squirrels (TGS) in a spatially explicit population model of TGS on the Snake River Birds of Prey National Conservation Area. Values were computed such that annual survival rates would approximate target values based on recapture rates (see text and Table 5.9). Additional criteria for computation of survival rates are described in text.

Habitat	Environmental Conditions	Period		
		1	2	3
Shrub	Good	0.9965	0.9965	0.9989
	Moderate	0.9916	0.9916	0.9974
	Poor	0.9815	0.9815	0.9903
Grass	Good	0.9962	0.9962	0.9986
	Moderate	0.9915	0.9915	0.9972
	Poor	0.9650	0.9650	0.0000

Table 5.11. Year- and habitat-specific estimates of litter size (LS), computed as the mean litter size among sites (see Table 5.4), with corresponding process variances ($\hat{\sigma}^2$) as estimated from bootstrap analyses. Also given are estimates of α and β for a gamma distribution function, calculated from the mean and variance. (See text for complete description of procedure and formulas).

Year	Habitat	Mean LS	$\hat{\sigma}^2$	α	β
1992	Shrub	2.42	1.89	3.11	1.28
	Nonshrub	5.40	1.62	17.98	3.33
1993	Shrub	0.29	0.06	1.47	5.00
	Nonshrub	0.94	0.06	14.08	14.92
1994	Shrub	0.82	0.26	2.58	3.15
	Nonshrub	3.24	1.48	7.08	2.18

Table 5.12. Habitat specific mean population growth rates (λ) calculated from simulation runs of a spatially explicit population model of Townsend's ground squirrels, where environmental conditions were held constant throughout the 10-year duration of the simulations. Means and standard deviations were calculated over 10 replications of each set of conditions, and are listed in order from highest to lowest λ.

Environmental Conditions		Shrub habitat		Grass habitat	
Early	Late	Mean λ	SD	Mean λ	SD
Good	Good	1.8161	0.0558	1.9254	0.0125
Mod	Good	1.5150	0.0023	1.5826	0.0015
Good	Mod	0.8943	0.0022	0.9932	0.0016
Poor	Good	0.8756	0.0015	0.9917	0.0010
Mod	Mod	0.8143	0.0015	0.9205	0.0008
Poor	Mod	0.6909	0.0023	0.7886	0.0010
Poor	Poor	0.6840	0.0033	0.6185	0.0018
Mod	Poor	0.5871	0.0029	0.6390	0.0021
Good	Poor	0.4679	0.0088	0.5897	0.0125

Table 5.13. Expected probability of occurrence for 3 groupings of 12 possible environmental condition combinations (4 early season × 3 late season categories), and their actual proportion of occurrence for different levels of population growth rates (λ) computed from 40 simulation runs, each of 10 years in length, of a spatially explicit population model for Townsend's ground squirrels. The groupings are of condition combinations that resulted in increasing, stable, or declining population growth rates in simulation runs where environmental conditions were held constant for 10 years (see Figure 5.9). Although combinations containing very poor early conditions were not included in the simulations summarized in Figure 5.9, they were placed in the declining group because no reproduction occurred in those conditions, resulting in a negative growth rate.

	Environmental conditions grouping		
	Increasing[a]: G/G, M/G	Stable: G/M, M/M, P/G	Declining: P/M, */P, VP/*
Expected probability	0.39	0.43	0.18
$\lambda < 1.05$ (n = 120)[b]	0.31	0.40	0.29
$1.05 \leq \lambda < 1.15$ (n = 120)	0.39	0.41	0.20
$1.15 \leq \lambda < 1.25$ (n = 70)	0.40	0.50	0.10
$\lambda \geq 1.25$ (n = 90)	0.57	0.31	0.12
All (n = 400)	0.41	0.40	0.19

[a]Early season/late season conditions: G=good, M=moderate, P=poor, VP=very poor, * = all conditions.

[b]n=number of years in the 40 simulations.

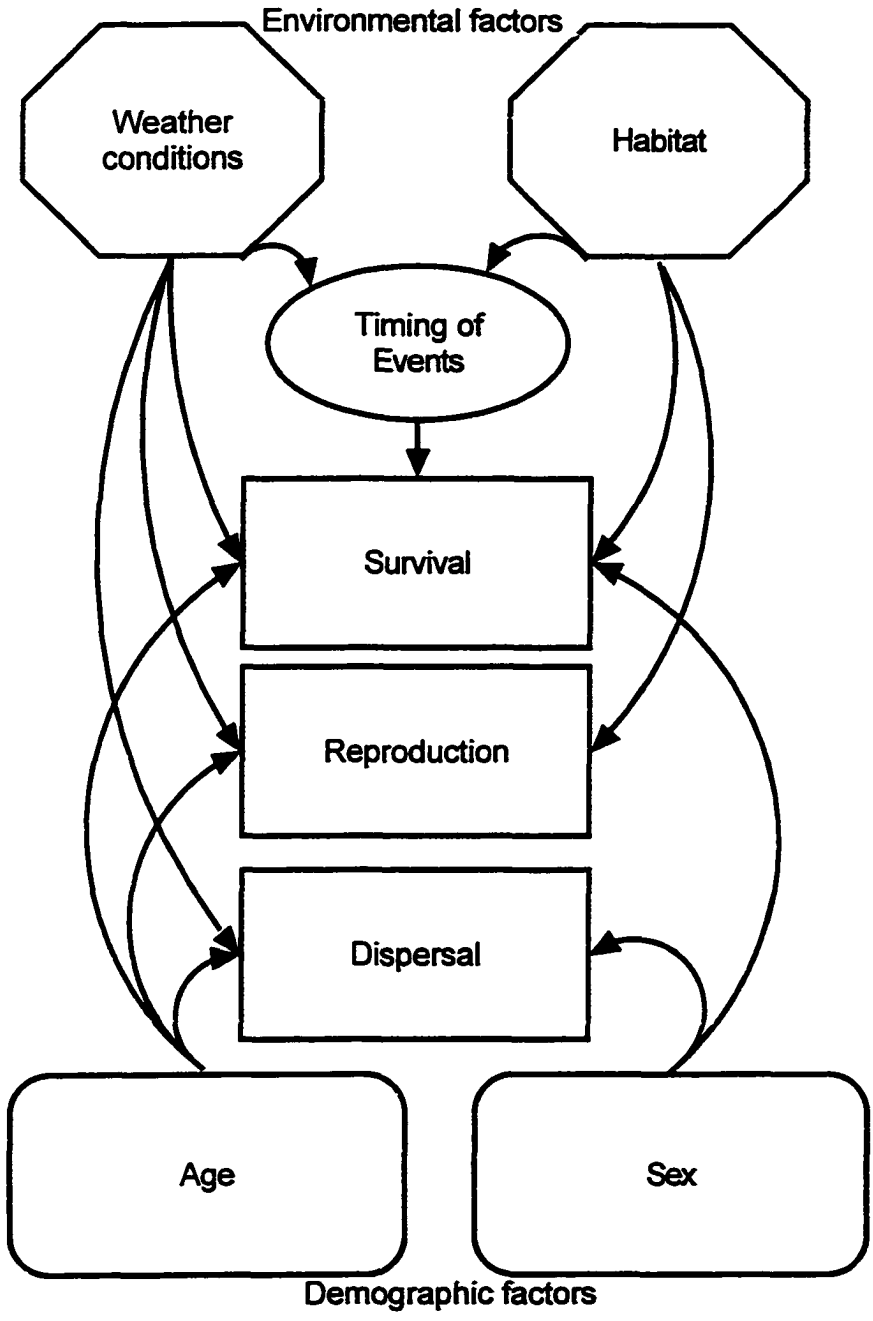


Figure 5.1. Relationships between environmental factors (weather and habitat) and demographic factors (age and sex) on the population dynamics of Townsend's ground squirrels (TGS), asmodeled in a spatially explicit population model of TGS on the Snake River Birds of Prey National Conservation Area, Idaho. Arrows denote the factors for which population parameter values are adjusted in the model; lack of arrows is not intended to imply a lack of relationship, but that the model does not account for it if one exists.

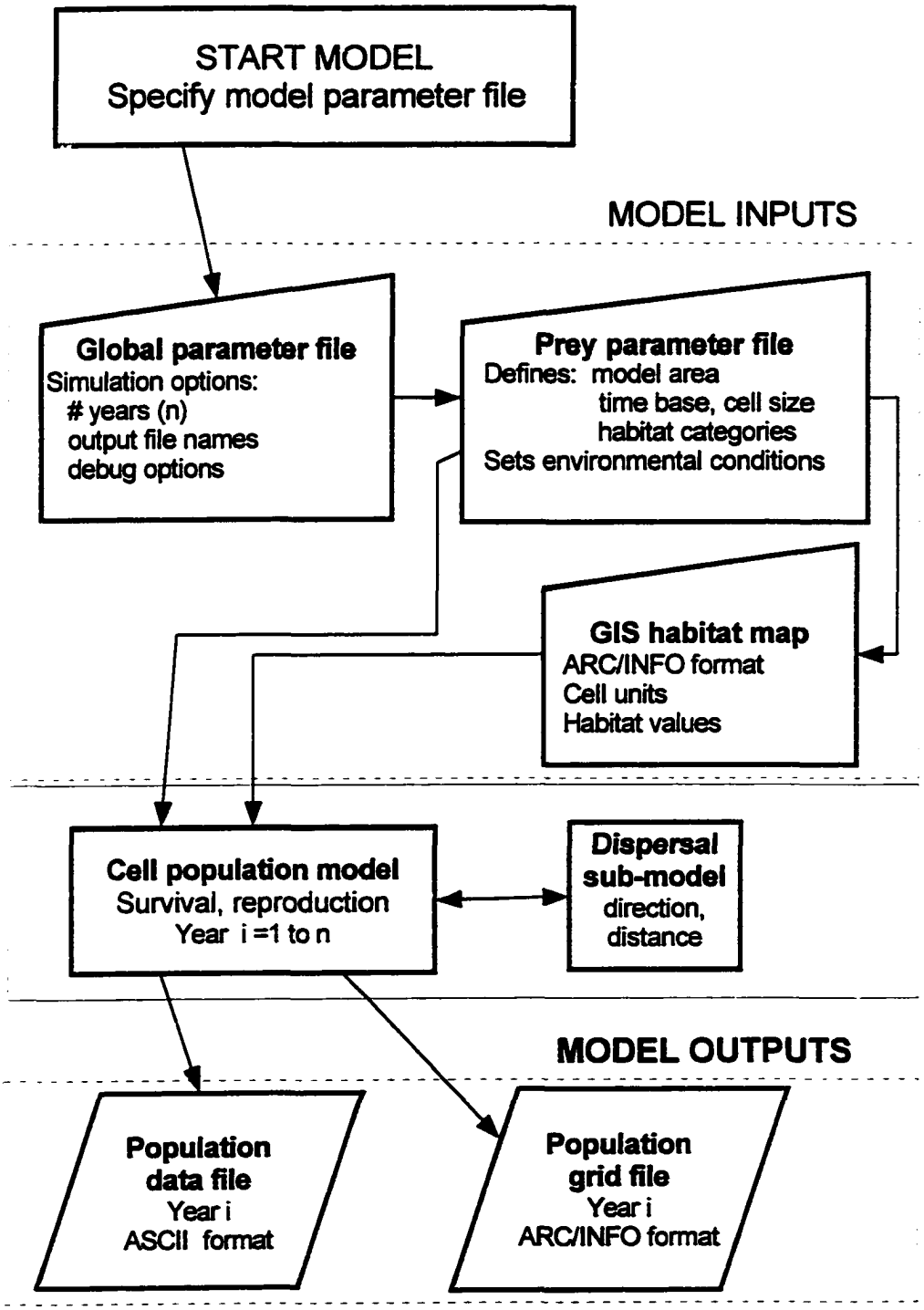


Figure 5.2. Flow chart of overall model structure for a spatially explicit population model of Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, Idaho.

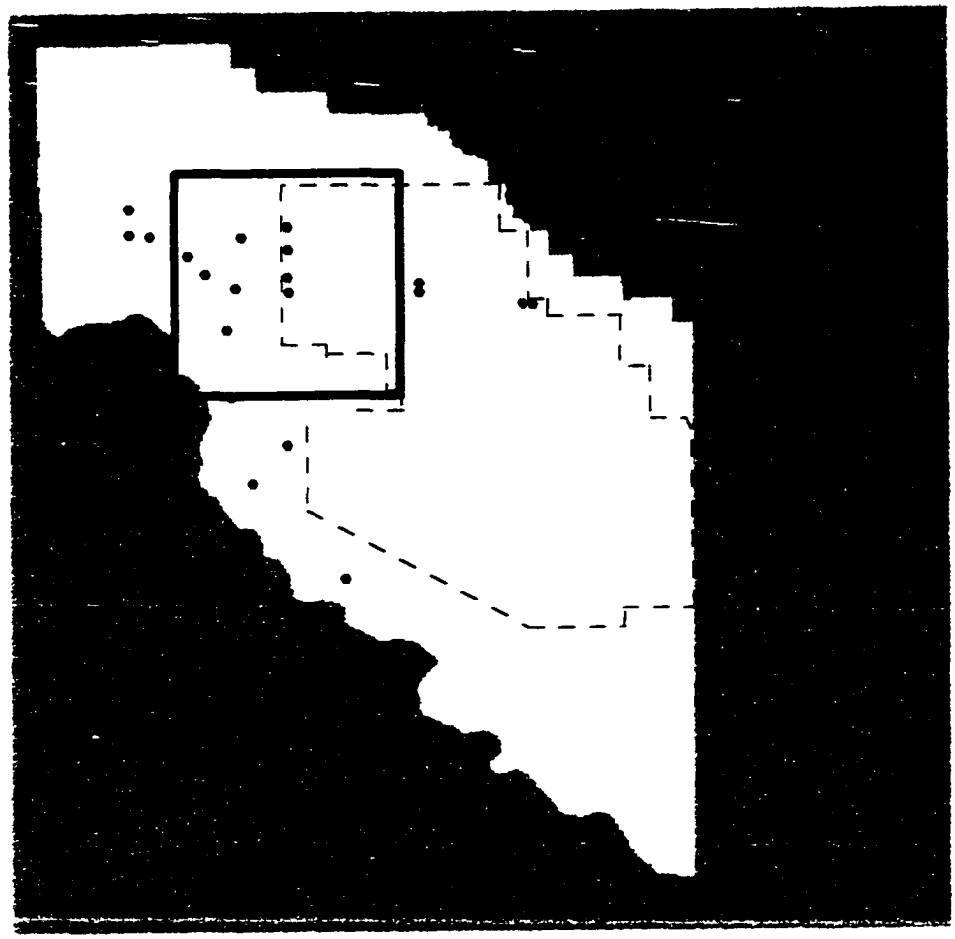
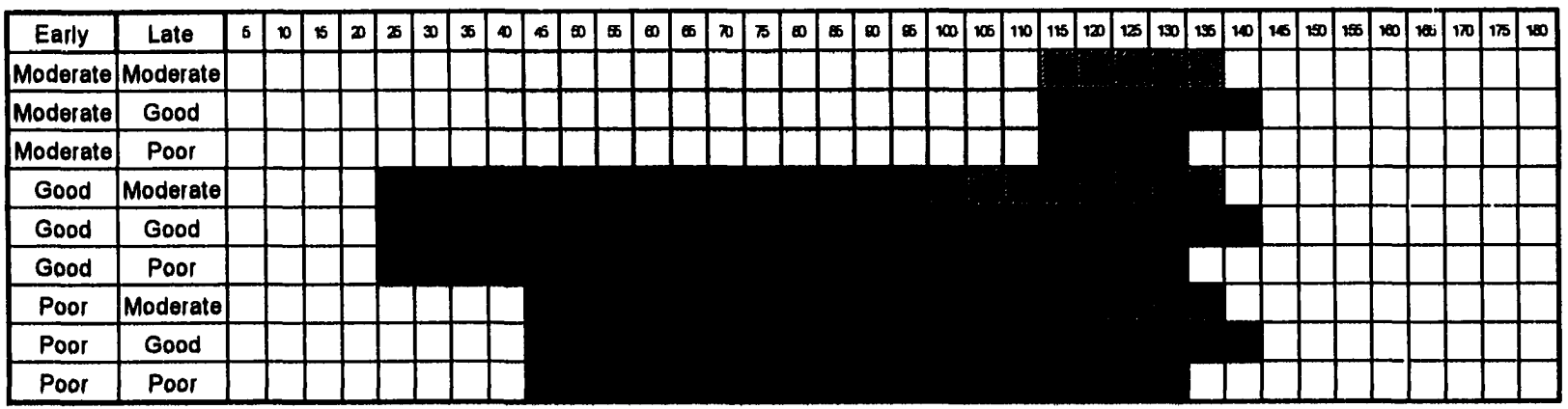


Figure 5.3. Map area (all area within shaded rectangle, including the non-shaded area), and model area (unshaded area) for a spatially explicit model of Townsend's ground squirrels (TGS) on the Snake River Birds of Prey National Conservation Area, Idaho. Only the area (22,500 ha) within the smaller box was used in simulation runs reported in this chapter. Black dots denote locations of TGS demography study sites, and the broken line approximately contains the Orchard Training Area. The map area is 390,298 ha, and the model area is 138,051 ha.

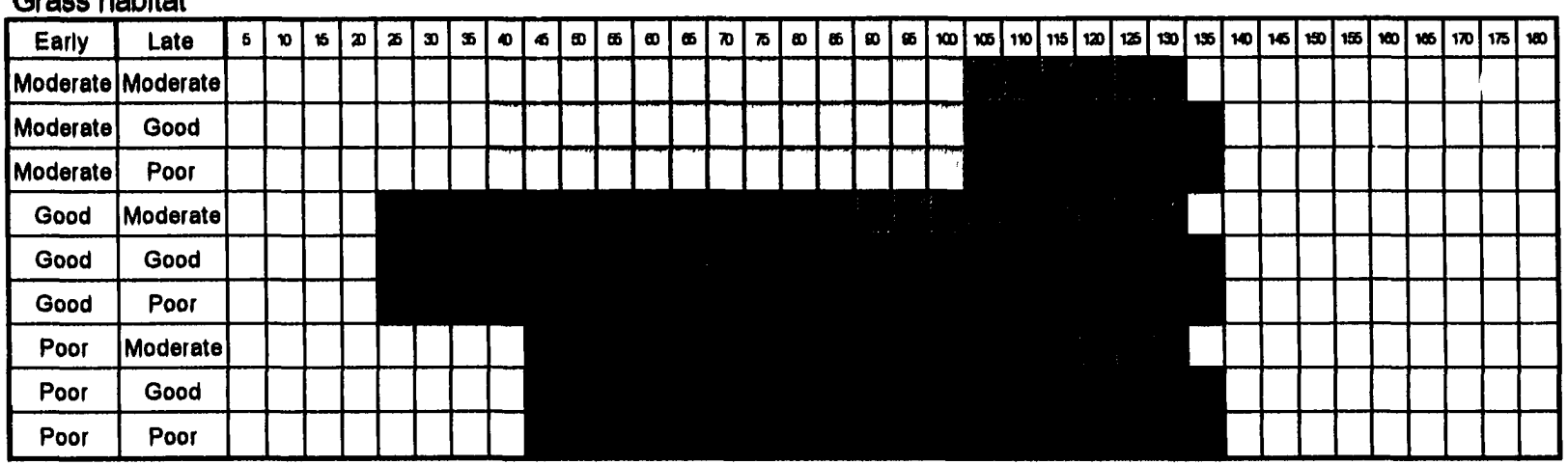
Figure 5.4 (following pages). Time lines showing the timing and duration of within year time periods modeled in a spatially explicit population model of Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area. Period definitions are adjusted for each age, sex, and habitat, and for environmental conditions at two times within the year, early and late. Figure A is for adult males, Figure B is for adult females, and Figure C is for juveniles of both sexes. Environmental conditions affecting the periods are shown in colors: green for good conditions, yellow for moderate conditions, and red for poor. Period 1 is in un-shaded colors, period 2 is in shaded colors, and Period 3 is left white. The number at the top of each column is the last day in the 5-day interval represented by the column. Days are numbered from the beginning of the model year (January 1) but only 180 days are shown; the remainder of the year (of 365 total days) is in Period 3.

A. Adult Males

Shrub habitat



Grass habitat



B. Adult Females

Shrub habitat

Early	Late	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180
Moderate	Moderate																																				
Moderate	Good																																				
Moderate	Poor																																				
Good	Moderate																																				
Good	Good																																				
Good	Poor																																				
Poor	Moderate																																				
Poor	Good																																				
Poor	Poor																																				

Grass habitat

Early	Late	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180
Moderate	Moderate																																				
Moderate	Good																																				
Moderate	Poor																																				
Good	Moderate																																				
Good	Good																																				
Good	Poor																																				
Poor	Moderate																																				
Poor	Good																																				
Poor	Poor																																				

C. Juveniles

Shrub habitat

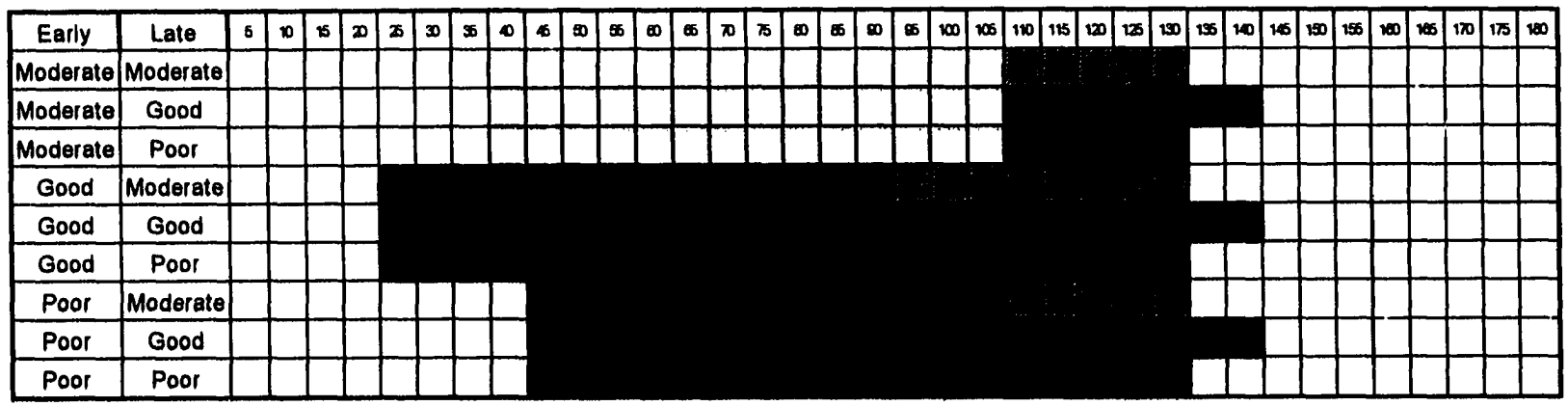
Early	Late	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180
Moderate	Moderate																																				
Moderate	Good																																				
Moderate	Poor																																				
Good	Moderate																																				
Good	Good																																				
Good	Poor																																				
Poor	Moderate																																				
Poor	Good																																				
Poor	Poor																																				

Grass habitat

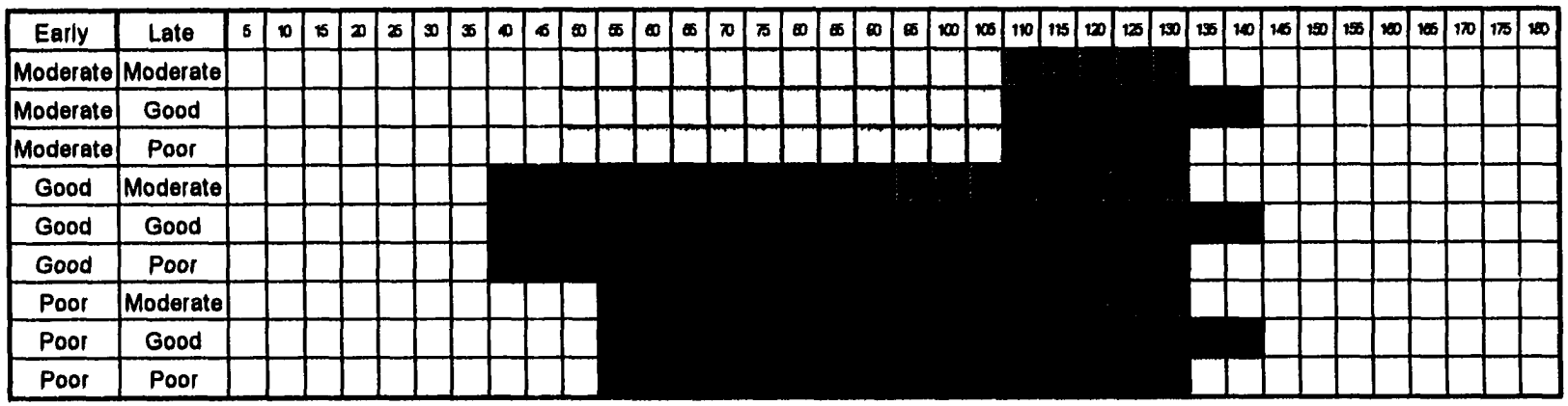
Early	Late	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	155	160	165	170	175	180
Moderate	Moderate																																				
Moderate	Good																																				
Moderate	Poor																																				
Good	Moderate																																				
Good	Good																																				
Good	Poor																																				
Poor	Moderate																																				
Poor	Good																																				
Poor	Poor																																				

Figure 5.5. (following pages). Time lines as depicted in Figure 5.4, without adjustments for habitat type. Figure A is for adult males, Figure B is for adult females, and Figure C is for juveniles of both sexes. See Figure 5.4 for complete description of format.

A. Adult Males



B. Adult Females



C. Juveniles

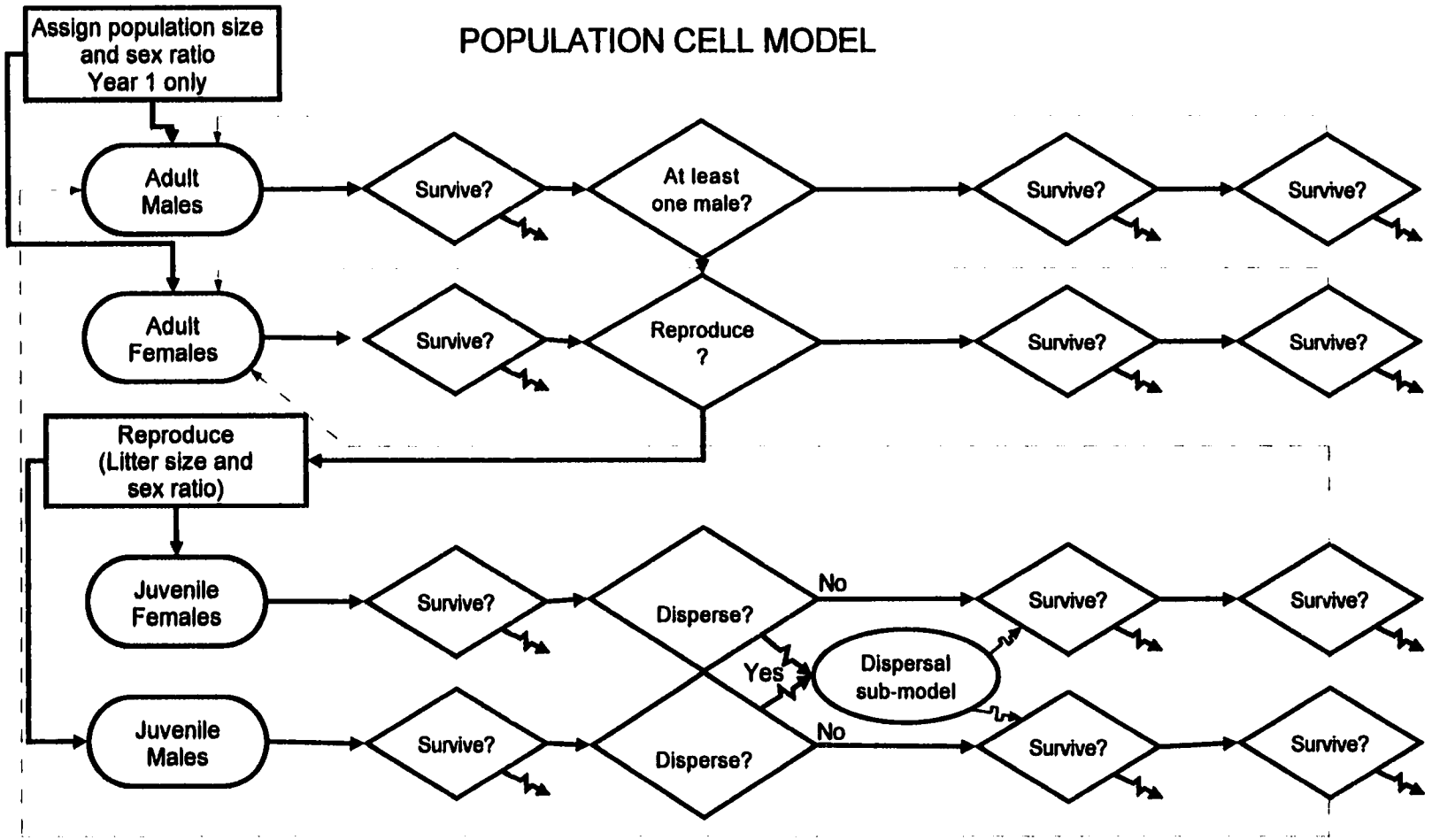


Figure 5.6. Flow diagram for population cell model for Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area. Cells are initialized with an adult population in year 1 of the model simulation, with size dependent on habitat type and an expected proportion of females = 0.60. Bent lines shown from survival boxes represent animals that do not survive and are lost to the system. Juveniles that enter the dispersal sub-model also leave the cell (see Figure 5.2), but are not necessarily lost to the model system. Crooked lines from the dispersal sub-model depict addition of immigrants from other cells. Dashed lines depict survival through torpor and emergence as adults in the cell population the following year.

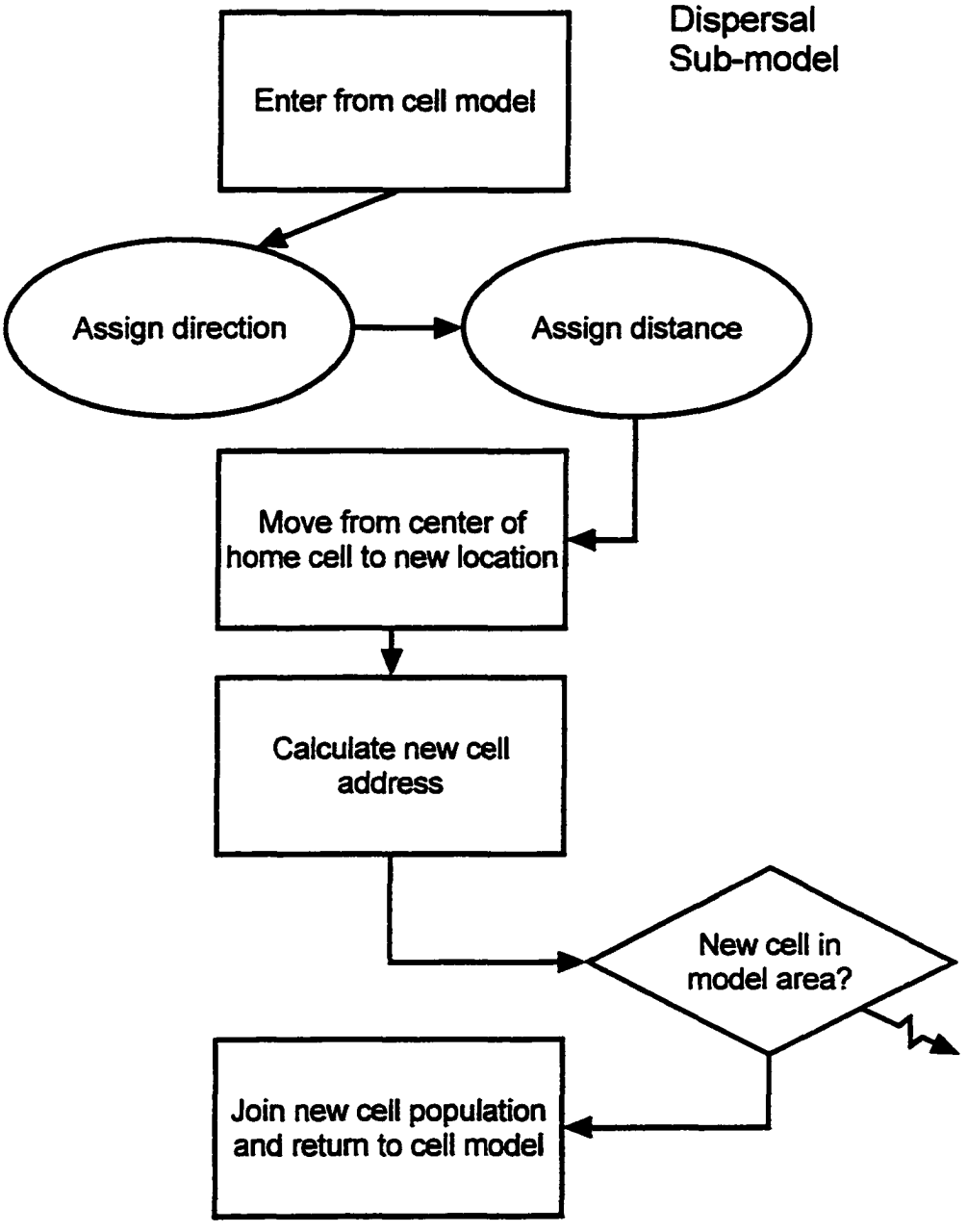


Figure 5.7. Flow diagram of dispersal sub-model in a spatially explicit population model of Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area, Idaho. Individual juvenile ground squirrels, identified as dispersers by the cell population model, enter the dispersal sub-model. Each receives a direction and distance chosen at random from designated distribution functions (see text for details), and are "moved" from the center of their originating cell to their new location. The cell address (in rows and columns from 0,0, which may be negative), is then calculated, and checked for whether it is within the model area. Dispersers moving to a cell address outside the model area are lost to the system (depicted by a bent arrow). Otherwise, they are added to the appropriate sex class in the population of the new cell, and return to the population cell model.

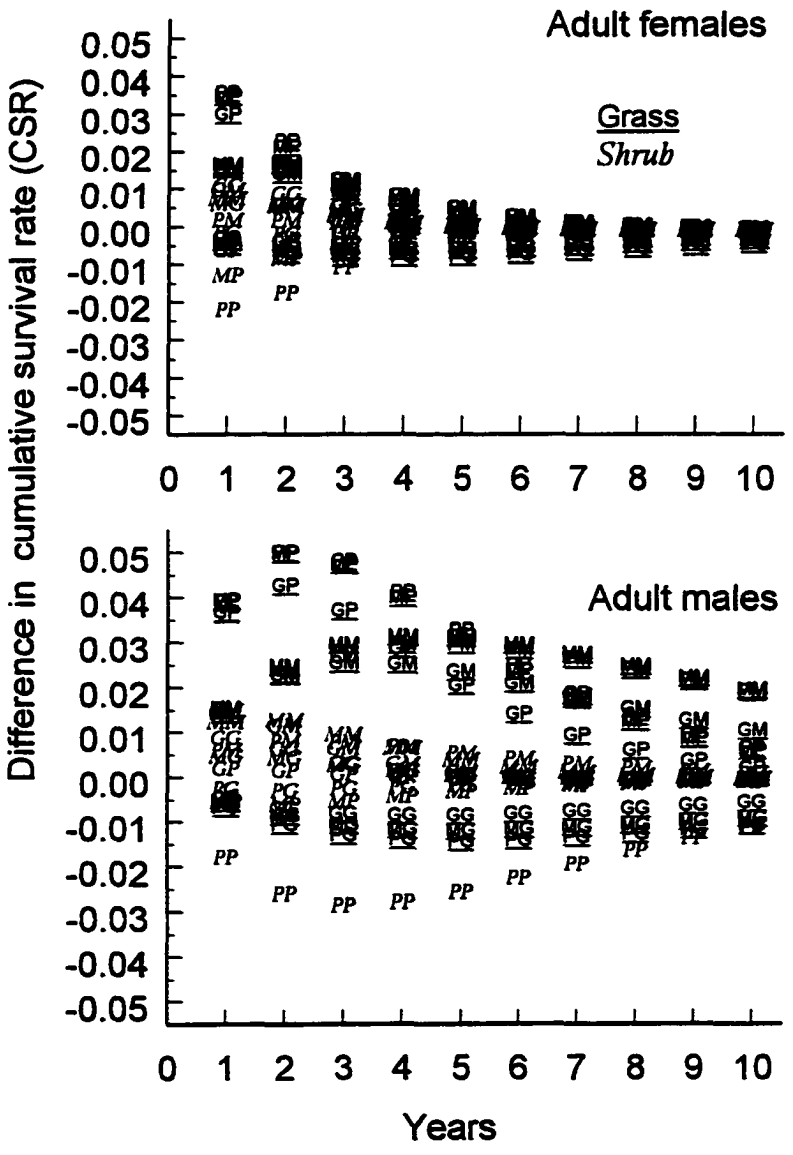


Figure 5.8. Difference in expected cumulative survival rates (CSR, calculated as annual survival rates raised to the *y* power, where *y* is number of years), with and without habitat-specific period definitions, for all combinations of environmental condition categories. Letters denote conditions as: G = good, M = moderate, and P = Poor; the first letter listed indicates early season conditions and the last letter indicates late season conditions. (Very poor early season conditions were not graphed because survival rates and period definitions are the same as for moderate early season conditions). Differences were computed by subtracting CSR from period definitions that are not habitat-specific, from CSR with habitat-specific definitions; thus a negative difference denotes an increased reduction in CSR when generic definitions are used.

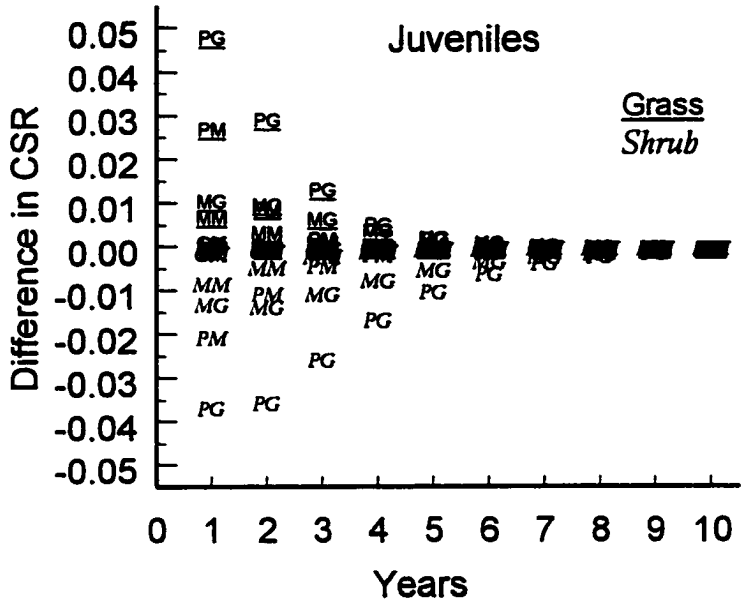
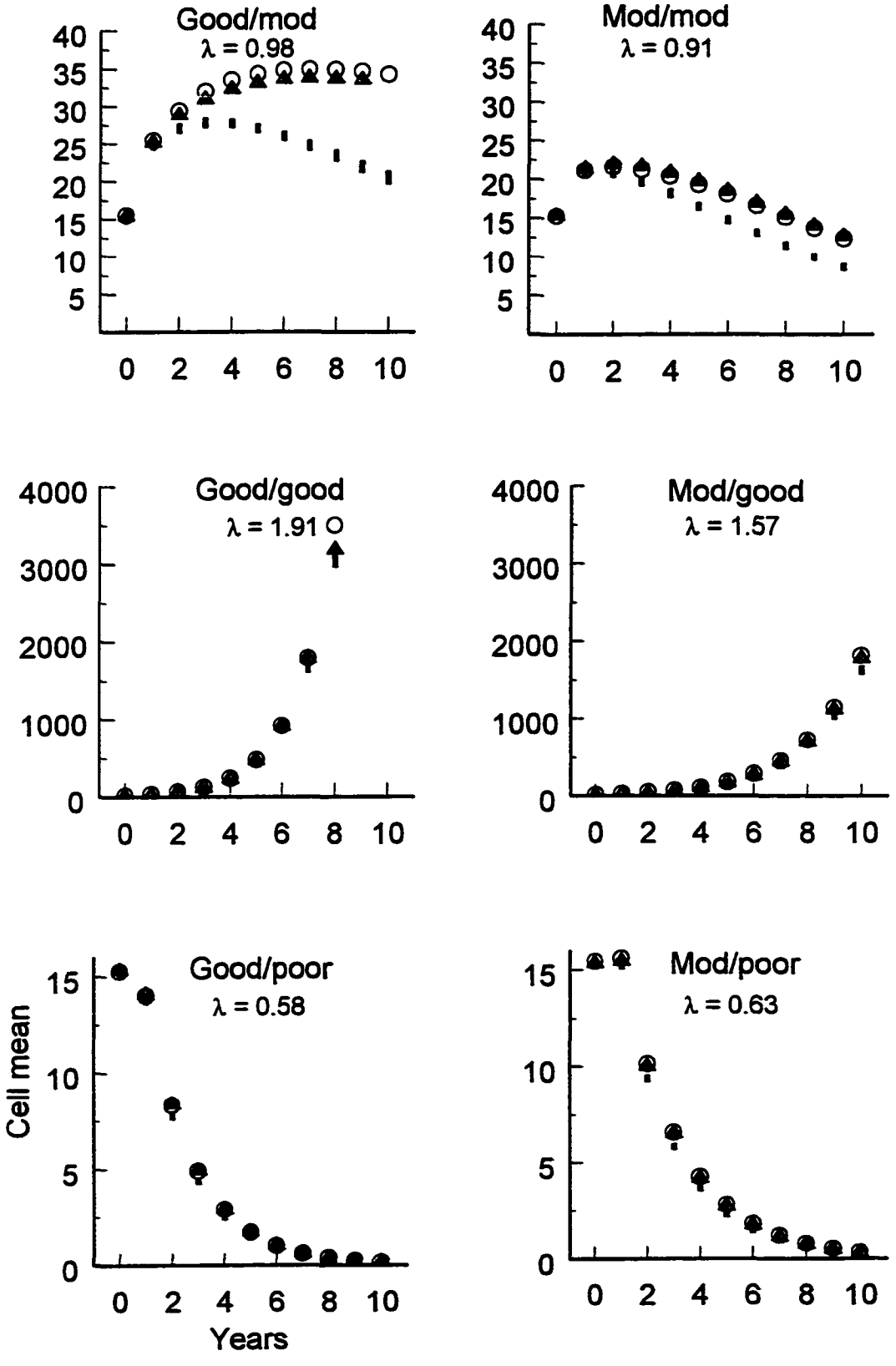


Figure 5.8 (continued).

Figure 5.9. (Following pages) Graphs of yearly cell population means from simulation runs of a spatially explicit population model for Townsend's ground squirrels, where environmental conditions are held constant for the 10 years of the simulations. The vertical bars depict the complete range of results from 10 simulation runs without spatial variability in adult survival rates. The length of the bars indicates the width of the range of values; note that nearly all of them are very short. The triangles and open circles depict the results from each of 2 simulation runs where spatial variability in adult survival rates was modeled as a random beta variable. The λ given with each graph is the mean population growth rate for the 10 simulations without spatial variance.



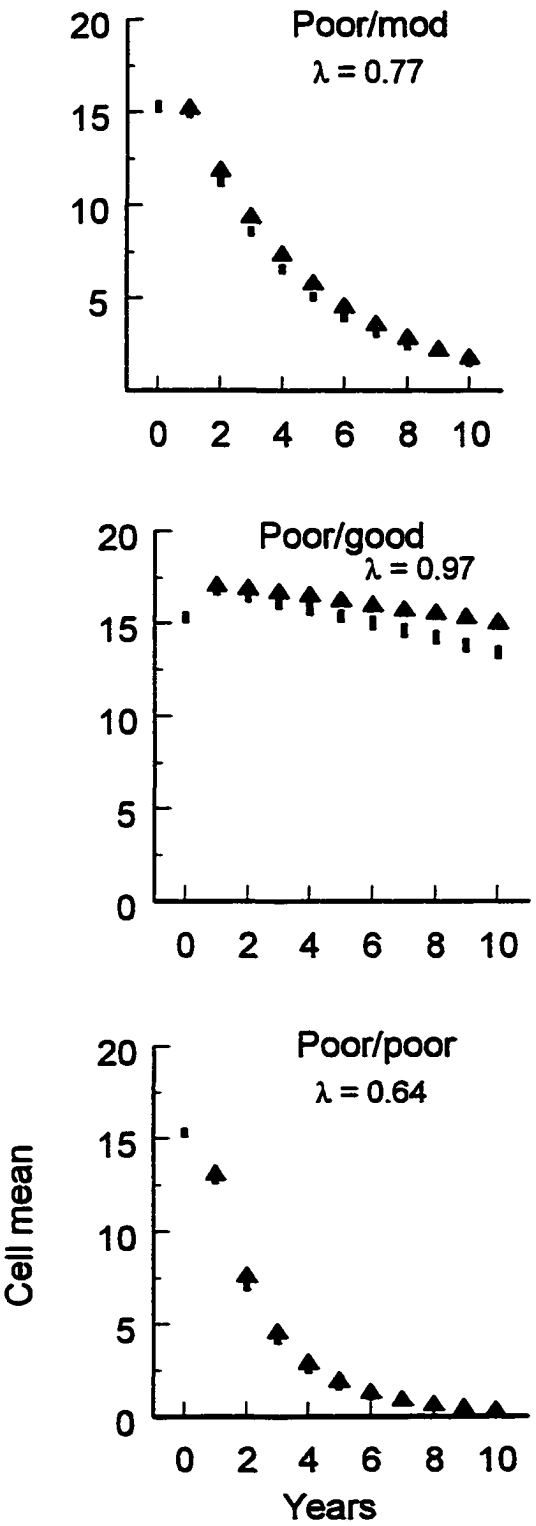
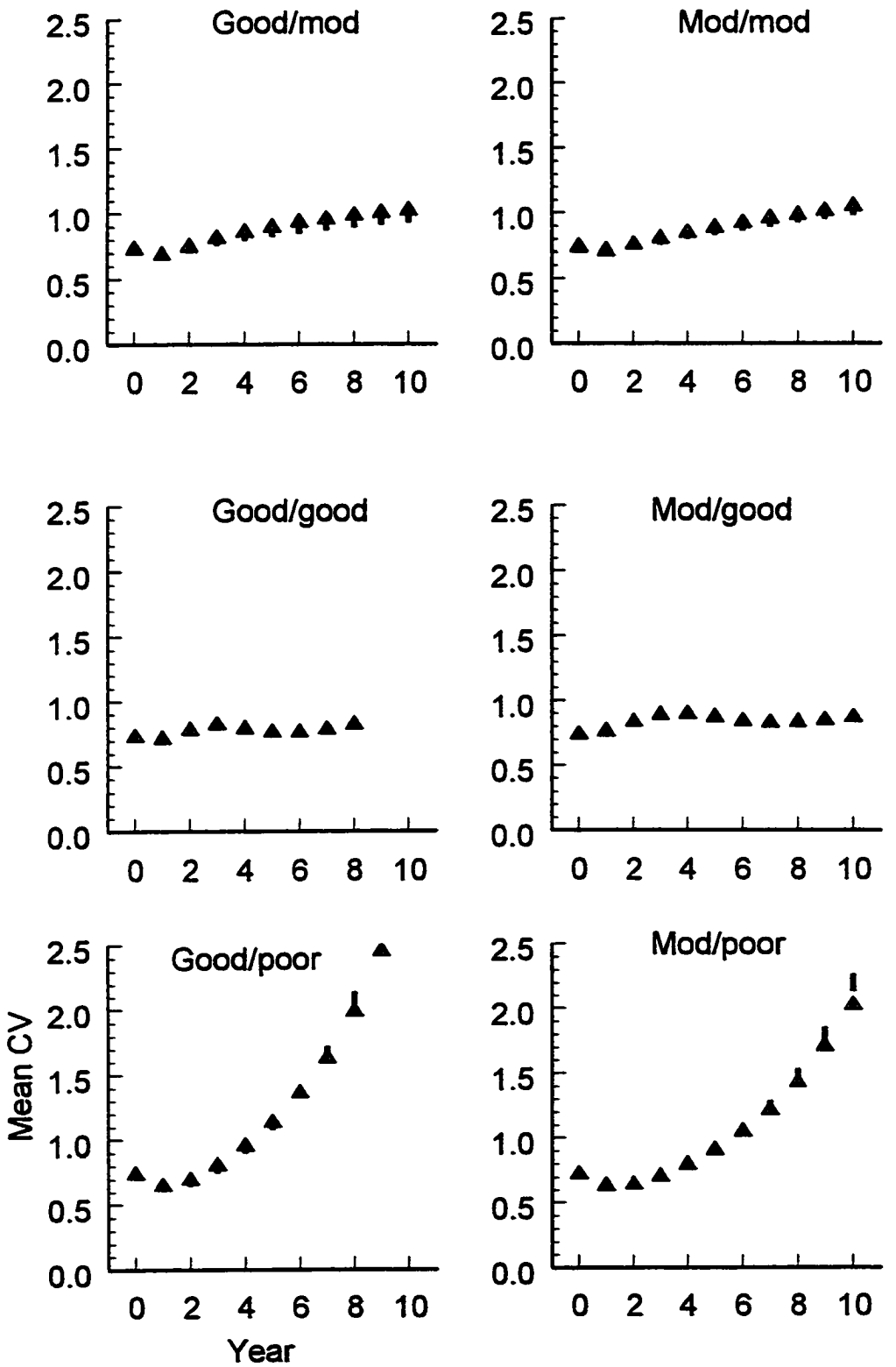


Figure 5.10. (Following pages) Graphs of yearly coefficients of variation (CV: calculated as the standard deviation among cells / cell mean) from simulation runs of a spatially explicit population model for Townsend's ground squirrels, where environmental conditions are held constant for the 10 years of the simulations. The lines depict the complete range of results from 10 simulation runs without spatial variability in adult survival rates. The triangles and open circles depict the results from each of 2 simulation runs where spatial variability in adult survival rates was modeled as a random beta variable.



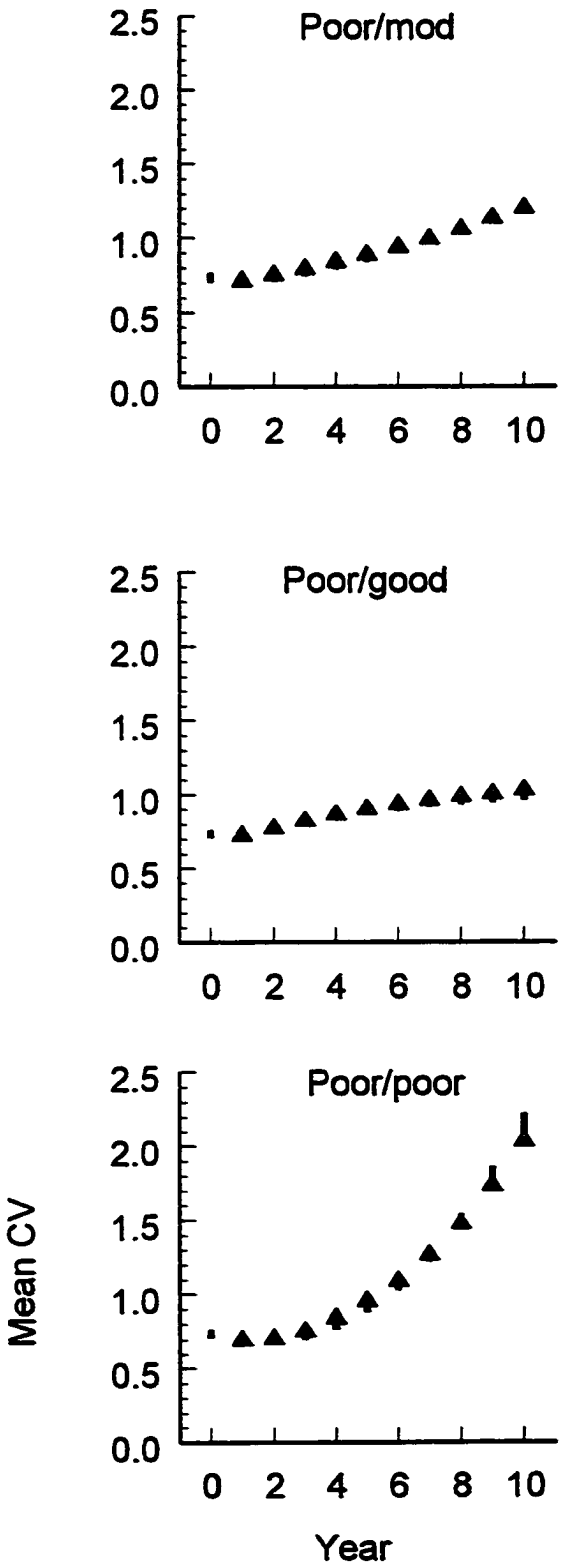
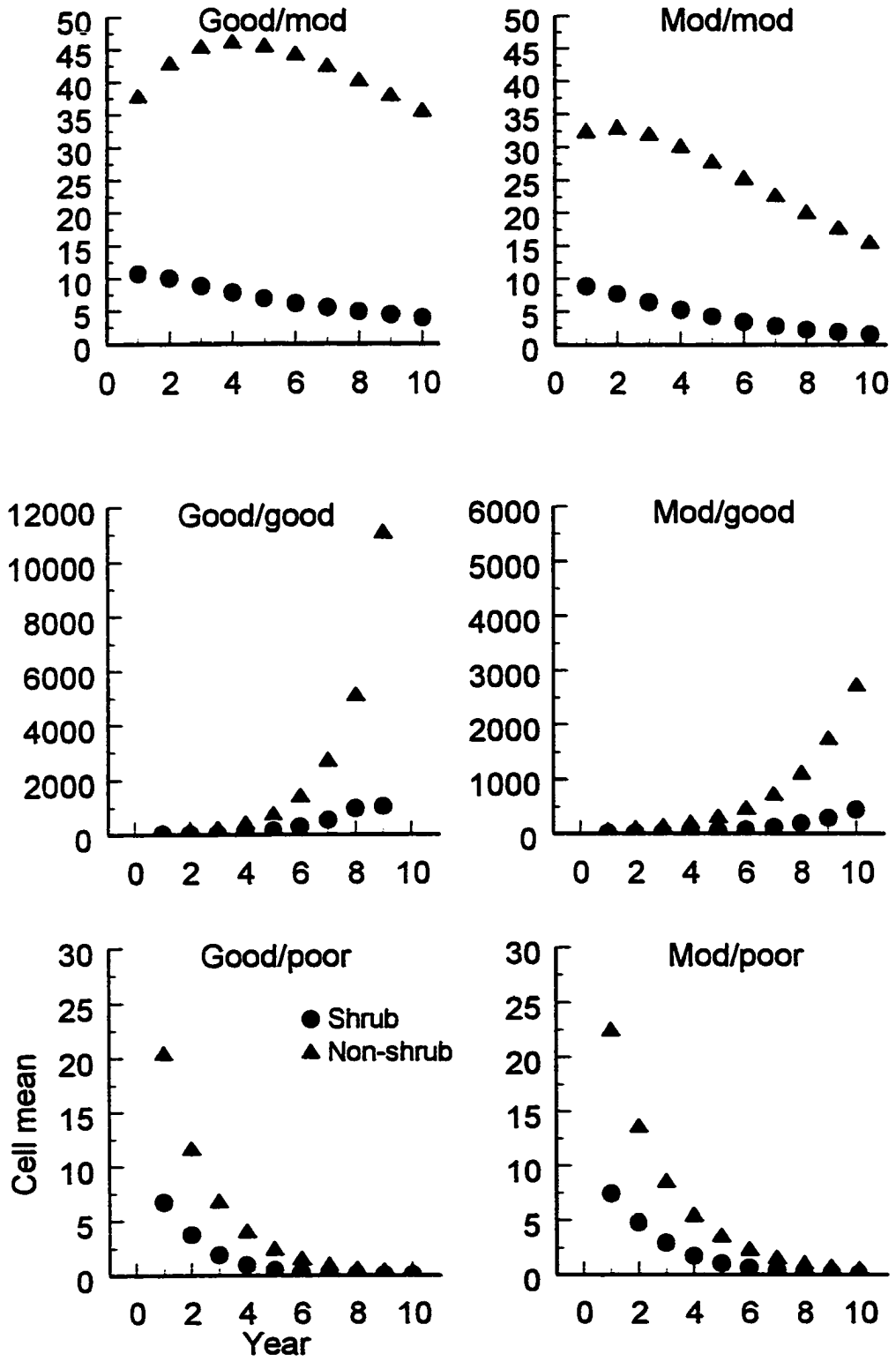
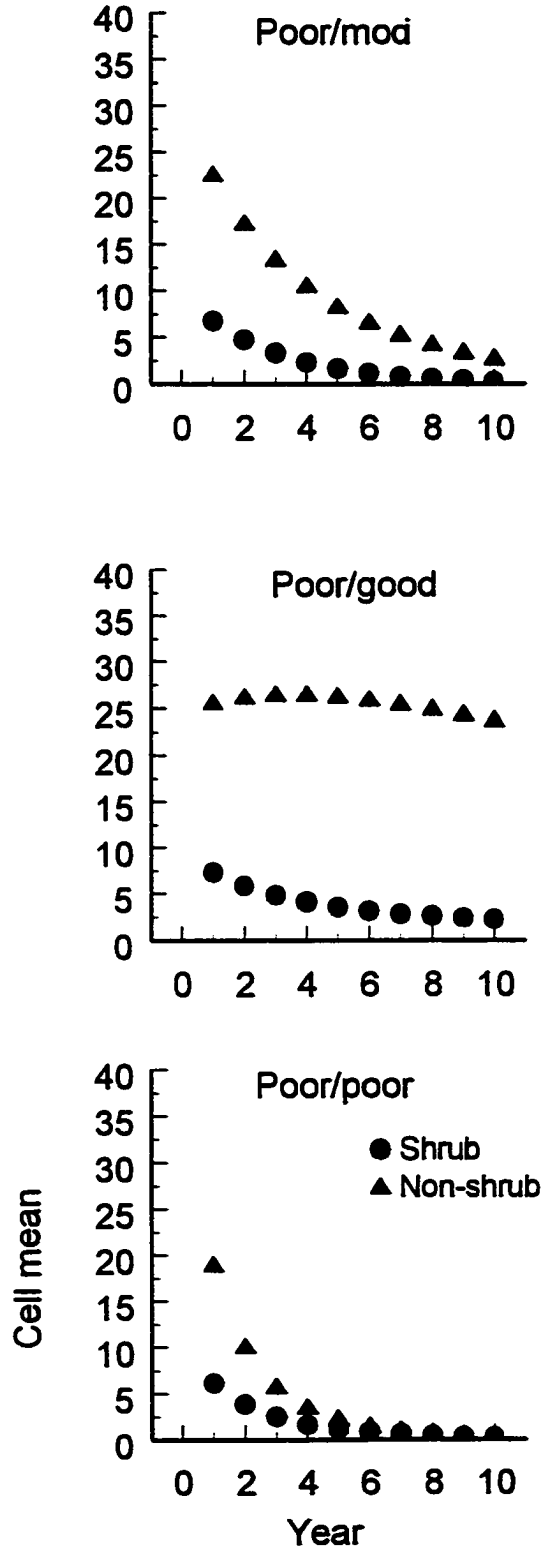


Figure 5.11. (Following pages) Graphs of habitat-specific yearly cell population means from simulation runs of a spatially explicit population model for Townsend's ground squirrels, where environmental conditions are held constant for the 10 years of the simulations. Each line plotted is the mean of 10 simulation runs without spatial variation in adult survival rates.





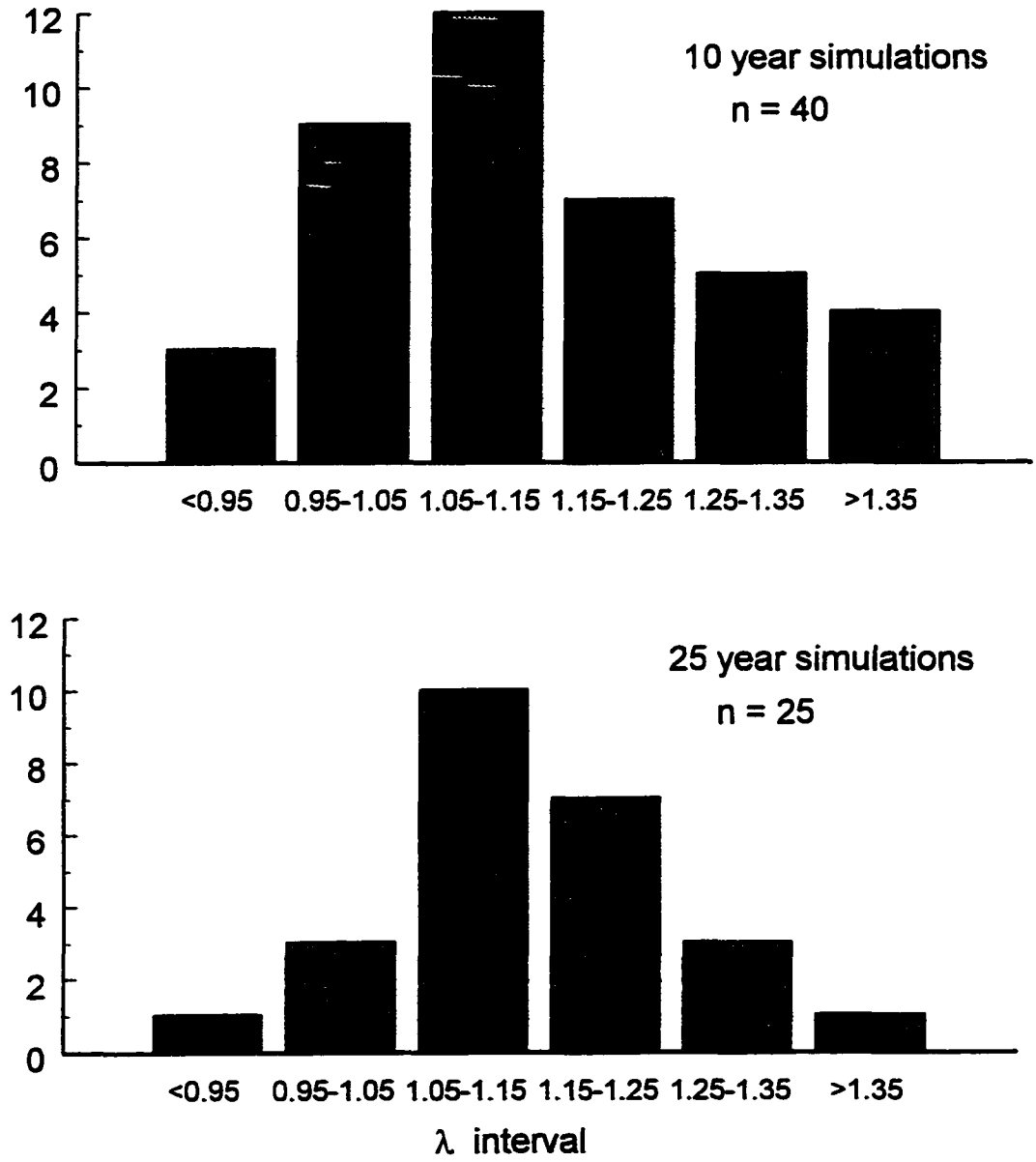


Figure 5.12. Frequency histograms of mean population growth rates (λ, calculated as a geometric mean over the number of years in the simulation) calculated from 2 sets of simulation runs of a spatially explicit model of Townsend's ground squirrel population dynamics. The top graph shows the distribution of λ for 40 replications of simulations 10 years in length, and the bottom graph shows the distribution for 25 simulations of 25 years.

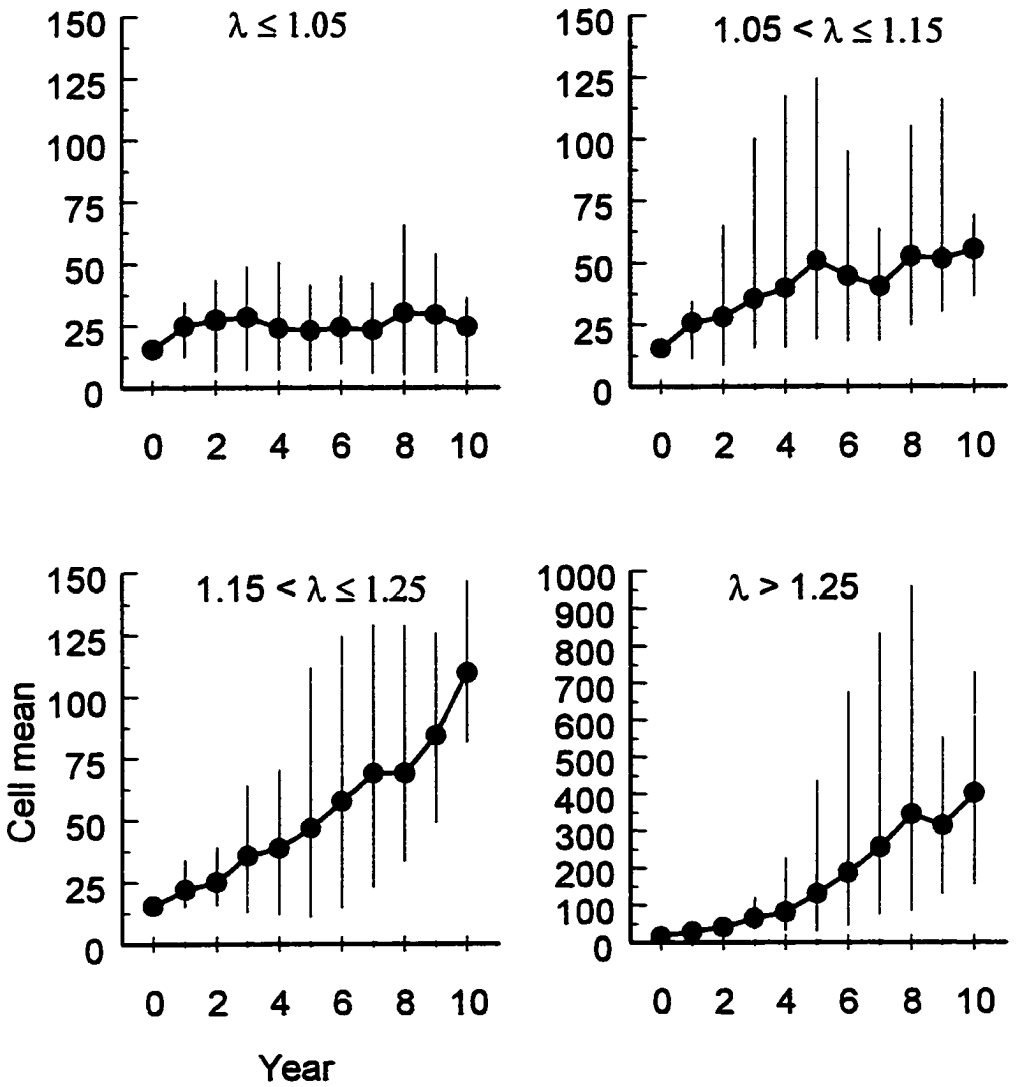


Figure 5.13. Trends in mean cell populations over 10 years from 40 simulation runs of a spatially explicit model of Townsend's ground squirrel populations, grouped by categories of population growth rates (λ). The solid circles are the means of all runs within the category, and the lines depict the entire range of mean cell population abundance.

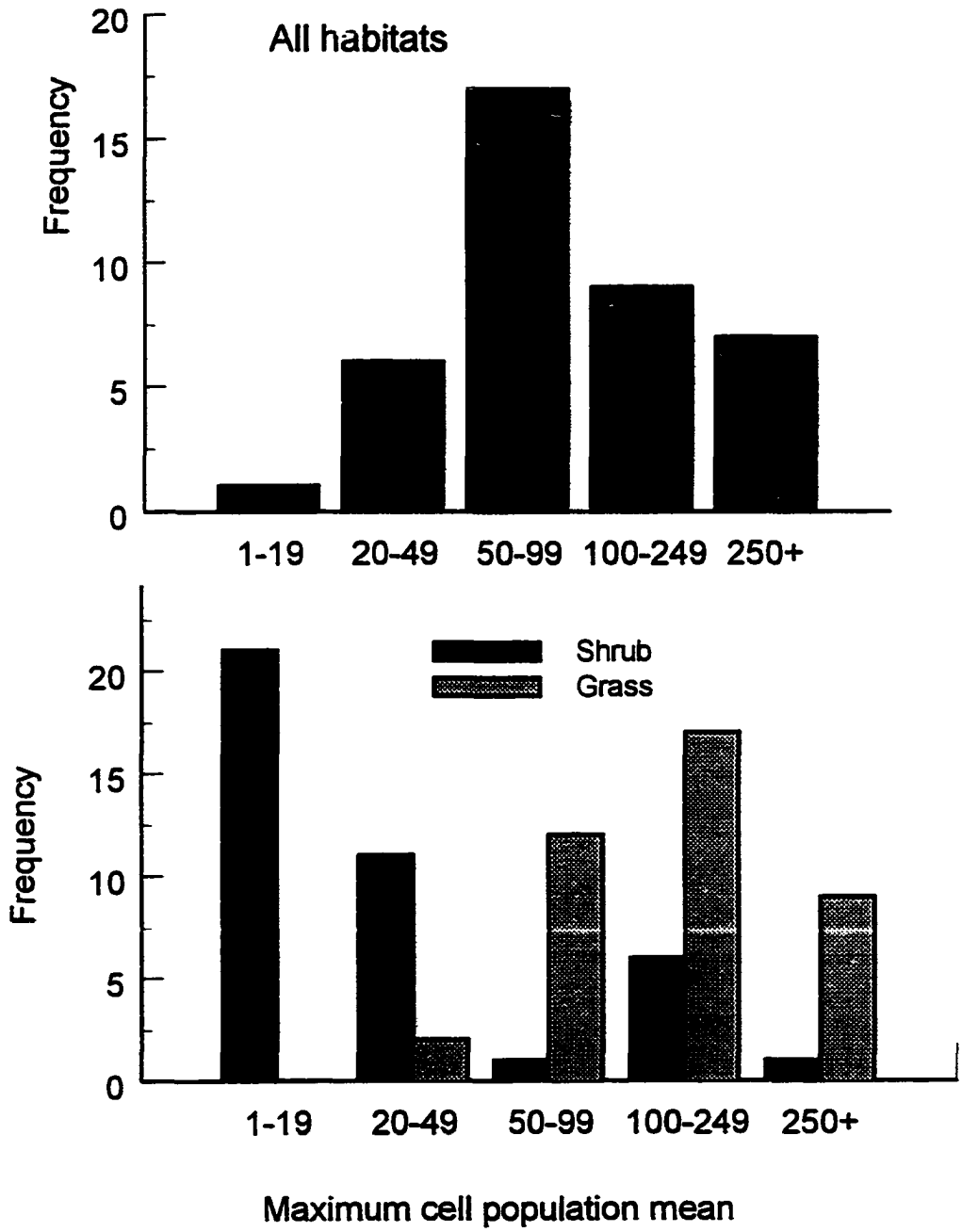


Figure 5.14. Frequency distribution of maximum cell population means achieved for 40 simulation runs of 10 years in length of a spatially explicit population model for Townsend's ground squirrels. The top graph is for all habitats combined, and the bottom graph is by habitat type.

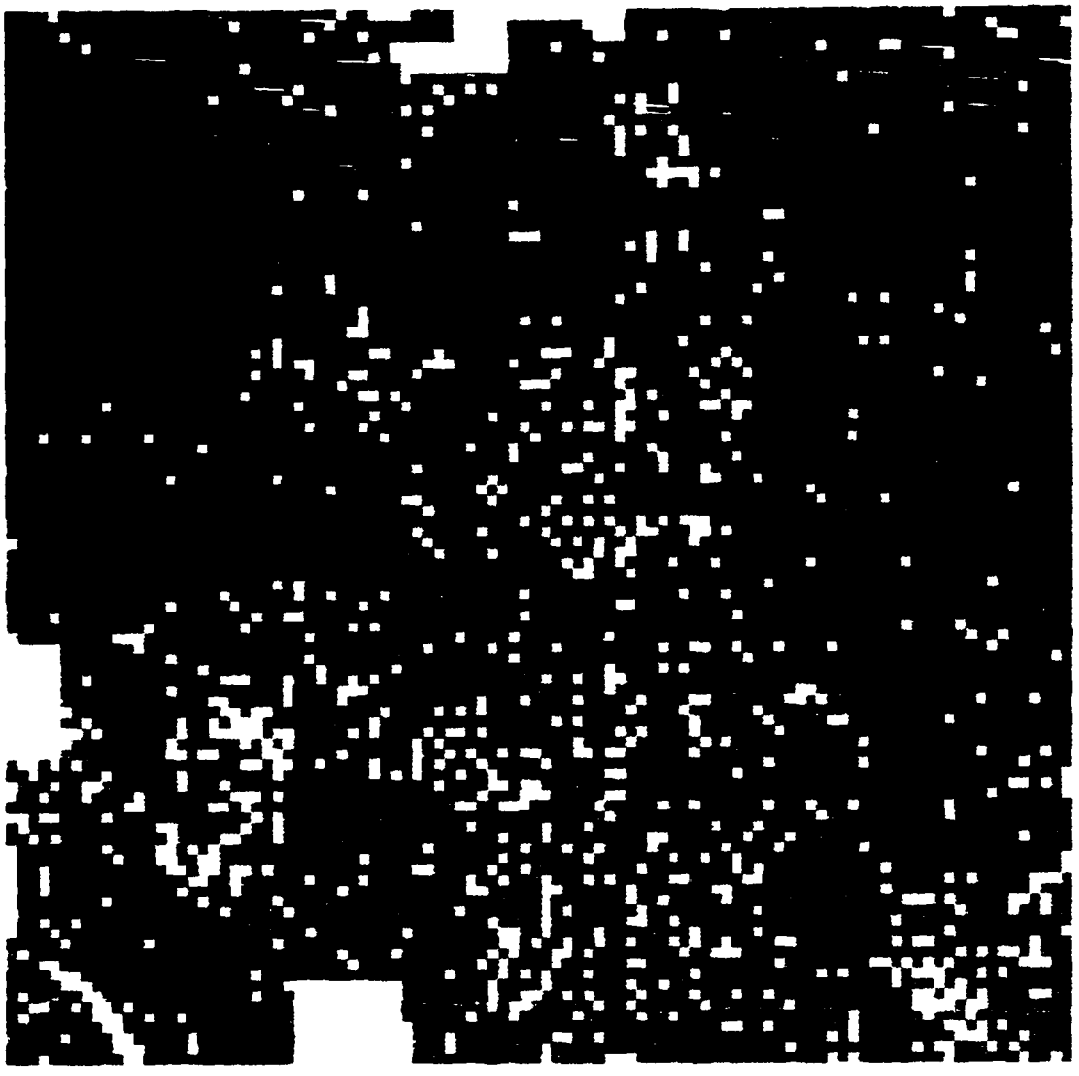


Figure 5.15. Habitat map used in conjunction with simulation runs of a spatially explicit population model of Townsend's ground squirrels. Each color square is a 2.25 ha (150 × 150 m) cell. Blue squares are shrub habitat cells, green squares are grass cells, and white cells are non-habitat.

Figures 5.16 - 5.19. (Following pages). Cell population grid maps showing Townsend ground squirrel population abundance in each cell during one 10-year simulation run of a spatially explicit population dynamics model. Each figure shows population abundance after initialization (top map), after year 5 (middle map), and after year 10 (bottom map). In all figures colors depict population classes as per the legend, below. The repetitions displayed were chosen at random from each of the 4 categories of λ, given in Table 5.14. In all cases, patterns of population growth or decline closely follow the habitat map (compare with Figure 5.15), and populations become more aggregated through time.

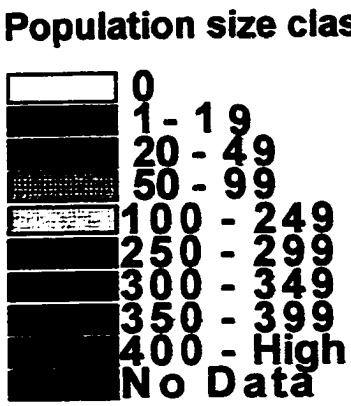


Figure 5.16. $\lambda = 1.02$.

Figure 5.17. $\lambda = 1.12$.

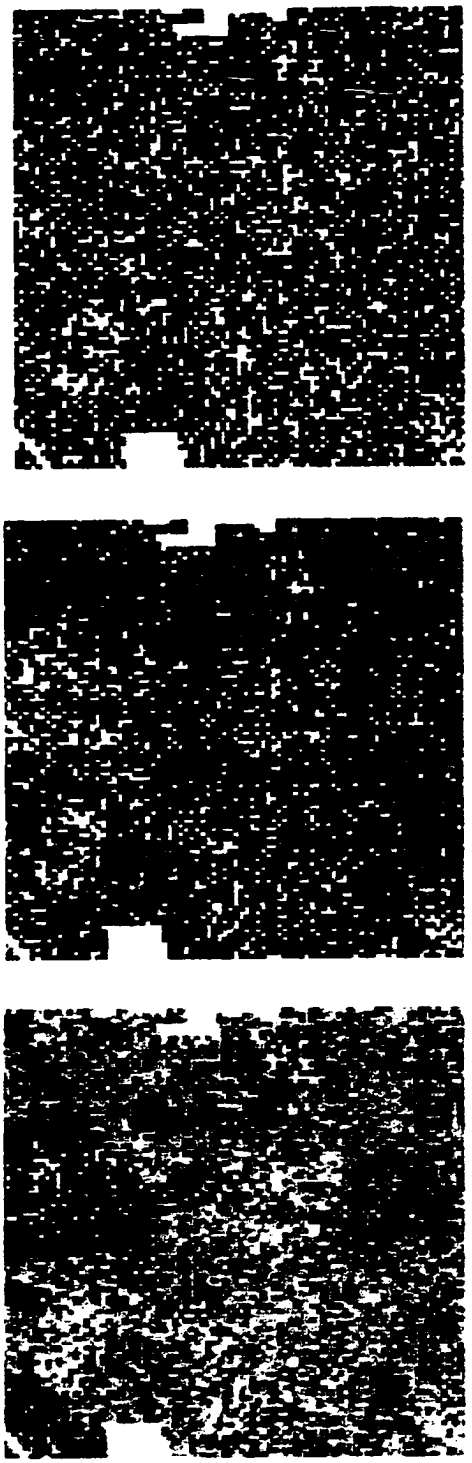


Figure 5.18. $\lambda = 1.22$.

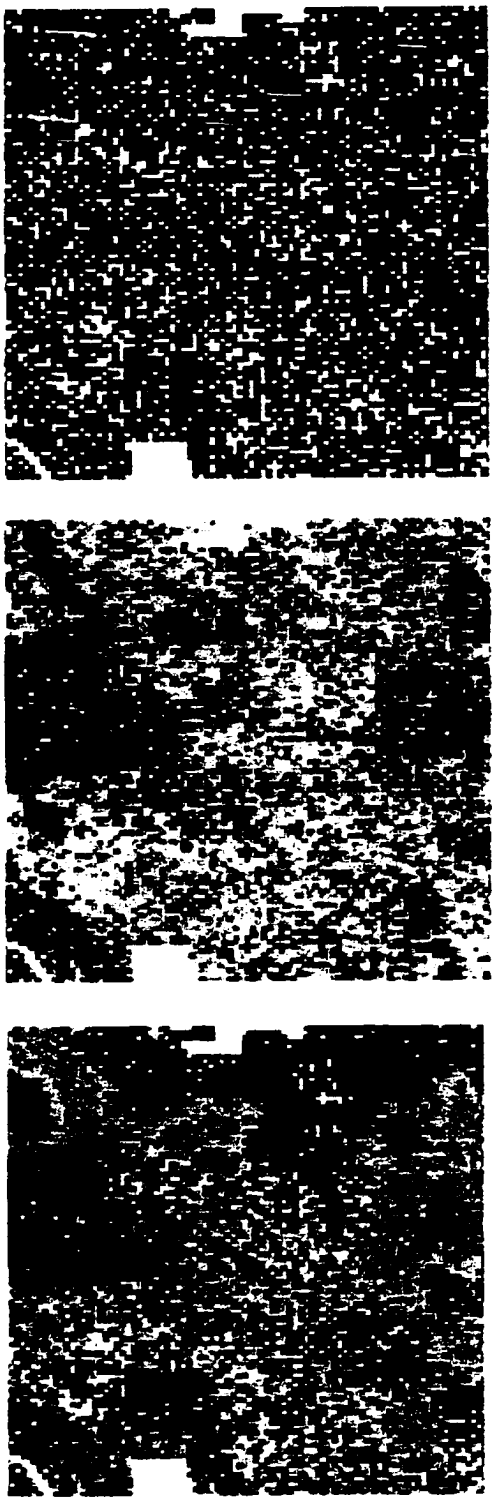


Figure 5.19. $\lambda = 1.33$.

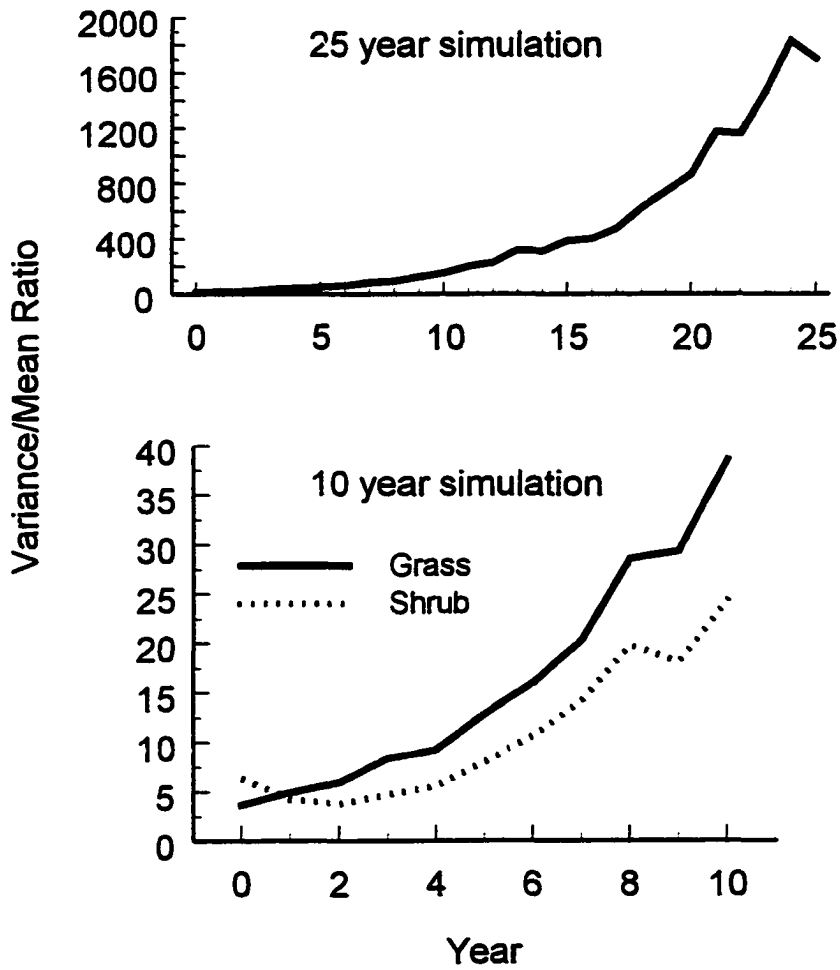


Figure 5.20. Plots of the ratio $s^2/\bar{x}$(cell variance/cell mean) for 25 (top graph, over all cells) and 10 year (bottom graph, by habitat type) simulation runs of a spatially explicit model for Townsend's ground squirrels. Increasing ratios indicate increasing aggregation of cell populations through time.

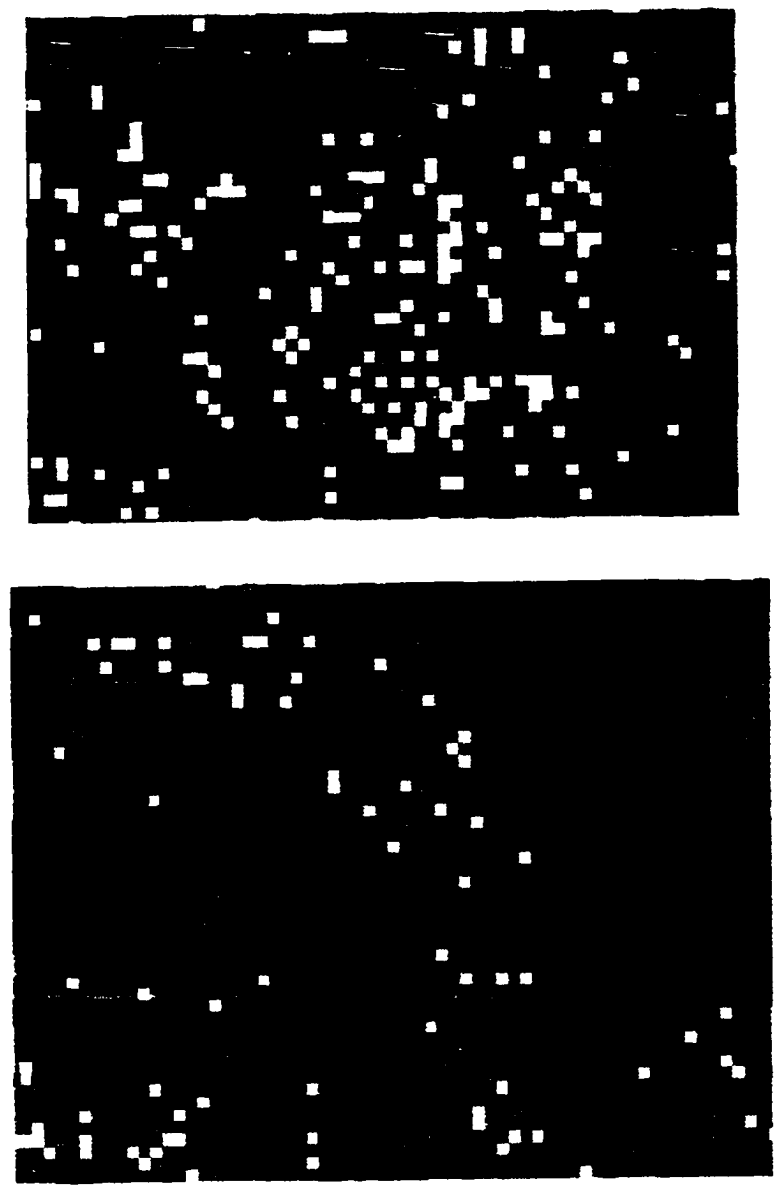


Figure 5.21. Locations of Townsend's ground squirrel study sites (black boxes) shown on habitat maps of portions of the Snake River Birds of Prey National Conservation Area, Idaho, generated by classification of satellite imagery (see text for more information). All sites shown were located within the Orchard Training Area (see Figure 5.3). All study sites were selected because of apparent habitat homogeneity within and surrounding the study site area. The 4 sites (each of 10 ha) in the top map were all chosen to represent grass habitats (green squares), and the 4 sites in the bottom map were chosen to represent shrub habitats (blue squares). Note that the shrub sites appear to better fit the habitat homogeneity criteria using this habitat classification.

CHAPTER SIX

SUMMARY AND CONCLUSIONS

Thus far, I have described how I estimated population parameters for Townsend's ground squirrels, and then integrated those parameters in a spatially explicit population model. My description of those efforts was at times exhaustive, but indicative of the work that went into those analyses. At this time, I think it is worthwhile to summarize what can be learned from my research, and make recommendations about the direction of future research efforts. I do so first on a chapter basis, and finish with some speculative remarks about the relationship between Townsend's ground squirrels and habitat.

Chapter 2. Abundance and density estimation.

The primary focus of this chapter was the methodology I used to estimate abundance: the no recruitment special case of the Jolly-Seber model, with the additional aspect of modeling of capture and survival parameters. Although the estimates themselves were also of interest, interpreting the relationships among those estimates is best done in combination with other sources of information, as was done by Van Horne et al. (1997). Therefore, my primary contributions were the application of methodology that heretofore has been little used for population estimation, the demonstration of the flexibility of these methods when trapping designs vary among sites, and the illustration of the potential for pooling data across data sets to improve abundance estimates.

I firmly believe that the use of the no recruitment special case, with parameter

modeling, is a substantial step forward in the search for better methods of abundance estimates. There are many situations where estimation by open population model methods is required, yet sample sizes are not sufficient for reasonable estimates to be calculated using the general Jolly-Seber model. Often, however, the main violation of population closure is due to losses, and not recruitment. Most biologists appear to be unaware of the existence of the no recruitment special case, or fail to see how its use may resolve their difficulties in using the general Jolly-Seber model. Certainly, few are aware of the applicability of capture and survival probability modeling to abundance estimation. I hope that my work will help to dispel ignorance of these techniques, and demonstrate their utility.

I recommend that when populations may be considered closed to recruitment for an appreciable time interval, that no recruitment methods be considered if estimates of abundance are desired. These methods should be especially useful when studying population of species, such as ground squirrels, that breed synchronously over a short period of time, that are relatively closed to immigration, and for which age classes are readily distinguishable during the time captures take place. These characteristics describe many game bird species and large mammals in general. The no recruitment methods I used should be especially useful for estimating breeding populations and/or pre- or post-harvest populations for these types of species.

Chapter 3. Within-year survival rates of Townsend's ground squirrels.

Survival rates, unlike estimates of abundance, are more amenable to direct analyses for influential factors, and the subsequent interpretation of the affects of those

factors. Consequently, this was the focus of Chapter 3. This was the first study of ground squirrels to estimate within-year survival rates on a broad scale, and also the first to examine habitat-specific differences. The results, when compared to the several biological hypotheses I listed, were not always as expected. Whereas the expected immediate effects of the 1992 drought, and subsequent prolonged winter in 1993, on survival were confirmed, lowered survival at later times in 1993 were not anticipated. Although the exact reasons for these lowered survival rates are unknown, they are probably caused by carry-over effects from the earlier poor conditions, as opposed to concurrent conditions. The potential for effects to linger, and the possibility they are realized at times other than those in which the causal conditions occurred, highlights the need for year-round assessment of survival. It is certainly not sufficient to estimate over-winter survival, as is most common in ground squirrel studies. I therefore recommend that future studies of ground squirrel survival included monitoring of populations throughout the active season, with particular attention paid to the periods immediately preceding and following the torpid period.

The survival estimation methods I used resulted in daily estimates of survival for each period of interest within the ground squirrel year. This made comparisons among factors fairly straightforward, but it was difficult to discern the true impacts of these factors without knowing the number of days in each period. Unfortunately, period length varied by many of the same factors that influence survival rates, and there was no reliable data available to determine period length. In addition, period lengths may differ appreciably among individuals; thus the use of generalized period definitions may not be

appropriate. However, as long as period-specific survival rates remain of interest, then accurate estimates of period length are important. For this reason, I would recommend that some areas be monitored on a daily basis (and if possible, individuals within those sites), during the times when the events that define period intervals occur; specifically, adult emergence, juvenile emergence, and immergence of both age groups.

Chapter 4. Dispersal patterns of juvenile Townsend's ground squirrels.

The radio-telemetry study of dispersal I conducted was not sufficient to detect differential patterns of dispersal, with the exception that a larger proportion of males disperse than females, at least under the conditions I studied. As the latter conclusion had been well documented for other ground squirrel species, it was not at all surprising. However, this was the first study of ground squirrels to investigate habitat-specific differences in dispersal characteristics, and this remains a worthy goal for future research. During the years I conducted this study, environmental conditions were moderate to good; and may not have been the conditions under which differences in dispersal between habitats occur. Under poor conditions, such as those encountered in 1992, it is more likely that habitat differences in dispersal might be noted. In addition, population densities in both habitats were relatively low. Differences in dispersal between habitats may also be detected in years where population densities are much higher in grass sites than in shrub. Such habitat-specific differences in dispersal may have considerable impact on the distribution of TGS across the landscape. This would be especially true if habitat imprinting (i.e., the selection by dispersers of ending dispersal movements in the same habitat type they left from) occurs, as was suggested by my study.

In addition to increasing sample sizes (i.e., radio-collared individuals), I recommend that study sites for future dispersal studies be selected to better investigate the relationships between habitat and dispersal movements. Specifically, the terrain surrounding sites should contain an equivalent mixture of habitat types, so that random dispersal movements should results in dispersers landing about equally in each. In addition, population densities within the study sites should be equal, thereby eliminating possible confounding between habitat and density. If possible, habitat patches should be mapped, and integrated with other information on topography and probable dispersal barriers, to create a map of dispersal probabilities to be compared to actual dispersal paths and endpoints.

In addition to these design features, I also advocate using manipulative experiments to resolve questions regarding dispersal under varying environmental conditions. Dispersal by juvenile females and adults (and perhaps juvenile males also) is likely to increase when food resources are poor, as demonstrated by Dobson and Kjelgaard (1985). Therefore, experiments that enhance or reduce food resources on treatment sites relative to control areas should be especially useful in assessing the influence of environmental conditions on dispersal rates.

Chapter 5. A spatially explicit population model for Townsend's ground squirrels on the Snake River Birds of Prey National Conservation Area.

I believe that my construction of the spatially explicit population model for TGS, described in Chapter 6, emphasized 2 important points: that a data-based modeling approach is worthwhile, despite the difficulties incurred, and that integration of

information into a model is necessary to focus future research efforts on the most important aspects of population dynamics. The broad scale nature of the TGS study allowed me to base nearly all model parameter values on actual data collected, and when specific data were not available, I made assumptions based on empirical results. Even when those results did not seem logical, I used them in the model unless I had good reason not to. Therefore, the model I constructed was based on the best knowledge I had about how the system I studied actually operates, and not any preconceived notions about how it should operate. Model results, therefore, are less tainted by my opinions, and more likely to reflect reality.

Despite this grounding in reality, the many assumptions I made while constructing the model render it nearly useless for prediction. Managers looking for guidance from my model on how to proceed with habitat improvements are urged to use extreme caution, as errors I may have made in assumptions may prove costly. Yet I believe the model is useful for other purposes, and especially as a means to identify the most important aspects of TGS population dynamics, and to develop testable hypotheses about population parameters and their relationships.

This generation of hypotheses could not be accomplished efficiently without a model. Although construction of a theoretical model might be sufficient to identify gaps in knowledge, it is the model simulations, and subsequent varying of parameters, that allows for the prioritization of efforts. Finally, those predictions that are useless for management, serve as null hypotheses, the rejection of which should provide more knowledge of TGS population dynamics. In my view, this method of hypothesis

generation, while advocated as a means to advance knowledge, is seldom applied in reality.

Habitat relationships of Townsend's ground squirrels

This study confirmed the importance of habitat to TGS, but revealed that their relationship with habitat is more complex than might be expected, given the relatively simplistic ecosystem in which TGS reside. The environment of the Snake River Birds of Prey National Conservation Area is harsh and variable. Neither shrub or grassland habitat can be easily identified as being of consistently higher quality for ground squirrels. Although ground squirrels in grasslands may exhibit higher growth rates under most weather conditions, they also experience greater declines when conditions become poor. Poor conditions may be the result of drought, but it's also conceivable that high populations of ground squirrels could lead to similar declines if TGS's ability to adjust population growth in response to density is relatively poor. Thus populations in grassland habitat may undergo wide fluctuations in density; a boom and bust cycle that occurs in many other species of small mammals. Ground squirrels in shrub habitat, on the other hand, fare less well under normal conditions, but are less affected by extremely poor ones.

It is probably not worth arguing whether grass is better than shrub, or vice versa, because the key issue may be how those habitats are distributed on the landscape. The wildfires that occurred in the 1980's created large expanses of grasslands, while other areas remain almost entirely shrub. If model results are reasonable depictions of reality, these large habitat patches may contribute to the instability of ground squirrel

populations, particularly those residing in grassland habitats. Only when habitats are intermingled did there appear to be more stable dynamics, under the presumption that there are no barriers to dispersal movements between habitat types.

Yensen (1982) extensively reviewed descriptive accounts of the Snake River plains by early overland explorers and subsequent travelers along the Oregon Trail. She concluded that sagebrush was the predominant presettlement vegetation type, yet an engraving from 1849 (Yensen 1982: p. 3) shows sagebrush intermingled with grassland. Although the status of Townsend's ground squirrel populations at this time is unknown, its conceivable that this mixture of habitat types is what TGS are best adapted for. Unfortunately, we are a long ways away from establishing this relationship as fact, and being able to use it to better manage the SRBPNCA for TGS populations.

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Yensen, D. 1982. A grazing history of southwestern Idaho with emphasis on the Birds of Prey Study Area. USDI-BLM Snake River Birds of Prey research project report, Boise, ID.