Establishment Limitations and Population Recovery of Giant Coreopsis (Coreopsis gigantea) on the California Channel Islands

A Dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in the department of Ecology, Evolution and Marine Biology

By

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December 2008
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By

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DEDICATION

To my parents John and Nancy Schwemm

To my children Annie Swank, Bridget Coonan and Carrie Coonan

To my husband Tim Coonan
VITA OF CATHERIN A. SCHWEMM

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ABSTRACT

Establishment Limitations and Population Recovery of Giant Coreopsis (*Coreopsis gigantea*) on the California Channel Islands

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*Coreopsis gigantea* (Asteraceae) is a dominant perennial shrub in coastal communities on the California Channel Islands. Mature stands of *C. gigantea* provide unique habitats for vertebrates and understory plants, and biodiversity in *C. gigantea*-dominated communities is determined largely by the population dynamics of this species. *C. gigantea* individuals are long-lived and mortality of adults is low, thus *C. gigantea* population growth is strongly influenced by impacts at early life stages. Mature *C. gigantea* stands persist for many decades in the absence of disturbance and represent the climax stage of shrub succession at many sites. Populations of *C. gigantea* were severely reduced in size and in some cases eliminated as a result of grazing and land management practices beginning in the 1850s. Recovery of *C. gigantea* populations in decades following the cessation of grazing has varied; in some areas *C. gigantea* has successfully recolonized historic sites, while in others the species is largely still absent and exotic plant species, especially exotic annual grasses, dominate. This project investigated the general hypothesis that ecosystem changes resulting from grazing impacts have altered the strength and/or mechanisms of limitations on early life stages of *C. gigantea*, reducing population growth at some sites and leading to altered successional patterns and persistent dominance of invasive
plant species. To identify the factors that most regulate *C. gigantea* abundance I investigated processes that act both pre- and post-seed dispersal, and gave particular attention to the role of native deer mice (*Peromyscus maniculatus*) as seed predators. Primary results from the study are: 1) fecundity did not differ between high and low growth populations; 2) pre-dispersal seed predation differed between high and low-growth populations but did not affect differences in pre-winter seed bank abundance; 3) post-dispersal seed predation limited establishment only at high *C. gigantea* densities; 4) low rainfall reduced seedling survival significantly, but this factor likely has influence only when rainfall is far below normal; 5) competition from exotic annual grasses had the strongest negative effect on seedling emergence; 6) future successional processes will likely be affected by continued persistence of invasive plant species in many areas.
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CHAPTER 1

Pre-dispersal seed predation and early life stage dynamics of a native shrub (*Coreopsis gigantea*) on the California Channel Islands

Introduction

The abundance of organisms is limited by processes that either prevent the establishment of new individuals or cause mortality to those already living (Pianka 1974). For most organisms the early stages of life are the most hazardous (Louda 1982, Fenner and Thompson 2005, Barbera et al. 2006), and species have adopted many strategies to overcome factors that reduce productivity and juvenile survival (Pianka 1974, Fenner and Thompson 2005). Given the rapid ecological changes caused by human disturbance, however, adaptations that have historically promoted the survival of individuals may no longer be sufficient (McDonald et al. 1996, Kearns and Inouye 1997, Greene and Pershing 2004). Recent, rapid impacts caused by invasive species, climate change, and habitat loss can result in limitations on growth and establishment to which species have not previously been exposed (McClure et al. 2003, Greene and Pershing 2004, Fish et al. 2005). Novel changes in selection may lead to extinction for many species unless management of impacted systems addresses factors that now constrain growth (Zahawi and Augspurger 1999, Satterthwaite et al. 2007). Species conservation requires that managers and scientists understand not only the sources of population regulation but also the degree to which
such limitations are caused by human activities (Bartolme 1979, Chambers and MacMahon 1994, Sherry and Holmes 1996).

In this study I investigated limitations on early life stages of *Coreopsis gigantea*, a deciduous shrub native to coastal Southern California and the California Channel Islands. *C. gigantea* is an important component of several coastal shrub communities (Junak et al. 2007), and on the smaller islands where trees are absent, mature stands of *C. gigantea* provide important habitat for vertebrates and associated understory communities. Nearly all of the island populations of *C. gigantea* were extirpated by the mid-20th century as a result of managed grazing, grazing by feral herbivores (primarily rabbits, *Oryctolagus cuniculus*) and land conversion practices.

All of these activities ended by the mid-1980s, and *C. gigantea* recovered rapidly in some areas. Many sites that would be expected to support populations of *C. gigantea* still do not, however, and instead remain dominated by exotic annual grasses or other non-native species (Junak et al. 1993, Halvorson 1994, Corry 2006). The continued absence of *C. gigantea* regeneration at these sites long after the removal of direct impacts suggests that there are either novel factors present that now limit growth, or that existing limitations have increased in strength in response to the presence of exotic competitors (Eliason and Allen 1997, Corbin and D’Antonio 2004), changes in soil conditions (Seabloom et al. 2003), increases in herbivore abundance (Peters 2007), or interactions of these factors with climate and disturbance patterns (Curtin et al. 1999).
Ecosystems on San Miguel Island (SMI), a medium-sized island within the Channel Islands chain, were heavily impacted by invasive species, and plant community response to the removal of anthropogenic impacts has varied. I selected three study sites on SMI that encompassed C. gigantea populations with differing dynamics - sparse and not increasing, abundant and increasing, and very dense but not increasing - to quantify and compare factors that limited seed abundance and reduced recruitment. The populations were in close proximity to each other (< 400m), so I assumed that large scale factors such as climate, topography, or consumer diversity did not contribute to the variable dynamics between populations (Louda 1982, Salas 1990, Kollmann et al. 2008). Deer mice (Peromyscus maniculatus streatori) are the dominant seed consumer on SMI, and are distributed island-wide. Because of the high population densities and generalist foraging habits of deer mice, I was specifically interested in whether there were conditions under which seed removal by mice could limit C. gigantea recruitment.

I divided the study into two parts. I first examined intrinsic rates of seed production, the pre-dispersal impacts of native consumers on seed production, and seed bank abundance in an observational study (Chapter 1). I then incorporated experimental work to investigate post-dispersal seed predation and microsite limitations on germination and seedling survival (Chapter 2). Cumulatively the two chapters examine the likelihood that a seed generated in each of the three populations will survive to become a seedling and the factors most responsible for seed loss. The study was designed to 1) better understand C. gigantea ecology, 2) examine in detail
the relationship between a dominant flowering plant and its primary seed consumer in a simple system, and 3) provide information useful to managers in planning restoration actions for recovery of shrub communities on the Channel Islands (Satterthwaite et al. 2006).

*Post-grazing Plant Community Dynamics on San Miguel Island*

The study was conducted on San Miguel Island (SMI), the westernmost of the eight California Channel Islands and one of five islands within Channel Islands National Park. The absence of land masses to the west of the island results in a windier and moister climate than is found on the other Channel Islands (Dorman and Winant 2000). The average precipitation on SMI is 39.15 cm (1993 – 2008), with much of that coming as fog drip (Estberg 1996), and there is a nearly constant 20-40 km/hr northwest wind. Annual weather patterns on the Channel Islands are characteristic of Mediterranean climates throughout the world, with rainfall during the winter followed by summer drought (Keeley and Swift 1995), though the dry season here is moderated somewhat by fog and humidity regimes that bring increased moisture to the islands (Dorman and Winant 2000).

From the 1850s to the 1980s, Euro-Americans and grazing livestock had both immediate and long-term impacts on island ecosystems. Domestic sheep (*Ovis aries*) were first transported to the island around 1850, and by 1860 there were nearly 6000 on the island (Ellison 1937). A severe drought in 1863-1864 caused most of the sheep
to starve, but not before they had eaten nearly every accessible, palatable plant
(Roberts 1991). Without the plants to hold the sandy soil in place, the prevailing
winds blew away much of the topsoil, leaving deposits of sand over nearly 80% of the
14.9 square miles of the island (NPS unpublished GIS data). Reduced numbers of
sheep remained until 1950, and burros (*Equus asinus*), another exotic species
destructive to vegetation, were finally removed in the late 1970s.

The impacts to vegetation communities from grazing and erosion on SMI
were severe (Hochberg et al. 1980, Junak et al. 2007). On this island and others
(particularly Santa Barbara Island), *C. gigantea* communities were nearly destroyed
by rabbit and sheep herbivory, and by management practices that specifically cleared
*C. gigantea* stands to open land for planting and grazing (Philbrick 1972, Daily
1993). It is possible that during the mid 20th century *C. gigantea* existed only in very
small remnant populations on SMI. Betsy Lester Roberti, who as a young girl lived
on San Miguel from 1933 – 1942, does not recall ever seeing the plants:

‘She didn’t recognize the head-high, black and brown coreopsis
stems. Coreopsis blooms yellow in spring and, in combination
with purple-bluish lupines, can make it seem like Easter on San
Miguel. But they didn’t have coreopsis in Betsy’s youth; she
surmised the sheep got to them.’

(Ventura County Star, August 24th, 2008).

By the 1960s few populations of *C. gigantea* remained on any of the Channel
Islands. Their destruction resulted in at least one vertebrate extinction; the Santa
Barbara Island song sparrow (*Melospiza melodia graminea*) was last seen prior to a
burn of the last \textit{C. gigantea} stand on that island in 1967 (Hunt and Hunt 1974). Since the early 1980s when exotic grazers were finally removed and the islands included within Channel Islands National Park, populations of \textit{C. gigantea} in some areas have responded quickly and are now at carrying capacity, while in others annual grasses dominate or lands are bare, and the only \textit{C. gigantea} plants present are over 20 years old with minimal regeneration (D’Antonio et al. 1992, Junak et al. 1993, Corry 2006).

\textit{Coreopsis gigantea} - Population and Community Structure

Giant Coreopsis (\textit{Coreopsis gigantea}; Asteraceae), as the name implies, is the largest species of \textit{Coreopsis}, and is one of only two perennial species in the genus (Crawford and Whitkus 1988). \textit{C. gigantea} is a deciduous shrub found in coastal bluff scrub communities in Southern California and on the California Channel Islands (Junak et al. 2007). Growth patterns, morphology and reproductive biology of this species have been little studied, and much of the information presented here is new. It should be noted that this information is for populations of \textit{C. gigantea} on the California Channel Islands only, and it is not known how similar mainland communities that include \textit{C. gigantea} are to those on the islands.

Very little is known about the natural pattern of succession and competitive interactions between \textit{C. gigantea} and other shrub species on the islands prior to the initiation of grazing. \textit{C. gigantea} is the dominant member of the giant coreopsis coastal bluff scrub community but occurs in other associations as well (Junak et al.}
Current observations of shrub aggregations on SMI suggest that *C. gigantea* in mixed shrub assemblages eventually outcompetes other species, resulting in monospecific *C. gigantea* shrub stands (Morin 1999, Chapter 4). The degree to which this process mimics pre-grazing succession in shrub communities or is influenced by past land use practices on the island is unknown (Fleischner 1994, Swetnam et al. 1999, Bonet 2004, Corry 2006).

Because observations of mature *C. gigantea* stands do not exist prior to grazing, the factors that contribute to the persistence of mature stands and why *C. gigantea* so dominates other shrubs under some conditions, is likewise unclear. Late successional stages of plant communities persist until disturbed (Morin 1999), however, natural disturbance events on the islands are rare. It appears from historical data and observations that the only source of mortality to mature *C. gigantea* plants, other than old age, are extremely high winds that accompany severe winter storms. These periodic blowdown events affect mature plants weakened due to age and possibly drought (this study), but have been observed in recent times only on small spatial scales. The presence of non-native grazers was by far the most significant disturbance affecting existing landscape patterns (Hochberg et al. 1980), and likely altered not only plant diversity but soil resources (Carmel and Kadman 1999) and consumer dynamics (Schiffman 2007). In lieu of disturbance, consumer effects, density dependent factors, and competition from exotic species may at present be important processes driving shrub community dynamics in island systems (Pickett et al. 1987, Morin 1999).
**Coreopsis gigantea - Morphology and Growth**

The morphology and productivity of individual *C. gigantea* plants vary depending on population density. In low to moderate density stands, a central trunk grows for 2-5 years, at which point the first branches and flowers are produced (Salas 1990, this study). (In the Asteraceae family two single-seeded flower types, ‘ray’ and ‘disk’, occur together and form a composite flower, termed a capitulum. For *C. gigantea* there is no evidence to suggest differences in pollination or seed survival between the two flower types, so for this study no distinction is made, and seed production is reported per capitulum. The terms ‘flower’ and ‘capitulum’ are used interchangeably.) Flowers grow off the ends of long (9-13 cm) peduncles at the ends of branches, so older plants with more branches have greater per capita flower production than younger plants (Salas 1990, this study). However, in high density stands many individuals can grow into adulthood without ever branching or producing flowers, effectively creating a self-thinning monoculture with low per capita flower production (Pyke and Archer 1991).

*C. gigantea* individuals can reach a maximum height of 3 meters with a trunk up to 40 cm in diameter, and live over 20 years (Salas 1990, this study). Consequently, while mature plants at low densities can have many long branches and be up to 2.5 meters wide, plants of the same age in very dense populations without branches are only as wide as the stem itself. These substantial physical differences
have important implications for variable consumer impacts between populations, as will be discussed.

The physiology of *C. gigantea* also affects community structure. This species is drought-deciduous, and as soil moisture declines through the summer and fall the leaves desiccate and water is lost from the branches, causing the plant to diminish in size. The dense canopy present in spring and early summer is thus severely reduced for the remainder of the fall and winter. Substantial water is retained in the main stem and larger branches, however, and leaves begin to appear almost immediately after the onset of first rains (Salas 1990, this study). Due to their semi-succulent physiology and lack of true woody tissue, *C. gigantea* plants are quite fragile given their relatively large size. Natural events such as vertebrate activity or strong winds that do not result in physical damage to other sympatric shrub species can result in broken branches or individual mortality (discussed below).

*Coreopsis gigantea* - Seed Development and Dispersal

There is no evidence of vegetative reproduction in this species and it is assumed that reproduction is by seed only. Salas (1990) examined the population dynamics of *C. gigantea* on Santa Barbara Island (California), and calculated estimates of fecundity based on the average number of inflorescences (capitula) per individual, but no estimate of seed production was presented. Because of its relevance to seed predator effects and the impact that differences in productivity between
populations could have on overall dynamics (Morgan 1998), seed production and
development was observed in some detail during this study.

The initiation of flower production in *C. gigantea* varies annually and is
highly dependent on rainfall (this study). Flower bud development begins with the
first winter rains, usually in late November or December, and blooms appear
approximately 4-5 weeks later. Though flowering phenology appears to be related to
the amount and timing of rain that occurs early in the winter (November through
March), there is no evidence that per capita flower abundance correlates with rainfall
amounts. Pollination takes place soon after flowers bloom, though specific pollinators
have not been identified. Hymenopterans, though, are a likely group; during one field
visit on late February 2008 hundreds of (unidentified) bees were observed visiting
flowers, but only on one day and only for a few of the warmest afternoon hours.

Seeds require approximately 10-12 weeks to mature, and seed set (dispersal)
commences in late spring and continues through mid-summer. Seeds enclosed in their
fruit (achenes) are 2-5 mm in length, oblong and somewhat flattened, and have a very
small pappus (wing). (Herein the term seed will be used to refer to the achene as it is
dispersed from the flower.) *C. gigantea* seeds are not adapted to wind dispersal
(Schiffman 1997) despite the high winds that dominate island weather conditions, and
seed dispersal is likely facilitated by rodents and passerine birds.
**Coreopsis gigantea – Soil Seed Bank**

The population of seeds in or on the soil surface that can potentially germinate is termed the seed bank (Leck et al. 1989, Fenner and Thompson 2005). Seed banks can be transient (seeds either germinate in the first year or they die), or persistent (the seeds remain viable for some period past the first year; Thompson 1992). Mediterranean annual grasses have a transient seed bank (Thompson 1992), and evidence strongly indicates that *C. gigantea* does as well. Greenhouse treatments of soil samples collected in the springs of 2005 and 2006 on SMI resulted in minimal emergence of *C. gigantea* seedlings (this study), suggesting that either few seeds were present, or that those that were present were not viable (Fenner and Thompson 2005). Further, an early rainfall event on SMI in October 2007 was immediately followed by a strong germination response of *C. gigantea* (personal observation), indicating that seed dormancy in *C. gigantea* is easily ended by rainfall, and that viable seeds would likely germinate given the amount of precipitation that occurs in a normal winter. However, the ability of *C. gigantea* seeds to survive multi-year drought is unknown.

For this study I use the term seed bank to specifically refer to *C. gigantea* seed abundance in the soil prior to winter rains (Simpson et al. 1989, Montiel and Montana 2003). Germination and seedling establishment for nearly all native and exotic species in Mediterranean climates occur in response to winter rainfall (Traba et al. 2006) and seed set (dispersal) of *C. gigantea* seeds ends by mid-summer. Consequently, the maximum number of *C. gigantea* seeds produced in a given year
that could eventually become established, (i.e., that are viable, have survived post-dispersal hazards, and are in a microsite without impediments to germination), will be some subset of the seeds present in the soil just before rains begin (Leck et al. 1989). For now I assume that this subset is proportionally consistent across populations, however I examine this assumption in detail in Chapter 2.

**Pre-dispersal Seed Predation**

The impacts of seed predation on plant populations vary temporally and spatially across species (Fenner and Thompson 2005, Kolb et al. 2007), as well as within species (Louda 1982, Boyd 1988, Figueroa et al. 2002). The strengths of seed predator impacts are related to multiple traits of seed physiology (Kelrick et al. 1986), plant population dynamics (Louda 1982, Crawley 1992), and consumer dynamics and behavior (Figueroa et al. 2002, Fedriani and Manzaneda 2005). Seed predation potentially has greater population impacts than other forms of herbivory because it removes an entire individual from the population, while herbivory generally involves only a portion of a plant’s tissue (Hulme 1998).

If a seed is consumed or damaged by herbivores while it is still on the parent plant the process is known as pre-dispersal seed predation, and includes not only the direct consumption of seeds but all interspecific processes that kill or damage seeds such that they never mature (Fenner 2000, Nilson 2000, Kolb et al. 2007). Losses to pre-dispersal seed predation alone can be as high as 100% of annual seed production
This study examines the impact of the two primary pre-dispersal seed predators of *C. gigantea*, insect larvae and deer mice.

**Insects** - Larvae of a species of tephritid fruit fly, most likely *Neotephritis finalis* (Diptera, subfamily Tephritinae), infested between 30 and 80% of all flowers examined (this study). Neither larvae nor adult flies were positively identified to species, however, all the larvae observed during the study were of similar size and imparted similar damage. Tephritid flies are common pre-dispersal seed predators on many species of Asteraceae (Headrick and Goeden 1998, Fenner et al. 2002), and I assumed that all of the seed damage caused by insects was due to larvae within this group and primarily from this species (Louda 1982). Adult flies lay eggs in developing flowers or flower buds, and hatched larvae damage seeds either by feeding on them directly or by causing seeds to abort (Louda 1982, Headrick and Goeden 1998, Fenner et al. 2002).

**Vertebrates** - Vertebrate diversity on San Miguel Island is low compared to equivalent mainland areas (Denslow 2001, Drake et al. 2002). Only six terrestrial vertebrate species exist on the island, including two endemic mammal subspecies (San Miguel island fox, *Urocyon littoralis littoralis*, and San Miguel Island deer mouse, *P. m. streatori*), and one non-native species (*Rattus rattus*). In addition to the mammals there are two lizards (*Sceloporous occidentalis becki* and *Elgaria multcarinata multcarinata*) and one salamander (*Batrachoseps pacificus pacificus*).
These species are primarily insectivorous, and while they certainly have impacts at lower trophic levels they are probably not relevant to this study. Of the vertebrate fauna only the deer mouse is granivorous. Deer mice are extremely abundant, with populations often exceeding 500/hectare, and are found in all habitats (Schwemm and Coonan 1991, Chapter 3). Hence, if seed loss to consumers is a potential regulating mechanism, the patterns of abundance and dynamics of deer mice are likely quite relevant and may have strong correlations to recruitment.

Seasonal dynamics of mouse populations on the Channel Islands are typical of temperate *Peromyscus* species (King 1968). Reproduction begins in the spring, largely in response to the amount and timing of winter rainfall and resulting plant growth (Chapter 3). If food resources are plentiful reproduction can continue through the summer and into fall, though more often the final litters of the year (females can have up to three) are born in mid-summer (Drost and Fellers 1991). Population densities peak in early fall, then decline over the winter to spring lows, when the cycle begins again. If spring conditions are poor, annual production is negatively affected and populations remain low throughout the following year. Seeds make up a large part of the diet of deer mice, but as dietary generalists mice also consume other foods including green plant tissue, invertebrates, carrion, and seabird eggs (Collins 1979).

Rodents, including several species of *Peromyscus*, are important seed predators in many systems (Reichman 1979, Borchert and Jain 1978, Sullivan and
Sullivan 1982, Crawley 1992). Past studies have demonstrated the ability of several *Peromyscus* species to consume large portions of available seeds (Mittelbach and Gross 1984), and to regulate plant abundance under certain conditions (Boyd 1991, Cabin et al. 2000, Maron and Simms 2001, Maron and Kauffman 2006). Deer mice are known to feed on flowers and seed heads of many plant species (Harney and Dueser 1987, Jekanski and Kaufman 1995), but few studies have specifically investigated the pre-dispersal impacts of deer mice on seed populations. Deer mice easily forage in the *C. gigantea* canopy, removing flowers by chewing the peduncle midway between the end of the branch and the flower. Mice may also be responsible for broken branches that are often found on the ground below large *C. gigantea* individuals. As mentioned, *C. gigantea* stems are easily damaged, and whether mice chew the branches or the branches simply break under the weight of one or more mice is not known, but in the absence of severe weather conditions there are no other logical explanations for this observation.

After cutting the flower peduncles (or whole branches), mice collect flower materials into large (30-40g) surface caches beneath the cover of the individual plant from which they were removed (Vander Wall et al. 2001). Four such caches were opportunistically collected in the spring of 2007 on SMI and examined, and each contained thousands of mature *C. gigantea* seeds. The fate of these seeds is relevant and will be discussed in Chapter 2, but for now it is assumed that these seeds do not survive, i.e., that this is not a case of seed dispersal (Chambers and MacMahon 1994).
Cumulatively, the abundance, island-wide distribution, behavior, and ecological niche of deer mice leaves little doubt that mouse populations consume immense portions of the seed populations of many plant species on the Channel Islands. This study investigates whether or not there are conditions under which seed consumption by mice results in reduced plant population growth for *C. gigantea*.

**Methods**

**Study Sites**

Three sites that differed in growth dynamics of *C. gigantea* were selected for study on San Miguel Island. The sites were all located on the north portion of the island within 1 km of each other, were without differences in slope or aspect, and were exposed to identical weather and local climate conditions.

The first site (‘**Grassland**’) was a homogenous annual grassland dominated by *Avena, Bromus* and *Hordeum* species with additional invasive annuals such as *Sonchus oleraceus* and *Medicago polymorpha*. *C. gigantea* density here was very low (0.01 individuals/m²) and all of the individuals were 8-10 years old (Chapter 4). This site was representative of the ubiquitous non-native annual grasslands that now exist in California as a result of European grazing practices of the last two centuries (D’Antonio et al. 2007). The presence of reproductive *C. gigantea* individuals here, albeit at very low densities, indicates that environmental conditions at the site are
conducive to growth, and that population limits are instead imposed by factors that strongly limit recruitment.

The second site (‘Transition’) was a mixed community where native shrubs, (C. gigantea at densities of 4.7/m², Lupinus albifrons, Isocoma menziesii, and Eriogonum grande var. rubescens) occupied approximately a quarter (26.8%) of the area and annual grasses and other herbaceous species the remainder. The understory was diverse, and included annual grasses, exotic perennials such as Carpobrotus edulis (exotic iceplant), native herbaceous perennials (Marah macrocarpa) and native annuals such as Escholzia californica and Dudleya greenei. The age structure of the C. gigantea population was highly skewed toward young individuals, with few individuals older than 10 years (Chapter 4). The abundance of young plants suggests that at present there are few limitations on C. gigantea recruitment and growth at this site.

The third site (‘Mature’) was a highly dense stand of C. gigantea (9.3/m²), where many individuals were unbranched and per capita flower production was lower than in the Transition population. Also in contrast to the Transition site, young C. gigantea plants occurred only in gaps where dead individuals created openings in the canopy. Most individuals were over 10 years old (Chapter 4). The understory, where present, was a mix of native and exotic annuals, including annual grasses. Understory plants were absent from much of the site, however, owing to the unbroken canopy that prevented direct sunlight from reaching the ground. At present, density
dependent mechanisms appear to be strongly limiting regeneration and the population is at carrying capacity. But in contrast to the persistent absence of recruitment in the Grassland population over the past several decades, germination and seedling establishment clearly occurred with great frequency here in the years after grazing ended.

**Study Design**

At each site, an area of habitat 50 x 40 m (2000 m$^2$) was identified within which all of the sampling described below was conducted. Each site was centered within the community type described (i.e., no edge or ecotone was included), and estimates of total seed production, losses to seed predation, fecundity, and seed bank density as reported for each population refer to these sites. A summary of parameters measured and methods used is presented in Table 1.1.

**Population Structure and Fecundity** - Demographic parameters for each population were estimated in February 2008 using sampling plots. Three transect lines, 50 m long and spaced 10 m apart, were centered at each site, and 1 m$^2$ plots established every 10 m along each line (n = 18/site). In each plot the number of individuals (total n = 145 in the Mature site, 43 in the Transition, and 9 in the Grassland) and their reproductive age (seedling, juvenile, flowering adult, non-flowering adult) were recorded. In past studies, (Salas 1990), the presence of branches was used to identify adult plants, however, individual plants can often be
quite old (>15 years) but without branches. Individuals without branches can either produce flowers from their main stem or have no flowers, so the presence or absence of flowers is also not a reliable indicator of age. Therefore, in this study, adults were classified simply as any individual greater than 0.5 meters in height, and individuals were either flowering or non-flowering at the time of sampling. The mean number of individuals calculated per m$^2$ at each site was multiplied by 2000 to obtain an estimate of population density for each site with associated confidence intervals. (Details of *C. gigantea* population structure at each site are presented in Chapter 4.)

*Flower Classification* - Per capita flower production at each site was estimated from spring sampling in 2007 and 2008. Flowers were classified as either ‘early’, ‘bloom’, or ‘late’. Early flowers (buds) were closed, without visible petals, and could not yet have been pollinated, but ovules had developed and could be counted. Flowers in bloom were those with petals that were fully open to pollinators and seed predators, and often contained a range of seed types, from unfertilized ovules to nearly mature seeds. Late flowers had lost their petals or the petals were completely dried, but retained the seeds which were nearly ready for dispersal and fell out easily when handled. Late flowers that upon examination had already lost some of their seeds were not included, nor were flowers in transition between these stages.

*Seed Classification* - Flowers were randomly collected to estimate seed abundance using two methods. In 2007 field personnel working on other island projects (island fox recovery) were requested to collect flowers of each type as they
worked in these areas and store them individually in paper bags. There were no other requirements for these collections other than the collectors record the location and not collect more than two flowers of each type from any one individual. In 2008, I blindly collected two flowers of each type (if present) from every fifth plant encountered during transect sampling. Because of the low number of individuals in the Grassland population, more than two flowers of each type were collected from individuals sampled here. Samples from the two years were pooled for analysis, and a total of 135 flowers included in the measurements, (n = 52 from the Mature site, 63 from the Transition, and 20 from the Grassland).

Flowers were dissected on the day of collection, and seeds classified as either unfertilized, immature, mature, or damaged. Very small ‘seeds’ were classified as unfertilized, although it was not always possible to differentiate between these and seeds that were pollinated but at a very early stage in development. Immature seeds were either smaller or the same size as mature seeds, but they were still partially green and/or did not separate easily. A mature seed was one that easily separated from a late flower and was completely brown (they are olive green during development). Damaged seeds were those at any stage that had sustained physical impacts due to larval development or direct consumption by larvae, and it was assumed that all seed damage was fatal. The number of larvae found in all flowers was also recorded; larvae were more common in late flowers than in blooming ones, and were never found in early flowers, though eggs could have been present at this stage (Headrick and Goeden 1998). Seed damage was calculated as both the actual
number of seeds damaged and as a proportion of total ovules (Headrick and Goeden 1998, Kolb et al. 2007), and measured from late flowers.

The ratio of mature seeds to ovules (S/O) indicates the relative success of pre-dispersal seed survival in relation to reproductive effort (Wiens 1984). The number of ovules produced was represented in any flower by the total number of all seed types, i.e. ovules could remain unfertilized, develop, or become infested, but it was assumed that they would not disappear. Consequently the mean number of ovules produced was calculated from the sum of all seed types in all flower types, while the mean number of mature seeds produced per flower was calculated only from late flowers. Because it was assumed that immature seeds that had survived predation by the late flowering stage would ultimately mature, immature and mature seeds from late flowers were combined to calculate the mean number of mature seeds produced. Finally, fecundity was defined as the number of viable seeds produced per flower, and was calculated as the mean number of mature seeds multiplied by the germination rate (below).

*Germination Rate* - Seldom will all of the mature seeds produced by a flower germinate, even under optimal conditions (Fenner and Thompson 2005). Greenhouse trials were used to determine the average proportion of *C. gigantea* seeds that would germinate from those produced (viability). Mature seeds were collected from flowers across all sites in late spring 2007 just prior to dispersal, maintained at room temperature in paper envelopes, and planted in February 2008. Fifty seeds were added.
to each of 16 trays in a mix of 3:1 potting soil and perlite. Separate trays were used only to facilitate planting and watering and there were no treatment differences between them. The trays were watered as needed to maintain soil moisture and the maximum number of seedlings observed over six weeks recorded (i.e. if a seed germinated but subsequently died it was included). The proportion of seeds germinating from the initial 50 planted in each tray was determined, these values arcsine transformed and the results averaged. Of 800 seeds planted, 149 germinated, (0.19) and the average proportion germinating per tray was also 0.19 (SE 0.02). Fecundity was therefore calculated as the average number of mature seeds produced per flower reduced by 0.19.

A final estimate of seed production in each population was calculated as fecundity multiplied by mean per capita flower production (after estimating removal by mice, below), multiplied by the population estimate at each site.

*Flower Cutting by Mice* - In January 2007, five large *C. gigantea* plants were non-randomly selected at each site prior to the onset of flower development. It was impossible to predict which plants (if any) mice would target, so in the absence of information on preferential selection of *C. gigantea* individuals by mice based on plant traits, I selected individuals for sampling that were of average size, (which I assumed would predict average flower abundance, Chapter 4), and were near the center of each study site. The plants were marked with aluminum tags and examined during subsequent field visits in February, March, and May. At each visit the total
number of flowers and cut flower peduncles was recorded, and for calculations the maximum count for each measure at the end of the season was used. In response to the high levels of flower cutting observed in 2007, in 2008 I resampled the 2007 plants, and recorded the number of cut peduncles for each flowering individual sampled in the demographic plots described above (which were less than the total number of individuals; n = 87 in the Mature site, 22 in the Transition, and 9 in the Grassland). The number of cut stems per individual was averaged for each site in each year, and this value multiplied by fecundity to determine estimated per capita seed loss to mice at each site.

*Plant Diversity* - Plant species richness was much greater at the Transition site than at the Grassland or Mature sites (where annual grasses and *C. gigantea* dominated, respectively) so plant community diversity was sampled here using point-intercept transects. Using a GPS (Garmin® eTrex) I collected the UTM coordinates of the corners of each site, then assigned random numbers to create new, 2-digit values for easting and northing coordinates (i.e. the new coordinates could be within 99 meters of any of the four corners). A list of 20 UTM locations was generated based on these coordinates, and each point located sequentially. If the coordinates were within the site and more than 10 meters from any previously selected set of coordinates, they were accepted, and became the south end of a new transect. Transects were 4 meters in length, with sampling points located every 10 cm along the transect (n = 40 points/transect). At each point the height and identification of all
individuals were recorded. Three transects were established and sampled in the fall of 2005, and 2 more in the fall of 2006.

*Seed bank* - To quantify the *C. gigantea* seed bank, soil samples from each site were collected prior to winter rains in November 2006 and in October 2007. Six samples of approximately 340 mL of soil (113 cm² of surface area to 3 cm depth) were collected at 10 m intervals along a transect through the center of each 2000 m² site described above. A subsample of 250 mL was moistened and placed in a refrigerator (5°C) for two weeks to accelerate seed development. These samples were then spread on plastic trays filled with the same soil mix used for the seed viability trials (3:1 potting soil and perlite). The trays were maintained under greenhouse conditions with daily watering and sampled weekly. All emerging seedlings were identified to genus, (species when possible), and seedlings removed after counting. The samples were maintained for approximately three months or until no new seedlings were noted for two weeks. The number of *C. gigantea* seedlings emerging from the six samples was averaged for each site, and this number multiplied by the proportion of the site represented by one sample (2000 m² /0.113 m²).

*Mouse Densities* - Mouse densities at the study sites were estimated by the National Park Service via mark-recapture trapping in the fall of 2006 and 2007 and the spring of 2007. Each session included two nights of trapping, with 12 or 18 traps each night. (The number of traps used was consistent within a session, but the maximum number of traps was not available for all sessions.) Two or three transects
of 6, 12-inch Sherman live traps (H.B. Sherman Co., Tallahasee, FL.) were placed in the center of each site. Traps were baited with dry oats and checked early each morning, and captured animals were identified to sex and age, marked with ear tags, and released. Traps were then closed for the day and re-opened at dusk.

In addition, annual population monitoring of deer mice was conducted by the National Park Service at two additional sites in the fall of 2006, and the spring and fall seasons of 2007 and 2008. Monitoring consisted of three nights of trapping on 10 x 10 grids with traps spaced 7 meters apart, and the same handling techniques used as described above (Chapter 3). Of the two monitoring sites, one (‘Willow Canyon’ – WC) was a homogenous annual grassland, very similar in composition to the Grassland site in this study. The other, (‘Nidever Canyon’ – NC), was in a mixed shrub community that included C. gigantea, but at lower densities than in the Transition site (Schwemm and Coonan 2001). All sampling was conducted by the National Park Service in accordance with the American Society of Mammalogists Guidelines for the Capture, Handling and Care of Mammals (http://www.mammalsociety.org/committees/index.asp).

**Statistical Analysis** - Measurements of ovules, seeds, larvae, the total number of damaged seeds and the proportion of seeds damaged were compared separately across sites using one-way ANOVA with t-test pairwise comparisons in JMP (Version 7.02, SAS Institute, Inc.). The propagation of error was relevant when calculating the function of two or more estimates (Box et al. 1978). A common
method for calculating error in these situations is the Delta method (Powell 2007, Cooch and White 2008). In lieu of information to the contrary, I assumed no covariance between reproductive measures, i.e., seeds/flower was independent of flowers/plant, etc.

Results

Seed Production

The number of ovules produced per flower differed significantly between all sites ($F = 18.10, P < 0.0001$). Flowers from the Grassland site (low population density) had the most ovules while those at the Transition site had the fewest (Table 1.2). Grassland flowers on average also produced more mature seeds than did flowers at the other two sites ($F = 10.0, P = 0.0001$), resulting in significantly higher fecundity here ($F = 5.40, P = 0.0065$; Table 1.2). The mature seed/ovule ratio was not significantly different between the sites, and ranged from 0.35 to 0.49 (Table 1.2), which was somewhat lower than the average found by Wiens (1984) for all perennial plants.
Seed predation

The number of larvae found in flowers was significantly higher in the Transition site than in either the Grassland or the Mature site \((F = 5.64, P = 0.0045)\), which were not different from each other. However, there were no differences between sites in the actual \((F = 0.05, P = 0.95)\) or proportional (arcsine transformed, \(F = 1.52, P = 0.220\)) amount of seed damage per flower (Table 1.2). When sites were pooled, there were significantly more larvae/flower in 2007 \((\bar{x} = 3.3, SE = 0.43, n=86)\) than in 2008 \((\bar{x} = 0.49, SE = 0.20, n=47; F = 21.70, P = < 0.0001)\).

When all sites and both years are pooled and pre-dispersal loss rates to larvae compared between flowers that bloomed early (January and February) versus later in the spring (March – May), there was a significant difference in larvae per flower \((\bar{x} = 3.59\) for early season blooms and 1.87 for late blooming flowers; \(F = 5.03, P = 0.028\)). There was also a strong significant difference in the proportion (transformed) of seeds damaged \((F = 9.92, P = 0.0023)\) between the two periods, and a nearly significant difference in the actual number of seeds damaged per flower \((F = 3.89, P = 0.052)\), with flowers blooming later in the season having a far greater chance of being infested. Sample sizes were not large enough to compare these differences separately across years.

The mean number of flowers removed by mice in 2007 from flowering adults at the Mature site was 38.8 (SE 10.96), compared to 5.0 (SE 4.4) at the Transition site, and this difference is nearly significant \((F = 8.66, P = 0.055)\). There were no
flowers removed from the Grassland in 2007, and almost none from any site in 2008, even with a much larger sample (Table 1.2).

**Flower Production and Population Density**

Per capita flower production was significantly higher at the Grassland site ($\bar{x} = 225.2$) than at either of the other two sites if all adult plants are considered, ($F = 3.71, P = 0.026$), but not if only flowering adults are included ($F = 1.019, P = 0.364$; Table 1.3). All of the Grassland individuals were flowering, while at the other sites many adults did not produce flowers (Chapter 4). The proportion of flowering/non-flowering adults was similar between the Mature and Transition sites (0.45 and 0.49 respectively), however, the number of non-flowering adults that were over 0.5 meter tall (and usually much taller) was three times greater in the Mature than in the Transition population, meaning that non-flowering adults in the Transition population were probably not yet mature, while those in the Mature population were very mature but mostly unbranched and without flowers (Chapter 4).

There were only 9 individual plants in the Grassland site, so a complete survey was possible. The estimates for flowering and total adults in the Mature population ($8,340 \pm 1,140$ and $18,560 \pm 4,540$ respectively) were each two times greater than the estimates for the Transition population ($4,660 \pm 740$ and $9,440 \pm 1740$). Estimates for the number of seeds produced per square meter was therefore greater in the Mature population than in the Transition population, both with and
without seed losses to mice considered (Table 1.3). However, the proportion of seeds lost to mice was much higher in the Mature than in the Transition population (0.86 versus < 0.1)

**Consumer Abundance**

Trapping in May 2007 (following what should have been the peak of the reproductive period), resulted in only one capture (from 18 trap nights) at both the Mature and Transition sites, and none in the Grassland (Table 1.4). NPS monitoring results for the same period resulted in mouse population density estimates that were the lowest seen at the grassland and shrub monitoring sites in a decade (Chapter 3). In May 2008, NPS grid trapping showed mouse densities in the grassland that were similar to 2007, but densities in the shrub habitat, which is similar in structure to the Mature study site, were substantially higher in 2008 (160/ha compared to 22/ha).

**Seed bank**

There were more *C. gigantea* seeds in the pre-winter seed bank at the Transition than at the Mature site in both 2006 and 2007. The estimated seed bank was 413.0/m² (± 99.0) at the Transition site and 162.3/ m² (± 100.0) at the Mature site in 2007, and 457.3/m² (± 20.6) and 29.5/m² (± 5.4) respectively in 2006 (Table 1.5). No *C. gigantea* seeds ever germinated from the Grassland soil samples, though
this result may be due to sampling design; if soil samples had been collected non-randomly from directly beneath the existing adult plants seeds would likely have been detected, albeit in low numbers.

Discussion

The landscape of San Miguel Island has changed over the last 25 years from one where *C. gigantea* survived only in hidden relict populations, to a mosaic of *C. gigantea* populations with variable growth dynamics. Climate and soil conditions support adult plant persistence at all sites, but important ecological differences exist across sites that affect the strength of factors that limit establishment. The possible connections between two of these factors, seed production and seed predation, and population growth at each site are discussed below.

*Productivity*

Variable reproductive effort between populations, caused by both genetic (Raijmann et al. 1994) and ecological (Herrera 1993) factors, can translate to temporal and spatial differences in growth dynamics within species (Ouborg and van Treuren 1995, Morgan 1998, Parciak 2002). The observation of significantly more ovules/flower in the Grassland population suggests that greater reproductive effort was allocated to seed production in this population than it was in the others (Samson
and Werk 1986, Albert et al. 2001). More ovules were also produced in the Mature than in the Transition population, meaning that plants in both low growth populations allocated more energy to reproduction than did the faster growing population. Prior studies have shown that resources in expanding populations may be allocated to biomass accumulation over reproduction (Fenner and Thompson 2005). Intrinsic differences in reproductive effort in these populations do not relate to growth dynamics, and are less important than ecologic impacts acting on seed populations at later stages.

**Pre-dispersal seed predation – Deer mice**

Vertebrate impacts on seeds varied considerably among populations (Ehrlen 1996, Kolb et al. 2007) and between years. Most importantly, the number of flowers removed by mice was substantially higher in 2007, when every plant examined in the Mature population had a high proportion of flowers removed. In 2008, few cut peduncles were observed in any of the populations despite more intense sampling. The stronger effect of mice on flowers in 2007 was not a result of higher consumer densities, as mouse abundance in 2007 was very low (Chapter 3). Hence, the extreme impact of mice on flowers observed only in the Mature population and only in 2007 is intriguing, and likely due to two related factors of resource availability and habitat structure.
The substantially higher rate of flower removal by mice observed in 2007 corresponded to lower precipitation in that year compared to 2008. From November 2006 through April 2007, total rainfall on SMI was 12.4 cm., much lower than the average of 32.5 cm (1992 – 2008) and the lowest amount recorded since 1993 (Chap. 4). As a result, the abundance of grass measured in the Transition community was the lowest recorded from 2004 – 2007, as was the relative cover of grass (this study). As will be discussed in detail in Chapter 2, exotic annual grass seeds are larger than \textit{C. gigantea} seeds, and provide a greater concentration of food than do most native seeds in Mediterranean systems (DeSimone and Zedler 1999, Howe and Brown 2001). Limited rainfall in 2007 reduced the abundance of grass biomass and seeds, leading to increased pressure by mice on other resources, specifically \textit{C. gigantea} flowers. Rainfall in 2008 was closer to average (25.8 cm), and though grass abundance was not measured, the density and average height of grasses appeared to be substantially higher in the spring of 2008 than in 2007 (personal observation). Mouse impacts on \textit{C. gigantea} were consequently less in 2008, in spite of higher mouse densities that year.

Larvae in flowers may have also provided an alternative and important food source for mice in 2007 (Pearson et al. 2000). Larvae were more abundant at all sites in 2007 than in 2008, and the removal of flowers may in fact have had as much to do with the larval resource as it did with seed availability (Pearson et al. 2000). Given the low numbers of mice in 2007 it seems likely that the intense impact on flowers by
the few mice occupying the Mature habitat resulted both from reduced grass biomass and the substantial larval resources available in *C. gigantea* flowers.

Differences in community structure were likely responsible for greater mouse impacts in the Mature over the Transition population in 2007. Optimal foraging paradigms suggest that mice will spend more time feeding where resources are most abundant (Morris and Davidson 2000), and risk is lowest (Bowers and Dooley, Jr., 1993, Fedriani and Manzaneda 2005). In the Mature population *C. gigantea* plants grow very close together, and branches (with their terminal flowers) nearly always reach across adjacent individuals. Mice can easily traverse this canopy and reach hundreds of flowers without having to descend to the ground (personal observation). While this behavior would be disadvantageous where aerial predators are abundant (Jekanoski and Kaufman 1995), on SMI the primary predator of mice is the island fox, which travels and hunts below the canopy. Owls, primarily barn owls (*Tyto alba*) are present, but were rarely seen by observers in the spring of 2007 (C. Schwemm and C. Drost, personal observations). The structure of the Transition population is quite different, and lower shrub density here results in much more open space between individuals, meaning that mice must travel on the ground to move from one plant to another, a much more risky and less efficient foraging behavior (Manson and Stiles 1998, Orrock et al. 2003).
Pre-dispersal seed predation – insects

There were no significant differences in pre-dispersal seed loss rates to larvae between sites or between years, even though there were many more larvae in flowers in 2007 than in 2008. Across sites and years the percentage of seeds lost to insects averaged 14.3% (Table 1.2), which is less than the loss rate reported by Kolb et al. (2007) for all perennial herbaceous species (23.2%).

Significant differences in larval abundance were observed, however, when flowers sampled in early versus late spring were compared. Flowering plants must adopt strategies that simultaneously attract pollinators and defend against insect herbivores (Brody 1997, Cariveau et al. 2004). For example, English-Loeb and Karban (1992) found that herbivory was reduced when flowering was asynchronous within a population. Flowering in *C. gigantea* occurs across many months, but there is usually an obvious (and brilliant) peak bloom that lasts about three weeks. In 2007 the bloom on SMI lasted for more than a month, and there was always a large proportion of flowers either still in bud or past bloom. Conversely, in 2008 the peak bloom was striking and lasted only a few weeks (Figure 13). This difference in phenology was due to very different weather patterns between the years, and specifically minimal January rainfall in 2007 nested within a year that would turn out to be far below average for total winter rainfall amounts (Chapter 4). As discussed, the higher larval infestation rates association with prolonged flowering in 2007 were also likely responsible for increased flower herbivory by mice that year. Variable
seed production between the populations in 2007 resulted from the interaction of ecological and abiotic factors at each site, but not from intrinsic differences in resource allocation (Ollerton and Lack 1992, Fenner and Thompson 2005).

Seed Bank

The abundance of viable *C. gigantea* seeds in the soil in November and December represents the maximum number of new recruits that can be added to the population in a given year (Ehrlen 1996, Traba et al. 2006), and seed bank differences across populations can translate to distinctive growth dynamics (Hille Ris Lambers et al. 2005, Buisson et al. 2006, Kolb et al. 2007). I was therefore specifically interested in two questions. First, was there a relationship between relative seed bank abundance in each population and population growth, and secondly, if there were, could low seed production or strong plant-herbivore interactions have reduced the seed bank to a level that limited population growth?

The pre-winter seed bank at the Mature site was much smaller than at the Transition site, and there was no measureable seed bank in the Grassland (Table 1.5). Therefore the populations with the lowest growth (Grassland and Mature) did in fact have smaller seed banks than the growing population (Transition). This difference did not, however, correspond to seed production, as the number of seeds produced in the Transition population was in fact only half of that in the Mature population. Instead, weaker negative effects of post-dispersal processes (seed predation) operating in the
Transition population, resulted in greater seed survival leading to a larger seed bank. In the Grassland, post-dispersal processes were not relevant given the absence of a seed resource, and the absence of a seed bank was instead due to the scarcity of adult plants (in spite of high per capita seed production).

Density-related factors operating pre-dispersal may also be important in regulating seed abundance in the Mature population (Ollerton and Lack 1992). As discussed, very high plant density in the Mature population results in many unbranched individuals that produce few flowers. If per capita flower production at the Mature site was equivalent to that of the Transition population, (i.e., branch growth was not constrained by high densities), and post-dispersal seed loss remained constant, the higher number of plants in the Mature population would produce an estimated 541 seeds/m², slightly more than that measured in the Transition population (413/m²). Hence, density-related processes that reduce per capita flower production, in addition to strong post-dispersal impacts, (which may also be density related), are responsible for a reduced seed bank in the Mature population and could further be associated with lower growth here.

Summary

Several conclusions are possible regarding the importance of seed production and pre-dispersal seed predation on C. gigantea dynamics on San Miguel Island. First, though both the Grassland and the Mature populations exhibit low growth and
are subject to identical environmental conditions, ecological processes acting upon early life stages within each are quite different. Fecundity is significantly higher in the Grassland population, resulting from greater ovule and flower production and reduced pre-dispersal seed predation. While very low adult density is a contributing factor to the absence of population growth in the Grassland, this is clearly not a factor in the Mature population. Consequently, neither high fecundity (Grassland) nor high adult densities (Mature) stimulate population growth at these sites. The population with the highest growth rate (Transition) has neither greater reproductive effort nor lower seed loss to insect consumers, and only under some conditions experiences reduced pre-dispersal seed loss to consumers.

Pre-winter seed bank abundance was the only factor measured in this study that when compared between the three populations corresponded to population growth. Seed bank abundance may be affected by pre-dispersal seed predation by mice under some conditions, but these circumstances have less to do with mouse dynamics than with rainfall and the associated availability of alternative foods. These results suggest that while processes that act on *C. gigantea* seeds prior to the onset of rains are related to the set of conditions experienced by each population, these factors may actually have little influence on population growth. Instead, the dynamics of *C. gigantea* appear to be dependent on post-dispersal factors that interact to reduce the seed banks at different rates during the winter, impact germination success, and affect seedling survival. Germination and seedling growth processes are in turn influenced strongly by microsite conditions, and at these stages invasive annual grass density and
precipitation amounts may become more important than consumer or density
dependent effects. Understanding the relative importance of pre- and post-dispersal
limiting factors on *C. gigantea* dynamics will allow managers to focus on addressing
the important factors regulate growth, both to aid in the recovery of this species and
to protect larger island shrub communities.
Table 1.1. Summary of parameters measured for demographic descriptions along with the procedures used.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Method</th>
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<tbody>
<tr>
<td><strong>A. <em>C. gigantea</em> population abundance</strong></td>
<td>Random plot sampling: (mean individuals/m²) * 2000</td>
</tr>
<tr>
<td><strong>B. Per capita flower production</strong></td>
<td>Number of flowers on all adult or flowering plants</td>
</tr>
<tr>
<td><em>Actual seeds removed by insect larvae</em></td>
<td>Number of damaged seeds in late flowers</td>
</tr>
<tr>
<td><em>Percent seeds removed by insect larvae</em></td>
<td>Damaged seeds/all seeds in late flowers</td>
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<tr>
<td><em>Ovules / flower</em></td>
<td>Total number of all seed types from all flowers</td>
</tr>
<tr>
<td><strong>C. Mature seeds/flower</strong></td>
<td>Total number of mature and immature seeds in late flowers</td>
</tr>
<tr>
<td><strong>D. Fecundity (viable seeds / flower)</strong></td>
<td><em>C</em> germination rate (0.19)</td>
</tr>
<tr>
<td><em>Germination rate</em></td>
<td>Seedlings / seeds planted in greenhouse</td>
</tr>
<tr>
<td><strong>E. Per capita flower removal by mice</strong></td>
<td>Average flowers removed / flowering adult</td>
</tr>
<tr>
<td><strong>F. Seeds removed pre-dispersal by deer mice</strong></td>
<td><em>A</em> <em>D</em> <em>E</em></td>
</tr>
<tr>
<td><em>Population seed production</em></td>
<td><em>(A * B * C) – F</em></td>
</tr>
<tr>
<td><em>C. gigantea seeds/ m²</em></td>
<td>*(C. gigantea seedlings/0.113) * 2000</td>
</tr>
<tr>
<td><strong>Mouse Densities</strong></td>
<td>Mark/recapture sampling: 2-night index and density estimates from grid trapping</td>
</tr>
</tbody>
</table>
Table 1.2. T-test comparisons of mean seed production and seed fate per flowerhead for Coreopsis gigantea at three sites on San Miguel Island, 2007-2008. Percent seed damage and seed/ovule ratios were arc-sine-transformed prior to analysis. Results with different superscripts were significantly different between sites at $P = 0.05$.

<table>
<thead>
<tr>
<th></th>
<th>GRASSLAND</th>
<th></th>
<th>TRANSITION</th>
<th></th>
<th>MATURE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{x}$</td>
<td>SE</td>
<td>N</td>
<td>$\bar{x}$</td>
<td>SE</td>
</tr>
<tr>
<td>Ovules / flower</td>
<td>86.9 $^1$</td>
<td>6.36</td>
<td>20</td>
<td>45.2 $^2$</td>
<td>3.56</td>
</tr>
<tr>
<td>Larvae / flower</td>
<td>0.58 $^2$</td>
<td>0.79</td>
<td>19</td>
<td>3.33 $^1$</td>
<td>0.47</td>
</tr>
<tr>
<td>Actual seeds damaged by larvae / flower</td>
<td>5.79 $^1$</td>
<td>3.05</td>
<td>19</td>
<td>6.93 $^1$</td>
<td>1.72</td>
</tr>
<tr>
<td>Percent seeds damaged by larvae / flower</td>
<td>7.37 $^2$</td>
<td>2.96</td>
<td>20</td>
<td>22.59 $^1$</td>
<td>5.9</td>
</tr>
<tr>
<td>Mature seeds / flower</td>
<td>36.5 $^1$</td>
<td>8.31</td>
<td>15</td>
<td>11.0 $^2$</td>
<td>3.42</td>
</tr>
<tr>
<td>Fecundity (viable seeds/flower)</td>
<td>7.64 $^1$</td>
<td>1.20*</td>
<td>15</td>
<td>3.02 $^2$</td>
<td>0.74*</td>
</tr>
<tr>
<td>Mature seeds / ovule</td>
<td>0.49 $^1$</td>
<td>0.08</td>
<td>15</td>
<td>0.35 $^1$</td>
<td>0.05</td>
</tr>
<tr>
<td>Flowers cut by mice / flowering adult - 2007</td>
<td>0.0 $^1$</td>
<td>-</td>
<td>5</td>
<td>5.0 $^1$</td>
<td>4.40</td>
</tr>
<tr>
<td>Flowers cut by mice / flowering adult - 2008</td>
<td>0.0</td>
<td>-</td>
<td>9</td>
<td>0.0</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 1.3. T-test comparisons of per capita flower production and estimated population densities for three study sites on San Miguel Island, 2007-2008. Results with different superscripts were significantly different between sites at $P = 0.05$.

<table>
<thead>
<tr>
<th></th>
<th>GRASSLAND</th>
<th></th>
<th>TRANSITION</th>
<th></th>
<th>MATURE</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\bar{x}$</td>
<td>SE</td>
<td>$N$</td>
<td>$\bar{x}$</td>
<td>SE</td>
<td>$N$</td>
</tr>
<tr>
<td><strong>Flowers / all adults</strong></td>
<td>225.2</td>
<td>35.1</td>
<td>9</td>
<td>84.0</td>
<td>17.0</td>
<td>50</td>
</tr>
<tr>
<td><strong>Flowers / flowering adult (includes mouse cutting)</strong></td>
<td>225.2</td>
<td>57.8</td>
<td>9</td>
<td>139.9</td>
<td>32.2</td>
<td>29</td>
</tr>
<tr>
<td><strong>Adults / m$^{-2}$</strong></td>
<td>0.005</td>
<td>-</td>
<td>-</td>
<td>4.72</td>
<td>0.87</td>
<td>18</td>
</tr>
<tr>
<td><strong>Flowering adults / m$^{-2}$</strong></td>
<td>0.005</td>
<td>-</td>
<td>-</td>
<td>2.33</td>
<td>0.37</td>
<td>18</td>
</tr>
<tr>
<td><strong>All adult abundance</strong></td>
<td>9</td>
<td>-</td>
<td>-</td>
<td>9,440</td>
<td>1,740</td>
<td>-</td>
</tr>
<tr>
<td><strong>Flowering adult abundance</strong></td>
<td>9</td>
<td>-</td>
<td>-</td>
<td>4,660</td>
<td>740</td>
<td>-</td>
</tr>
<tr>
<td><strong>Population seed production / m$^{-2}$</strong></td>
<td>8.6</td>
<td>-</td>
<td>-</td>
<td>949.2</td>
<td>66.1</td>
<td>-</td>
</tr>
<tr>
<td><strong>Seeds / m$^{-2}$, fall 2007, from soil samples</strong></td>
<td>0.0</td>
<td>-</td>
<td>-</td>
<td>413.0</td>
<td>20.6</td>
<td>-</td>
</tr>
</tbody>
</table>

* - actual count
Table 1.4. Capture rates of deer mice in 2006-2008:

Table 1.4a. *C. gigantea* population study sites, November 2006 and May 2007

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Trap Nights</th>
<th>Individuals</th>
<th>Total Captures</th>
<th>Trap Success</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>Nov. 5-7</td>
<td>24</td>
<td>7</td>
<td>7</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>Nov. 29-Dec. 1</td>
<td>36</td>
<td>16</td>
<td>16</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>May 11-12</td>
<td>24</td>
<td>1</td>
<td>1</td>
<td>0.04</td>
</tr>
<tr>
<td>Transition</td>
<td>Nov. 5-7</td>
<td>24</td>
<td>9</td>
<td>11</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>Nov. 29-30</td>
<td>36</td>
<td>18</td>
<td>26</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>May 11-12</td>
<td>12</td>
<td>1</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Mature</td>
<td>Nov. 6-7</td>
<td>24</td>
<td>22</td>
<td>28</td>
<td>1.17</td>
</tr>
<tr>
<td></td>
<td>Nov. 29-30</td>
<td>36</td>
<td>19</td>
<td>22</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>May 11-12</td>
<td>12</td>
<td>1</td>
<td>0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Table 1.4b. NPS Monitoring at two grids, 2006 – 2008

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th>Density Estimate mice/ha</th>
<th>se</th>
</tr>
</thead>
<tbody>
<tr>
<td>Willow Canyon (Grassland)</td>
<td>May 2006</td>
<td>144</td>
<td>32.3</td>
</tr>
<tr>
<td></td>
<td>May 2007</td>
<td>30</td>
<td>13.4</td>
</tr>
<tr>
<td></td>
<td>Nov 2007</td>
<td>82</td>
<td>28.7</td>
</tr>
<tr>
<td></td>
<td>May 2008</td>
<td>41</td>
<td>21.0</td>
</tr>
<tr>
<td>Nidever Canyon (Shrub mix)</td>
<td>May 2006</td>
<td>157</td>
<td>29.1</td>
</tr>
<tr>
<td></td>
<td>Nov 2006</td>
<td>419</td>
<td>72.8</td>
</tr>
<tr>
<td></td>
<td>May 2007</td>
<td>22</td>
<td>16.1</td>
</tr>
<tr>
<td></td>
<td>Nov 2007</td>
<td>152</td>
<td>8.6</td>
</tr>
<tr>
<td></td>
<td>May 2008</td>
<td>160</td>
<td>49.7</td>
</tr>
</tbody>
</table>
Table 1.5. Results of soil sampling for seed bank estimates

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>C. gigantea seed density estimate per m²</th>
<th>C. gigantea seedlings (0.68 m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>Grassland</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Transition</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Mature</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2006</td>
<td>Grassland</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Transition</td>
<td>457.3</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Mature</td>
<td>29.5</td>
<td>2</td>
</tr>
<tr>
<td>2007</td>
<td>Grassland</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Transition</td>
<td>413.0</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>Mature</td>
<td>162.3</td>
<td>11</td>
</tr>
</tbody>
</table>

Figure 1.1 – Exotic annual grass and C. gigantea germination from soil samples at two sites, 2006 and 2007, with SE
CHAPTER 2

Post-dispersal factors limiting regeneration of the native shrub

*Coreopsis gigantea*

Introduction

For flowering plants the transition from seed to seedling is often the least successful stage of the life cycle (Fenner 2000). A viable seed must survive post-dispersal mortality, land in a location that has the physical requisites for germination, survive the tenuous life of a small plant, and ultimately reproduce, to become part of the next generation (Naylor 1985, Fenner and Thompson 2005). Limitations at each of these steps reduce the likelihood of success, and few seeds survive even the first of these stages (Fenner 2000). In response, plant species have adapted by producing many more seeds than will survive, so that a combination of the total number of seeds produced reduced by early stage mortality factors on seeds and seedlings ultimately determines annual reproduction for an individual (Thompson and Grime 1979, Watkinson 1997).

*Coreopsis gigantea* (Asteraceae) is a perennial shrub, restricted in distribution to the California Channel Islands and portions of the Southern California coast (Junak et al. 2007). On the Channel Islands *C. gigantea* populations were severely reduced by grazing and land-use practices during the last 150 years, and much of their historic
distribution remains dominated by exotic annual grasses several decades after grazing ended. Because they are long-lived plants, processes that limit success at early life stages are important regulators of *C. gigantea* dynamics. Prior work showed that up to 40% of *C. gigantea* seeds were removed by pre-dispersal seed predators (Chap. 1), but that pre-dispersal seed predation had little impact in low-growth *C. gigantea* populations where exotic annual grasses dominated. Fecundity was also high in low growth populations, meaning that neither low seed production nor high pre-dispersal seed mortality explained why *C. gigantea* populations have failed to expand into grasslands.

For this portion of the study I used manipulation experiments to examine three factors - seed predation, microhabitat (ground cover), and seed density – that act on seeds post-dispersal to influence germination success. The experiments tested two treatment levels for each factor on seeds introduced at three sites on San Miguel Island (SMI), one of the California Channel Islands. I hypothesized that a higher abundance of exotic annual grasses would correspond to increased seed predation and stronger negative effects of ground cover, but that the effect of seed density on germination would be unrelated to grass abundance, with higher seed densities resulting in greater germination rates at all sites. At the conclusion of the chapter I include a brief discussion of how incorporating the results of these experiments in management and restoration plans might lead to increased population growth for this species and faster regeneration of coastal shrub communities following grazing (Chambers and MacMahon 1994).
Post-dispersal seed predation

Post-dispersal seed predation is a substantial source of seed mortality for many plant populations (Crawley 1983, Hulme 1998, Howe and Brown 2000), in some cases removing the entire seed crop in a given year (Crawley 1997, Fenner and Thompson 2005). Consumer impacts at this stage can be significant but also temporally and spatially variable, even within a single plant population or season (Maron and Simms 2001). Multiple factors of consumer dynamics and behavior (Maron and Simms 2001), plant reproductive characteristics (Fedriani and Monzaneda 2005), habitat (Maron and Kauffman 2006) and environmental conditions (Boyd 1988, Hulme 1998) interact to determine the effects of post-dispersal seed predation.

Post-dispersal seed predators include invertebrates, birds, and small and medium-sized mammals. Of these, rodents have been studied extensively and been shown to have significant impacts at both population and community levels (Crawley 1992, Hulme 1997, Fenner and Thompson 2005). While many studies have looked at the impacts of entire rodent guilds on seed abundance, many studies do not differentiate impacts among individual species (Kelrick 1986, Hulme 1998, Blaney and Kotanen 2001). The genus *Peromyscus* is ubiquitous in distribution and a dietary generalist, (King 1968), and often included in a larger group of small mammal and invertebrate consumers responsible for seed losses (Anderson and MacMahon 2001, Beckage and Clark 2005). When the unique role of *Peromyscus* species as seed
consumers has been studied, results strongly suggest that this genus can have important impacts on plant populations in systems where they are abundant (Mittlebach and Gross 1984, Boyd 1991, Maron and Simms 2001).

Deer mice (*P. maniculatus*) are the only native small mammal on SMI, and are present in high densities in all habitats (50-500/ha; Drost and Fellers 1991, Schwemm and Coonan 1995, Chap. 3). Mice on SMI take a large proportion of *C. gigantea* seeds from the population via pre-dispersal predation (Chap. 1), with the highest proportion of seeds removed where *C. gigantea* is most abundant. Pre-dispersal impacts, which remove seeds directly from flowers, occur in the spring, when mouse densities are lowest (Chap. 3). Mouse populations increase throughout the summer, coincident with the presence of dispersed seeds on the ground. Therefore mouse impacts on the seed population post-dispersal could be expected to be as great or more important than pre-dispersal removal (Sullivan and Sullivan 1982, Cabin et al. 2000). Moreover, seeds in communities with higher densities of seed consumers would be expected to have less likelihood of survival. To quantify the role of mice as post-dispersal seed consumers I introduced seeds into small plots at all three study sites, excluded mice from half of the plots, and compared germination success between the two treatments.
Resource Competition

If viable seeds survive consumers and environmental mortality factors they have the potential to germinate. Germination is the end of seed dormancy, and occurs in response to environmental cues such as changes in temperature, light and/or moisture (Rees 1997, Fenner and Thompson 2005). In addition to ambient factors, seeds must be physically situated where conditions will facilitate root establishment and growth of the new seedling. (The transition from seedling to juvenile is largely physiological [Fenner and Thompson 2005], so for this study the term ‘seedling’ will refer to a young plant throughout the spring of its first growing season.)

The physical and environmental parameters of a seed’s final location are cumulatively termed its microsite. If these conditions facilitate establishment, (i.e., they ‘protect’ the seed from mortality and support germination), the location is also termed a safe site (Fenner and Thompson 2005). Microsite conditions are critical regulating factors for nearly all flowering plants (Barbera et al. 2006), and the likelihood of an individual seed within a population actually arriving at a safe site is extremely low (Naylor 1985). The presence of exotic annual grasses alters microhabitat conditions near the ground, and may substantially reduce the availability of safe sites. In this study I removed the ground cover from half of the treatments at each site to determine the effect of microsite variability on germination and seedling survival.
Seed Density

One strategy adopted by plant species to overcome microsite limitations for both seeds and seedlings is to produce many times more seeds than the number of seedlings required to replace annual losses of adult plants (Barbour et al. 1999). Along with successful dispersal adaptations, high fecundity makes it much more likely that some portion of the seed rain will find safe sites (Crawley 1997). But adaptations of plant species to factors that reduce reproductive success evolved in the absence of human impacts, and factors that now often limit native plant population abundance, such as competitive interactions from invasive species, have occurred too quickly, in an evolutionary sense, for populations to respond (Seabloom et al. 2003). For example, prior work (Chap. 1) showed that *C. gigantea* plants growing at low densities in invasive grasslands did produce more seeds than plants in communities with high adult *C. gigantea* densities, but that this factor did not translate to active recruitment at this site.

To examine whether seedling recruitment is limited by seed supply, two treatments of seed density were used. A significantly greater germination response to higher seed densities would indicate seed limitation as a regulating mechanism, and suggest that restoration programs that included seed addition strategies might overcome this limitation and result in population growth (Seabloom et al. 2003).
I tested the importance of each of these factors on limiting germination by applying a factorial experiment to seeds artificially introduced into the environment at three sites.

Methods

Study Sites

Three sites on San Miguel Island were selected that varied in the relative conditions of alien annual grass abundance and rate of *C. gigantea* growth. The location and vegetation composition of each site were described in Chap. 1; here I provide details on the microsite conditions at each that might affect mouse foraging behavior, seed germination success, or seedling survival. The three sites were identified as ‘Grassland’ (a homogenous invasive annual grass community consisting primarily of *Avena, Bromus, Hordeum* and *Vulpia* species), ‘Transition’ (a community with approximately an equal mix of *C.gigantea* and other native shrubs and annual grasses), and ‘Mature’ (a dense stand of *C. gigantea* with a mostly continuous canopy and open understory largely without grasses).

For a seed to germinate it must be located where environmental conditions support germination. It must also be in contact with the ground so that developing roots can reach the soil before embryonic resources are depleted (Fenner and Thompson 2005). Germination success is thus strongly affected by the ground cover
layer in place at a given microsite. During the period when *C. gigantea* seeds germinate (December – March), the ground at the Grassland site is covered by a thick (1-5 cm) layer of dead grass litter which has accumulated over time. Unlike most mainland systems, few disturbance processes, (e.g., gopher activity, fires) exist within island systems to remove or reduce this layer, or to facilitate the establishment of invading species (D’Antonio 1993).

In contrast, ground cover at the Transition site is much more diverse, with a low-growing vegetation layer that includes small annuals (*Escholzia californica, Gnaphalium* sp.), spreading (*Marah macrocarpus, Carpobrotus chilensis*) and low-growing perennials (*Achillea millefolium, Dudleya greenei*), and exotic annual grasses. While the relative amount of litter cover here was not significantly different that at the Grassland site, the composition was much more diverse and the layer substantially thinner overall (C. Schwemm unpublished data). Demographic sampling of *C. gigantea* (Chap. 4) indicated canopy cover of these shrubs was approximately 30% of the area, and additional shrub species provided additional cover of about 5-10% of the area.

Finally, the sparse ground cover at the Mature site consisted of low-growing native plant species (*E. californica, D. greenei*) and occasionally soil crusts and mosses, but most of the ground surface consisted of exposed mineral soil. The microenvironment here received much less sunlight and was cooler and moister than all other coastal scrub communities on the island. Occasional gaps in the canopy were
created by the death of mature *C. gigantea* plants, and in these spaces plant diversity was greater than below the canopy; these were also generally the only areas within the community where *C. gigantea* recruitment was occurring.

**Experimental design**

A factorial seed-addition experiment utilizing small mouse-proof cages was used to cross three treatments testing mouse accessibility, ground cover, and seed density as limiting factors on seedling recruitment of *C. gigantea*. Cages (30 x 30 x 10 cm) were constructed of small-mesh (1/4 inch) hardware cloth. Each set of eight cages (two levels of mouse accessibility x two levels of ground cover x two seed densities) was replicated 6 times at 10 m intervals along transects centered in each of the 2000 m² study plots described in Chap. 1 (8 cages x 6 replicates = 48 cages at each site). Treatments were assigned randomly to cages within a replicate.

To test for rodent effects, a small opening was cut on one side of half of the cages to allow mouse access (treatment levels of ‘open’ and ‘closed’). The openings allowed mice access to the seeds prior to and during the winter germination period. The cages allowed access by invertebrates but prevented access by ground-feeding birds. To test the effects of ground cover, half of the treatments were hand-cleared prior to seed addition while in the others the ground cover was left in place (treatment levels of ‘cleared’ and ‘uncleared’). Hand clearing the existing vegetation and upper 1-2 cm of soil likely removed most, but certainly not all, of the existing seed bank. To
test whether seed abundance affected seed predation impacts or whether there were density-dependent effects on germination, two seed densities were used (treatment levels of ‘high’ and ‘low’). The densities were selected to span the range of the high limit of the natural seed bank (approx. 670/m²; 60/cage) and what might be used for a restoration seeding application (1500/m²; 135/cage). The total number of seeds broadcast at each replicate was 780, and the total at each site was 4680.

Cages were fixed to the ground in November of 2006, and seeds scattered randomly through the top of the cage. A small amount of adjacent *in situ* soil was used to lightly cover the seeds. Cages were checked three times between January and April, 2007. During each check all *C. gigantea* seedlings were counted and marked with colored toothpicks, and mortality was calculated by subtraction between observations. The abundance of live grasses, litter (dead plant material of any kind), herbaceous species and bare ground in each cage was measured as percent cover and classified from 1 to 5, (1 = 0-20%, 2 = 21-40%, etc.) for analysis. To account for multiple layers, the percent cover described the percent of the area occupied by each cover type, not the percent of total cover. For example live grass could have covered 60-70% of the area, with an underlying herbaceous layer covering 50% of the ground surface. Identifying different cover types was important because I suspected that exotic annual grasses were stronger competitors than native species, so percent cover alone, without cover type, was not a sufficient comparative metric (Eliason and Allen 1997).
Seedling abundance increased from January to February, but after February no additional seedlings were observed and mortality increased. Consequently I used seedling and relative cover counts from February only. Because of the lack of rain all the cages were watered once in January in an attempt to sustain the seedlings, though as will be discussed this effort was unsuccessful and no further watering was conducted after this date.

*Mouse densities* - Mouse population sampling was conducted by the National Park Service in the fall of 2006, prior to seed sowing, and in late spring and fall of 2007. Sampling techniques are described in detail in Chap. 1, and consisted of live trapping along transects at the study sites, and grid trapping in habitats similar to the study sites.

*Seed Bank* - Soil samples were collected from all sites to measure seed bank composition. Details of soil sample collection, greenhouse protocols, and data analysis methods are described in Chap. 1.

*Statistical Analysis* - The fully-crossed 3-factor randomized block design was analyzed using 3-way ANOVA, testing the effects of rodent access, ground cover, and seed density on the proportion of seeds germinated (Gotelli and Ellison, 2004). Response data were arc-sine transformed prior to analysis. To examine the effects of specific ground cover types on germination, the response variable was regressed against categorical variables describing existing live grasses, litter, other herbaceous species (that were not grasses or *C. gigantea*) and bare ground.
Results

*Germination Success*

The effects of each of the treatments - rodent access, ground cover, and seed density - on germination success differed between sites, with an apparent interaction effect between relative density of *C. gigantea* and cover by annual grasses. Where there were more grasses (Grassland and Transition) consumer effects were reduced, and where there was less grass litter (Transition and Mature) the existing ground cover had a positive effect. Seed density had an effect only where grass density was lowest (Mature).

Rodents significantly reduced germination in the Mature population (*F* = 6.53, *P* < 0.0001), had a weaker but significant effect in the Transition population (*F* = 2.07, *P* = 0.045), and had no effect in the Grassland (Table 2.1). Of the 2340 seeds placed in both open and closed treatments at each site, 237 (10%), 208 (9%), and 106 (5%) germinated in the mouse exclosures in the Mature, Transition and Grassland community, respectively, compared to 63 (3%), 140 (6%), and 89 (4%) in the open treatments.

The impacts of ground cover on germination were strongly site dependent (Table 2.1). In the Grassland, the ground cover consisted almost exclusively of thick grass litter, and germination increased significantly when this material was removed (*F* = 37.6, *P* < 0.0001). In contrast, in the Transition and Mature populations, there was a strong but negative effect of removing ground cover. The effect was stronger at
the Mature site, \( F = 6.14, P < 0.0001 \) than at the Transition site \( F = 3.58, P = 0.0009 \), even though there was less material at the Mature site initially.

The results were similar when relative abundance of ground cover was regressed against seedling abundance (Table 2.2). In the grassland there was a strong negative correlation between litter abundance and germination success, and a positive correlation between both herbaceous vegetation and bare ground and germination success. At the Transition site there were positive correlations with litter abundance and live grass, but a negative correlation with bare ground. At the Mature site there was a strong positive correlation with herbaceous cover that was not present in the Transition population, a positive relationship with litter that was also seen at the Transition site, and a strong negative correlation with bare ground.

There was a small positive effect of seed density on germination at the Mature site \( F = 3.11, P = 0.003 \), and no effect at the other sites. Interaction effects explained very little of the additional variation in germination success, except in the Mature population where there was a small negative effect of the interaction of ground clearing and rodent access \( F = 3.29, P = 0.002 \).

*Seedling survival*

Seedling abundance varied between treatments and sites, with a total of 838 seedlings alive across all sites in February. Despite the application of supplemental
water in January equivalent to 1 cm of rainfall, by early April there was nearly 100% mortality of seedlings at both of the Mature and Transition sites, and similar results in the Grassland a few weeks later. Seedling mortality was almost completely due to physiological stress of desiccation, and there was very little if any observed herbivory on live seedlings from either mice or invertebrates.


t

Mouse Densities

Results of mouse population sampling using both index methods and density estimation via grid trapping in the fall of 2006 indicated greater mouse abundance in the shrub habitats than in the grassland (Table 1.4), though populations were high in all cases compared to published estimates from other systems (Chap. 3). Index values of capture success from the study site transects ranged from 0.29 in the Grassland to 1.17 in the Mature site. Values greater than 1.0 mean that there were more captures than there were trap nights, in this case resulting from several instances of multiple captures in one trap at the Mature site during the first November session. This conditions is known as trap saturation, and depending on sampling design, indicates very high population densities in a sampled population (Efford 2004). Results from the grid trapping methods provided more precise population estimates, in this case a value of 419 mice/hectare (SE 72.8) on the NC grid, which is a mixed-shrub habitat, similar in structure to the Transition site (Chap. 3).
Trapping the following spring (May 2007) revealed substantial declines at all sites from fall densities. The life cycle of deer mice on the islands is one where young are born in spring and early summer, and adults rarely survive through the following spring (Chap. 3). Low over-winter survival of deer mice occurred in 2006-2007, and the absence of rain in January, an important period for plant growth, likely reduced mouse reproduction in the spring due to lack of food resources for mice (Ostfeld and Keesing 2000). Consequently, populations estimated at between 400-1000/ha at all sites in the fall of 2006 declined to unusually low densities of < 20/ha in the spring of 2007. Similarly, population estimates from NPS grid trapping were the lowest in a decade. Sampling results along with minimal evidence of mouse activity therefore indicated unusually low mouse densities in the spring of 2007 (Chap. 3).

Discussion

Experimental manipulation of three potential limiting factors revealed significant differences in *C. gigantea* germination rates between sites and between treatments. As hypothesized, in the Grassland the presence of litter and live grass seedlings had a significant negative effect on germination. Surprisingly, mice had no effect in the Grassland, though they were present in relatively high numbers at the start of the winter. At the Transition and Mature sites removing the ground cover had a negative impact on germination success, as did seed predators. These results suggest that in the absence of dominant invasive grasses, microsite conditions support *C. gigantea* recruitment, and native consumers may have a regulating role under some
conditions. Density dependent processes within mature *C. gigantea* populations may also limit survival of seedlings, however, this hypothesis was not tested experimentally. Community interactions within exotic grasslands and shrublands operate very differently to affect *C. gigantea* dynamics.

**Germination Success – Microsite Effects**

Germination success was lower in the Grassland site when the litter layer was left in place compared to when it was removed, while the opposite result occurred at the other two sites. Many studies have demonstrated the negative impacts of an existing grass litter layer on seedling emergence and survival of native species (Williams and Hobbs 1989, Martinez and Fuentes 1993, Eliason and Allen 1997, Maret and Wilson 2005). I suggest that the negative effects of annual grasses on *C. gigantea* were caused by two primary mechanisms: the physical impacts of grass litter that limited resource availability to *C. gigantea* seeds, and biotic competition from grass seeds and seedlings.

**Negative Impacts of Grasses** - The presence of a deep grass litter layer can reduce the availability of both light and water to seeds on the soil surface, reducing seed germination and seedling growth (Fenner and Thompson 2005). Changes in light regimes are often the cue that ends seed dormancy (Fenner and Thompson 2005), and in the presence of thick litter seeds may receive insufficient stimuli. Increased moisture often ends dormancy, and a thick litter layer can impede the transport of
water from the atmosphere to the surface. Because so much of the moisture available to seeds and seedlings on San Miguel Island results from fog drip (Estberg 1996), the presence of thick litter may have a particularly strong negative effect on seeds; fog drip does not have the force of rainfall to move the water through the litter to the soil, so the moisture simply remains on the litter surface, unavailable to seeds, until it evaporates (Corbin et al. 2005). The presence of litter could also influence microsite factors such as temperature, which could be too high or low, or the abundance of seed pathogens or fungi that reduce seed survival (Chambers and MacMahon 1994, Fenner and Thompson 2005). Though the specific mechanisms are unknown, the presence of grass litter in some way alters microsite conditions such that fewer seeds germinate under these conditions than in the absence of a thick litter layer.

In addition to litter effects, the presence of grass seeds at the Grassland site likely had additional negative impacts once grass seeds germinated. Invasive annual grass seeds are larger than *C. gigantea* seeds (and most other seeds in this system), and are capable of more rapid germination and seedling growth in response to rainfall (Eliason and Allen 1997, Corbin et al. 2007). For example, because grass seeds emerge sooner and grow more quickly than do native seeds, grass seedlings are often stronger competitors for available soil moisture (Williams and Hobbs 1989, Martinez and Fuentes 1993, D’Antonio and Vitousek 1992, Coleman and Levine 2007) and may limit light to smaller native seedlings (Williams and Hobbs 1989). As expected the relative cover of live grasses in the spring was significantly higher at the Grassland site than at the other sites, and grass seedlings likely combined with litter
to outcompete *C. gigantea* seeds and seedlings for light, water, and space (Coleman and Levine 2007).

The competitive interactions between exotic annual grasses and native species during early development persist throughout the growing season (Williams and Hobbs 1989, Cione et al. 2002, Coleman and Levine 2007). Due to the sampling interval (3-4 weeks), it is possible that some *C. gigantea* seeds germinated, but were quickly outcompeted and died before they could be counted (Fenner and Thompson 2005). If so, the results of fewer seedlings in the Grassland in uncleared treatments were caused not only by reduced germination, but also perhaps by the death of very small seedlings between sampling periods that were never seen. In this case there would have been higher germination success and lower seedling survival than observed (Chamber and MacMahon 1994).

*Positive Effects of Ground Cover* - In contrast to the negative effect of existing ground cover on germination in the Grassland, in the Mature and Transition sites conditions created by leaving the ground cover in place resulted in higher rates of germination. The layer at these two sites included native annuals, low growing perennials and little or no cover by exotic annual grasses. Any negative effects that the accumulation of litter at the Mature and Transition sites had on either changing the physical environment or producing competing seedlings for *C. gigantea* were apparently less important than the supportive microsite conditions created by the material (Kirkman et al. 2004). Not only were fewer seedlings present in the cleared
treatments, but desiccation effects of low rainfall were noted sooner in the cleared areas than in the uncleared ones.

Interactions between soils and ground cover at each site may also have contributed to differences in seedling survival. Soils at the Grassland site, though not directly measured, had a visibly higher clay content and retained more water, than did the more sandy soils at the Transition and Mature sites. The cleared treatments at all sites dried out more quickly after rains than did the uncleared treatments (personal observation), but the seedlings at the cleared sites in the Grassland survived longer than did seedlings at the sites with sandy, non-clay soils, indicating delayed water stress in the Grassland soils. Soil crusts at the Mature site may also have aided germination in some way, though they were only present in areas where the canopy was very dense.

**Germination Success – Consumer Effects**

In contrast to the Grassland and Transition sites where rodents had no effect, at the Mature site, germination rates were significantly lower when mice had access to seeds. Mouse densities were higher at both the Mature and Transition sites than they were in the Grassland, likely because of the increased cover afforded by shrubs (Phelan and Baker 1992, Nilson 2000, Orrock et al. 2004). Although increased mouse densities likely contributed to reduced germination in the open cages at the Mature site, the absence of alternative food sources may have been more important. This
would explain why the rodent effect was highly significant at the Mature site and much less so at the Transition site (where mouse abundance was also high). Soil samples showed that invasive annual grass seeds were more abundant at the Transition than at the Mature site (Figure 1.1), and they were essentially the only seeds available in the Grassland. Consequently, exotic grass seed abundance was inversely related to the relative strength of seed predation on *C. gigantea*.

Many studies have demonstrated that granivores select seeds based primarily on food value, which is often directly related to seed size (Reichman 1979, Mittelbach and Gross 1984, DeSimone and Zedler 1999, Howe and Brown 2001). A brief field trial conducted within the scope of this study suggested that this is also true for deer mice on the Channel Islands. In 2005 I compared removal rates by mice of *C. gigantea*, *Nasella pulchra* (a native perennial grass), and *Avena barbata* (an exotic annual grass), three plant species that coexist on the islands in deer mouse habitats. Seed sizes ranged from smallest to largest as listed. For three nights I placed similar quantities of each seed type in several replicates in three habitats. On each night the proportion of seeds removed was directly related to size; *A. barbata* was taken most often and *C. gigantea* the least, and these results held across sites similar in structure to those studied on San Miguel (personal observation). So while the larger size of invasive grass seeds affords them ecological advantages (such as faster root growth, discussed above), it also makes them more susceptible to seed predation (Borchert and Jain 1978, Blaney and Kotanen 2001, Celis-Diez et al. 2004, Peters 2007).
In the fall of 2006 when the experimental seeds were introduced on SMI, abundance of both *C. gigantea* and annual grass seeds was higher at the Transition than at the Mature site (Figure 1.1). At the same time mouse densities were estimated to be slightly higher at the Mature site. This condition resulted in greater consumer pressure on the experimental *C. gigantea* seeds at the Mature site compared to the Transition site. The *C. gigantea* seeds in the open cages likely made them easier for mice to find and consume than the ambient seeds (i.e. they were not buried or damaged; Bowers and Dooley Jr. 1993). At the Transition site seeds were still taken, but less often than at the Mature site because other seeds were more less readily available there than at the Transition site.

*Germination success and population dynamics*

To connect early life stage limitations with population growth, observations of treatment responses should be followed by measurements of survival of the treatment cohort through to adult stages (Crawley 1997, Barbour et al. 1999). In spite of supplemental watering, physiological stress on seedlings from low rainfall in late winter 2007 resulted in the death of all seedlings. Because of total recruitment failure at all sites, it was not possible in this study to relate germination rates to any measures of growth past the seedling stage. While this outcome was somewhat unanticipated, it provided important information on *C. gigantea* dynamics at early stages; in some years water limitation at the seedling stage is a much stronger population regulating
factor than anything that acts earlier (Fenner and Thompson 2005, Corbin et al. 2007, Chap. 4).

Site Comparisons

Grassland - Very little recruitment of *C. gigantea* is presently occurring in the Grassland. Results showed that in the Grassland, 1) seed predation did not reduce germination, 2) greater seed densities did not increase germination, and, 3) clearing away the existing litter layer significantly increased germination. These results indicate that safe site limitation caused by competitive effects of exotic annual grass litter had a strong negative effect on annual *C. gigantea* regeneration, and is the most likely explanation for the absence of *C. gigantea* in the grassland (Corbin et al. 2007). Poor microsite conditions are strong limiting factors on germination in many systems (Etherington 1982, Fenner and Thompson 2005, Barbera et al. 2006), and in exotic annual grasslands may be nearly insurmountable obstacles for native seeds.

The absence of seed predator effects in the Grassland countered conclusions from several past studies of island plant ecology suggesting that the high densities of *P. maniculatus* on the Channel Islands are artificially supported by the food resource provided by invasive annual grass seeds (Salas 1990, Murray et al. 1983, Halvorson et al. 1997), resulting in apparent competition (Veech 2001). My results show that larger deer mouse populations are not responsible for the persistence of annual grasslands on the Channel Islands. Not only are mouse populations less abundant in
grasslands, in all cases they appear to prefer grasses over smaller native seeds. Instead I suggest that the islands have always provided optimal habitat for deer mice, and that this generalist species was supported at high levels long before human arrival by abundant food resources, mild climates, and the absence of competition (Schiffman 2007). While mice can consume significant quantities of native seeds, this is a limitation to which *C. gigantea* has adapted, since in the absence of microsite limitations *C. gigantea* populations are stable or increasing even when mouse populations are high, and there is no evidence to suggest that consumers are at present preventing *C. gigantea* range expansion.

Unlike at the other sites, few gaps exist within the litter layer in the Grassland to facilitate germination and seedling growth of native plants (D’Antonio 1993, DeSimone and Zedler 1999). However, the existence of scattered plants within the grassland suggest that recruitment does happen here occasionally, and that there is some set of conditions within which *C. gigantea* seeds can germinate under grassland conditions. The plants in the grassland all appear to be the same age (Chap. 4), indicating that at some point in the past conditions conducive for germination and seedling survival occurred concurrently. By spring 2008 there had been no further regeneration of *C. gigantea* in the Grassland, though the individuals present produce many flowers and are highly fecund (Chap. 1). Cumulatively these observations suggest the episodic but relatively infrequent occurrence of supportive conditions that overcome physical and biotic limitations acting on *C. gigantea* in grasslands.
Transition - Post-dispersal seed predation during the winter slightly reduced germination at the Transition site. A comparison made in Chap. 1 of the proportion of the seed rain lost to post-dispersal processes over the summer also indicated fewer seeds lost during this period at the Transition site than at the Mature site. Microsite limitation was not a factor at the Transition site, likely reflecting increased facilitation of recruitment by established individuals and the importance of microsite diversity to seed survival (van Andel 2005, Barbera et al. 2006).

Overall, I suggest that processes operating in the Transition habitat are more dynamic than those at the other sites. In the Grassland and Mature sites the species that dominate those communities (exotic annual grasses and C. gigantea, respectively), have apparently served to limit plant diversity and promote community stability for some time. In each case the absence of disturbance contributes to maintaining lower plant diversity by preventing the creation of gaps that could potentially allow recruitment of additional (native and invasive) species (Hobbs and Humphries 1995, DeSimone and Zedler 1999). In contrast, the plant community at the Transition site seems to be changing rapidly, as evidenced by the high proportion of young C. gigantea individuals and the presence of adult and juvenile individuals of other native shrub species that are rare at the Mature site and completely absent from the Grassland site.

The observation of C. gigantea population growth at the Transition site, where exotic grasses are abundant (but not dominant) and consumer densities are high,
provides insight on how consumers, climate, and habitat structure may interact to
direct succession of *C. gigantea*-dominated communities. When *C. gigantea* seeds
arrive in grasslands, (via as-yet unidentified means), it appears that they are relatively
safe from seed predation given the availability of exotic grass seeds as an alternative
and preferred consumer resource. Instead it is the availability of gaps in the grass
litter and sufficient rainfall that determines the success of *C. gigantea* germination
and seedling survival. If *C. gigantea* do establish, relative abundance of grasses
should decline as individual shrubs reduce water and light availability for annual
grasses, and as *C. gigantea* individuals mature and reproduce (Cabin et al. 2000,
Barbera et al. 2006). Shrub establishment can also result in greater consumer densities
accompanied by increased seed predation (Gill and Marks 1991). In this case seed
predators could potentially drive this system toward a *C. gigantea*-dominated
community, if, as Howe and Brown (2001) suggest, ‘…plant communities…reflect
what small vertebrates fail to eat…’.

**Mature** - The high proportion of old individuals within the *C. gigantea*
population at the Mature site and the substantial difference in plant morphology
(apparently caused by self-thinning, Chap.1), suggest that this population is at or near
carrying capacity (Crawley 1997). Late successional communities are normally
subject to strong density dependent processes (Barbour et al. 1999), exhibited by high
consumer densities (in response to structural characteristics of a dense shrub
population), and low seedling survival due to light limitations. Both pre- and post-
dispersal seed predation removed many seeds from the Mature population, and the
strongest limiting factor is apparently the negative effect of adult density on recruitment.

Consequently the observation of high seedling production here in both 2007 and 2008 (personal observation) was unexpected. Very few seedlings appear to survive in this population (as evidenced by the absence of young age classes), and the advantage of producing seeds that germinate so easily but rarely survive as seedlings is unclear. One explanation is a strategy that assures seedling resources in the event of a major disturbance, for example a blowdown. Seedling recruitment of shrub species in mature Mediterranean communities is rare, and usually happens on a large scale only when gaps are created by the death of older individuals (Etherington 1982, Parker and Kelly 1989). High production of non-refractory seeds by C. gigantea may have been an adaptation to episodic periodic disturbances and high densities of seed predators on the islands (Barbour et al. 1999).

Summary, and Implications for Coastal Shrub Recovery

In the Grassland minimal recruitment of C. gigantea will likely continue under existing conditions due to microsite limitation and possibly seed limitation. Periodic events combining seed dispersal and high rainfall may overcome obstacles to seedling establishment, but these events are rare. In the Transition population, C. gigantea population growth should continue given good microsite conditions, sufficient rainfall, and the continued moderation of mouse abundance as island fox
are reintroduced to the system (Chap. 3). The Mature population appears stable, and will likely remain so until many of the adult individuals are removed either because of old age, or as a result of disturbance that impacts the population on a large scale. Until that time consumer densities and normal climate conditions should have little impact on population dynamics in the Mature community.

This study showed that regulating mechanisms shift in response to the levels of exotic plant invasion and density dependent processes operating in native plant communities on the Channel Islands. Conditions are supportive of *C. gigantea* germination in the Grassland, as evidenced by high seedling abundance in the experimental treatments where litter was cleared. Conditions here are also sufficient to sustain adult *C. gigantea* individuals that are highly fecund (Chap. 1). Consumers are present but don’t limit recruitment, as shown by the absence of significant differences in germination between treatments open and closed to mice. Consequently the primary factor preventing *C. gigantea* population expansion in the Grassland is the persistent presence of exotic grass litter, and the absence of disturbance processes to remove it.

This information could be applied to conservation and protection efforts of coastal shrub communities where exotic annual grasses are dominant. First, to overcome the strong physical and biotic limitations of annual grasses on native seeds, grass litter must be removed to allow germination and/or seedling growth of native species (George et al. 1992, Seabloom et al. 2005, Corbin et al. 2007). Also, while
management efforts that introduce established individuals to potential sites seem intuitively less risky, (i.e., seeds have been germinated under greenhouse conditions and the resulting seedlings or juveniles are transplanted to island sites), in locations where the logistical challenges of on-site projects are significant, like the Channel Islands, seeding projects may be much more cost and labor effective than planting (Barbera et al. 2006). Results from this study suggest that native seeds that are smaller than grass seeds should be relatively protected from rodent granivores, but an approach that presents a mixture of sterile annual grass seeds (or other large, sterile seeds) and native seeds to the environment might provide the native plants even greater protection (Sullivan and Sullivan 1982, Chambers and MacMahon 1994). If seeds are introduced and some portion of the existing grass layer removed, with normal rainfall this study suggests that germination success for C. gigantea or other native shrubs could be high. Because rainfall is critical to success of planting or seeding efforts, if possible such projects should be conducted only in years when rainfall is forecast to be at least average and if possible above average. Finally, if seedlings survive their first year, studies have shown that established plant survival for native species in grasslands can be high, leading to the beginning of exotic annual grassland conversion (Eliason and Allen 1997, Cione et al. 2002).
Table 2.1. Three-way ANOVA for the effects of rodent access, ground clearing, and variable seed density on germination success. *P* values in bold are significantly different at *P* < 0.05 within habitat type.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>df</th>
<th>Grassland</th>
<th></th>
<th>Transition</th>
<th></th>
<th>Mature</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>F</em></td>
<td><em>P</em></td>
<td><em>F</em></td>
<td><em>P</em></td>
<td><em>F</em></td>
</tr>
<tr>
<td>Rodent Access (A)</td>
<td>1</td>
<td>1.45</td>
<td>0.24</td>
<td>2.07</td>
<td><strong>0.0452</strong></td>
<td>6.53</td>
</tr>
<tr>
<td>Ground Cover (C)</td>
<td>1</td>
<td>37.6</td>
<td>&lt;0.0001</td>
<td>3.58</td>
<td><strong>0.0009</strong></td>
<td>6.14</td>
</tr>
<tr>
<td>Seed Density (S)</td>
<td>1</td>
<td>0.15</td>
<td>0.70</td>
<td>0.48</td>
<td>0.63</td>
<td>3.11</td>
</tr>
<tr>
<td>A x C</td>
<td>1</td>
<td>1.90</td>
<td>0.17</td>
<td>1.59</td>
<td>0.12</td>
<td>3.29</td>
</tr>
<tr>
<td>A x S</td>
<td>1</td>
<td>0.54</td>
<td>0.47</td>
<td>0.22</td>
<td>0.83</td>
<td>1.58</td>
</tr>
<tr>
<td>C x S</td>
<td>1</td>
<td>1.91</td>
<td>0.18</td>
<td>0.62</td>
<td>0.54</td>
<td>1.97</td>
</tr>
<tr>
<td>A x C x S</td>
<td>1</td>
<td>0.25</td>
<td>0.62</td>
<td>1.21</td>
<td>0.23</td>
<td>1.08</td>
</tr>
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</table>
Table 2.2. ANOVA table for regression analysis of live grass, herbaceous vegetation, litter, and bare ground, against proportion germination. *P* values in bold are significant at the 0.05 level.

<table>
<thead>
<tr>
<th></th>
<th>Grassland</th>
<th>Transition</th>
<th>Mature</th>
</tr>
</thead>
<tbody>
<tr>
<td>df</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Regression</td>
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<td>0.011</td>
</tr>
<tr>
<td>Residual</td>
<td>46</td>
<td>0.049</td>
<td>0.035</td>
</tr>
<tr>
<td><strong>Grassland</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>df</td>
<td>1</td>
<td>0.002</td>
<td>0.014</td>
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<tr>
<td>Regression</td>
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<td>4.50</td>
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<tr>
<td>Residual</td>
<td>1.45</td>
<td>0.0142</td>
<td>0.013</td>
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<tr>
<td><strong>Herbaceous Layer</strong></td>
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<tr>
<td>df</td>
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<tr>
<td>Regression</td>
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<td>0.0013</td>
<td>12.28</td>
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<tr>
<td>Residual</td>
<td>0.150</td>
<td>0.0011</td>
<td>0.049</td>
</tr>
<tr>
<td><strong>Litter</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>df</td>
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<td>0.0111</td>
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<td><strong>Bare Ground</strong></td>
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<tr>
<td>df</td>
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<tr>
<td>Regression</td>
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<tr>
<td>Residual</td>
<td>0.121</td>
<td>0.0012</td>
<td>0.043</td>
</tr>
</tbody>
</table>

*P* values in bold are significant at the 0.05 level.
CHAPTER 3

Density Estimation Techniques for Highly Variable Populations of Consumers on San Miguel and Santa Barbara Islands, California

Catherin A. Schwemm, Larissa L. Bailey and Charles A. Drost

Introduction

Techniques for estimating population abundance and density for closed animal populations have been discussed in the literature for many years, particularly for populations and communities of small mammals (Nichols and Pollock 1983, Menkens and Anderson 1988, Boulanger and Krebs 1994, Parmenter et al. 2003, Efford 2004, Hopkins and Kennedy 2004, Conn et al. 2006). These investigations have generally concluded that population estimates based on statistical models of mark-recapture data that incorporate variable capture probabilities (likelihood of detection) are far less biased than count-based indices (Nichols and Pollock 1983, Conn et al. 2004, but see McKelvey and Pearson 2001). Specifically, models that incorporate the influence of individual heterogeneity have performed best in simulations and in studies where true population values are known (Otis et al. 1978, Parmenter et al. 2003). However, many factors that vary between trapping sessions, including capture probabilities, sample size, and average movements of individuals can contribute to the level of bias and precision of abundance and density estimates
for a given dataset, so that the consistent application of one model to a population over time may or may not be justified (Boulanger and Krebs 1994, Slade and Blair 2000).

When sample sizes are small, average measurements of individual animal behavior are insufficient to evaluate capture probabilities (Hammond and Anthony 2006) or effective sample area using statistical models (Menkens and Anderson 1988). In these cases investigators often calculate an index of population abundance from the data (Nichols and Pollock 1983, Slade and Blair 2000, McKelvey and Pearson 2001) that can then be applied to a measurement of area to quantify density. Such indices are usually based only on actual counts of individuals, and are known to be negatively-biased because they do not include any consideration of how many additional animals were present but not detected (Nichols and Pollack 1983, Slade and Blair 2000). Moreover, a valid comparison of indices over time for the same population requires that there be a consistent relationship between the index (however calculated) and the true population measure (McKelvey and Pearson 2001, but see Bart et al. 2004). Because the probability of detection for individual animals varies in space and time due to intrinsic behavioral and extrinsic environmental factors, this condition is likely never met in real populations (Otis et al. 1978, Conn et al. 2006). Yet when the data are inadequate for statistical analysis, investigators are left with limited alternatives, and often choose an index or relative abundance approach (McKelvey and Pearson 2001).
These issues arose in our efforts to describe (via population monitoring) the dynamics of two island populations of deer mice, *Peromyscus maniculatus elusus* on Santa Barbara Island (SBI), and *P. m. streatori* on San Miguel Island (SMI), in Channel Islands National Park, California. These populations are of interest for several reasons. Both populations fluctuate widely, in contrast with most populations of island rodents where dynamics are generally stable (Gliwicz 1980, Drost and Fellers 1991). The absence of land-based predators on SBI results in greater population variability there, and densities can reach levels higher than previously published for the species (over 1000/ha), followed by declines to levels where animals are undetectable during some periods (Drost and Fellers 1991, Schwemm and Coonan 2001, NPS unpublished data). On SMI, the presence of island foxes (*Urocyon littoralis littoralis*) historically moderated mouse populations. However, during the period when foxes were extirpated from the island from 1998 – 2005, numbers of mice fluctuated between higher and lower extremes than when foxes were present, closely mimicking SBI dynamics (Drost et al. in prep).

Understanding the true dynamics of changes in deer mouse populations in relatively simple ecosystems (as are found on these islands) will lead to greater insight into predator regulation of prey populations (Berry 1983). Moreover, because mice are by far the most dominant consumer on the islands, they potentially have significant top-down effects on their resources, which include seeds, plants, and small eggs (Collins et al. 1979, Drost and Fellers 1991, Schwemm
and Martin 2005, Chapters 1 & 2 this study). Finally, long-term observations of
deer mouse dynamics in the absence of interspecific competition will provide
important information regarding the fundamental niche ecology of *P. maniculatus*
(Llewellyn and Jenkins 1987, Morin 1999).

Selecting a consistent analysis method for mark-recapture data from highly
variable populations is problematic (Slade and Blair 2000, McKelvey and Pearson
2001, Parmenter et al. 2003). Using indices in all cases will provide consistency but
most likely an underestimation of real population numbers and variability under
most conditions (Slade and Blair 2000), while models will fail to function in some
instances due to low sample sizes (Skalski and Robson 1992). Suggestions of how
best to address the challenge of sampling highly variable animal populations have
been proposed, however we are not familiar with any published studies applying an
array of analysis techniques to a long-term mark-recapture dataset to compare the
dynamics resulting from each approach, nor do there exist standardized data
analysis methods for monitoring variable small mammal populations via mark-
recapture sampling (Thomas 1996).

For this effort we applied several of the most widely-accepted population
density estimation techniques to our datasets and posed three questions. First, were
there differences in observed population trends when a count-based analysis method
was applied in all cases compared to when estimation models were applied
whenever possible? Examination of the data revealed periodic instances of low
captures where it was obvious that models would fail, and we wanted to investigate whether an approach that utilized indices or enumeration methods in all cases would reveal dynamics different from an approach that primarily incorporated models.

Second, when applying estimators to as many cases as possible, were there any observed differences in overall patterns using consistent versus variable estimators? In many cases mark-recapture data lend themselves reasonably to more than one estimator and the selection of the best estimator can be somewhat subjective (Parmenter et al. 2003). To limit investigator bias over the course of a long-term study, one approach would be always to apply the best-fit model as determined by, for instance, the discriminant function analysis procedure in program CAPTURE (White et al. 1978). This utility is often invoked to select an appropriate estimator for a particular dataset (Hammond and Anthony 2006), however there are equivocal opinions on its reliability. Menkens and Anderson (1985) found in simulations that the correct estimator was selected less than 20% of the time, and Manning et al. (1995) noted that estimator performance varied with population size. To address these potential deficiencies, several studies have recommended the consistent use of the Jackknife (M_k) estimator, both to avoid selecting an inappropriate estimator and to incorporate the individual heterogeneity that likely exists in all animal populations (Manning et al. 1995, Boulanger and Krebs 2000, Davis et al. 2003, Parmenter et al. 2003).
Finally, we investigated whether the nested subgrid (Wilson and Anderson 1985), inverse prediction, and maximum likelihood (Efford 2004) methods (described below) provided comparable density measurements when using the same population estimators. Single-session data analyses for deer mouse populations on the islands have historically utilized the nested-subgrid method (Drost and Fellers 1991, Schwemm and Coonan 2001), however, newer methods may better reveal the true dynamics of this species.

Long-term monitoring of small mammal populations can have many objectives, including providing detailed information on demography and relationships of populations to habitat and environmental conditions (Ernest et al. 2000, Solari et al. 2002, Letnic et al. 2005). In its most basic form population monitoring simply measures changes in abundance at regular intervals over time. While we collected sex and age information as part of the monitoring program (Schwemm and Coonan 2001), the focus of the current effort was to determine how best to quantify the abundance and density of mice (old enough to independently enter a trap) during each sampling event. From this perspective the mechanisms that determine abundance at one point in time are of less interest than the change in abundance across time, (i.e. whether higher survival or increased reproduction caused greater abundance at time B over time A is irrelevant if what we are interested in is the change in the food resource available to predators). Individual density estimates are presented in this study without associated demographic parameters, which will be examined in future analysis (Drost et al. in prep.)
Methods

Santa Barbara Island

Santa Barbara Island (33° 28.5’N, 119° 02.2W) lies centrally within the eight California Channel Islands, and is the eastern- and southernmost of the five islands within Channel Islands National Park. The island is 2.6 km² in size, and ranges in elevation from sea level to 200 m. Rainfall averages 46 cm per year, and day time maximum temperatures during the spring average 19º C (Channel Islands National Park, unpublished data). Exotic grasslands are the most common vegetation community on the island, and likely replaced coastal shrub communities, particularly those dominated by giant coreopsis (Coreopsis gigantea) that once covered much of the island (Halvorson et al. 1988, Junak et al. 1993). In addition to deer mice the island fauna includes only one terrestrial vertebrate, the island night lizard (Xantusia riversiana). Large colonies of nesting seabirds, including brown pelicans (Pelecanus occidentalis), western gulls (Larus occidentalis) and Xantus’s murrelets (Synthliboramphus hypoleucus), cover large portions of the island from December to July, and several pinniped species are resident in coastal areas.

Deer mice on Santa Barbara Island (SBI) exhibit a life history characterized by the initiation of reproduction in the spring, with timing at least partially dependent on the cessation of winter rains and increased temperatures, reproduction throughout the summer, and potentially significant population declines throughout the winter. Sexual maturity can occur as early as six weeks of age, and females can
have up to three litters per year with between three and six pups/litter (Layne 1968, Collins et al. 1979, Drost and Fellers 1991). In the wild *P. maniculatus* on the islands seldom live more than 18 months, however captive individuals have lived upwards of five years (CS personal observation).

Sampling sites for deer mice were selected to monitor population trends in common vegetation types on the islands (Fellers et al. 1988). On SBI the terrace coreopsis (TC) grid is situated in an area dominated by *Coreopsis gigantea* shrubs. These shrub stands typically have a thick canopy about 1.5 to 2.5 meters high, but provide a relatively open understory where grasses and annual herbaceous species are common. *C. gigantea* are semi-succulent and deciduous, so that although the foliage dies back during the dry season (mid-summer to early winter), the stems retain a high moisture content and provide an additional water source in the drought season that mice can use during these periods (CS and CD pers. obs.). The terrace grassland grid (TG) is approximately 150 m distant, located in relatively homogenous habitat strongly dominated by exotic wild oats (*Avena* spp.) and brome grasses (*Bromus* spp.). Plant species composition on both sites has changed little since the beginning of the study, however annual productivity in both areas varies dramatically in response to winter rainfall amounts (Johnson and Rodriguez 2001, NPS unpub. data).
San Miguel Island

San Miguel Island is the furthest west of the Channel Islands, with a climate characterized by persistent northwest winds and prevalent fog. The topography of SMI is more diverse than that of Santa Barbara Island; several small to medium sized valleys radiate from two hills on the central and northwest parts of the island with sloping terraces between them. Two of the largest canyons have perennial water and associated riparian vegetation, but the majority of the island is windswept with low-growing vegetation. Seasonal rainfall (November – April) from 1993 – 2008 averaged 32.5 cm (NPS unpublished data).

Perennial grasslands, coastal scrub vegetation (including *C. gigantea*-dominated communities), and riparian vegetation likely comprised the pre-European landscape of the island (Hochberg et al. 1979). The removal of vegetation by sheep during the peak of grazing (1850 – 1930) caused much of the topsoil to be lost, and eventually sand covered approximately 50-70% of the island (Hochberg et al. 1979). The vegetation on SMI has recovered substantially since the removal of sheep. Common shrub species of *Lupinus albifrons, Coreopsis gigantea*, and *Isocoma menzeseii* dominate coastal scrub communities on the island, but exotic annual grasses and iceplant (*Carpobrotus edulis*) remain abundant at many sites. Faunal diversity on SMI is very similar to that on SBI, with the important addition of island fox (*Urocyon littoralis*) as a top terrestrial carnivore. In addition to foxes and mice, there are two reptiles and one amphibian, and non-native rats (*Rattus*...
rattus, in low numbers). Common raptors include barn owls (*Tyto alba*), short-eared owls (*Asio flammeus*) and northern harriers (*Circus cyaneus*).

Sampling grids for deer mice on SMI are located in three habitat types, *Isocoma* scrub (‘Airstrip’ grid, AS), *Lupinus* scrub (‘Nidever Canyon’ grid, NC), and exotic annual grassland (‘Willow Canyon’ grid, WC). The AS grid is located in habitat characterized by *I. menzeseii* shrubs at low densities (approximately 0.1/m-2) with an understory of exotic annual grasses and iceplant, *Dudleya greenei*, many native and non-native herbaceous annuals, and approximately 10% bare ground. The NC grid is similar in structure, with open areas, invasive species and shrubs, but the dominant shrub is *L. albifrons* at densities of approximately 0.5/m-2. The WC is an homogenous annual grassland without shrub species and with few native herbs (Fellers et al. 1988).

**Sampling Protocols**

Mice were sampled semi-annually on both islands in the spring, (March-May, designated as S) and fall (September-December, F), using 10 x 10 trapping grids with traps spaced 7 meters apart. (On SBI there were 3 occasions when grids were 7 x 7; these sessions are specified in Table 3.1) One medium-sized (12-inch long) Sherman trap (H.B. Sherman Co., Tallahassee, FL) was placed at each location and baited with dry oats. Fingerling ear tags (#1005-1, National Band and Tag Co., Newport, KY) were applied, and animals released at the point of capture.
Traps were checked each morning, closed for the day, and reopened in the evening. The grids were sampled for a minimum of 3 nights. Because of the short time span of the trapping sessions we considered each estimate to be independent and collected from a closed population (Parmenter et al. 1999). All sampling was conducted by the NPS in accordance with the American Society of Mammalogists Guidelines for the Capture, Handling and Care of Mammals (http://www.mammalsociety.org/committees/index.asp).

Capture data were compiled from sampling conducted on SBI from March, 1991 to April, 2008 (n = 55 events), and on SMI from March 1993 to April 2008 (n = 74). We chose to focus on population density as a state variable rather than abundance to address the importance of changes in effective area sampled (Converse 2005), which we suspected were significant. For the statistical analyses, all datasets were analyzed using three estimation methods: the nested subgrid method applied with program CAPTURE (Otis et al. 1978, White et al 1982), and the inverse prediction (IP) and maximum likelihood (ML) methods applied with program DENSITY (Carothers 1979, Pledger and Efford 1998, Efford et al. 2004; www.landcareresearch.co.nz/services/software/density). The nested subgrid (NS) approach simultaneously estimates both population size (\( \hat{N} \)) and the width (\( \hat{W} \)) of a boundary strip about the sampling grid to determine the effective area trapped and thus density, \( \hat{D} = \frac{\hat{N}}{\hat{A}} \) (Otis et al. 1978). \( \hat{N} \) is derived using estimation models, incorporating capture probabilities, and \( \hat{W} \) is calculated as a function of the mean
maximum distance moved (MMDM) of all animals trapped more than once. It is
generally agreed that there is a positive relationship between the number of animals
captured and the likelihood that these methods converge on the true values (White

The inverse prediction (IP) estimation method involves a spatial detection
model for a given trapping grid, and a numerical application for model fitting. This
method is conceptually consistent with distance sampling (Buckland et al. 1993,
Thomas et al. 2002), with a spatial detection function, \( g(\sigma) \), where the probability of
detecting an individual animal is a decreasing function of the distance, \( \sigma \), between
the animal’s home range center and the trap. Inverse prediction estimates three
parameters: density, \( D \), detection probability at the center of an animal’s home
range, \( g(0) \) and \( \sigma \), roughly interpreted as an animal’s home range size. This method
uses 3 closed-population statistics obtained from the data to numerically obtain
estimates of \( D \), \( g(0) \), and \( \sigma \) (Efford et al. 2004). These closed-population statistics
include: population size, \( \hat{N} \), mean detection probability, \( \hat{p} \), and the mean distance
moved between detections of the same individual, \( \bar{d} \) (Efford et al. 2004). The
Maximum Likelihood (ML) method is similar to the IP method, in that it
incorporates spatial distribution of captures, but it further maximizes the likelihood
of possible animal locations using mixture models (Borchers and Efford 2007).

We assumed a Poisson spatial point process, a half-normal detection
function, and set the detector type option to ‘single-live’, all default settings in
program DENSITY. (While it is often assumed that Sherman traps can only sample one animal [Hanski et al. 1994], our experiences contradict this assumption; we often caught 2-3 live animals in one trap, and in one case caught 5 animals in one trap on SMI when densities were extremely high. However, applying the ‘multiple live’ option had little effect on the resulting estimates in these cases, so to maintain consistency we applied the ‘single live’ option only.) In program DENSITY we manually set the initial density value to the estimate provided by CAPTURE. Pledger full-likelihood heterogeneity models (Pledger 2000) were considered for analysis; however, because simulations using capture probabilities and samples sizes similar to ours suggested poor performance with less than 4 sampling occasions, this method was not applied (Conn et al. 2006). We made the assumption of closure for three nights of trapping based on the short trapping period, and further assumed no tag loss during the period.

The most appropriate model and associated recommended estimator selected by the discriminant function model selection procedure in CAPTURE, and the Jackknife estimator, were applied using all methods. (There is currently no goodness-of-fit or model selection procedure within program DENSITY). If the discriminant function suggested a model with both time and individual variation in capture probabilities, Chao’s second coverage estimator was used for model $M_{th}$ in the IP and ML analysis as recommended by Efford et al. (2004). For cases where no estimator was available the Jackknife estimator was applied to all datasets; earlier exploration of a subset of the data (Schwemm and Coonan 2001) revealed that
variation in capture probabilities were most likely due to heterogeneity, and because it has performed well in comparative studies and in studies where the abundance of rodents was known (Manning et al. 1995, Davis et al. 2003, Parmenter et al. 2003, Hammond and Anthony 2006).

We did not attempt to apply estimation methods to data from sessions where the total number of individuals captured was less than 10 (n = 9 events on SBI [16%]; n = 1 on SMI [< 1%]). Because the null model (M_o) likely does not apply to real animal populations (White et al. 1982) when the null estimator was selected we instead applied the next most appropriate model. Finally, for all sampling periods we calculated a naïve density index (McKelvey and Pearson 2001) by dividing the number of unique individuals caught (M_t+1) by the size of the trapping grid (3969 m² [~0.4 ha] for 10 x 10 grid, and 1764 m² for 7 x 7 grids).

Results

Population Dynamics

Santa Barbara Island - All of the methods resulted in patterns of density change reflecting of the extreme variability previously noted in the mouse populations on Santa Barbara Island (Drost and Fellers 1991, Schwemm et al. 2005; Figure 3.1). The highest estimate calculated was 2217/ha for the TC grid in the fall of 1991, using the IP method with the Jackknife estimator, and the lowest (when
Mt+1 > 10), was 3/ha on the TG grid in the spring of 1991, using the NS method with the Jackknife estimator (Table 3.1). Within years, all methods consistently showed spring densities that were either less than or the same as fall densities, except in two years (2002 and 2004) when densities calculated by all methods showed substantial declines from spring to fall in both populations. Among years, peaks were suggested by all methods in the fall seasons of 1991, 1993, 1998, 2001 and 2003, though the magnitude of the peaks differed among years and methods. Very low fall densities, indicating population crashes, were noted in 1995, 1997, 2002, and 2004. The greatest within-year increase was noted by all methods in 1991, when the number of individuals caught on the TC grid increased from 37 in the spring to 331 in the fall. In only 5 cases (3 on the TG grid and 2 on the TC grid) did one or more of the methods provide a value that indicated an upward or downward trend in contrast to that provided by other values.

San Miguel Island – The data collected on San Miguel from 1993 – 2008 captured the dynamics of a prey population responding dramatically to the complete removal of its most important predator (Drost et al. in prep.; Figure 3.2). The highest mouse density estimates were recorded on the NC and AS grids in fall 1998 when island fox populations were declining rapidly. The lowest estimate (when Mt+1 > 10) was 17/ha on the AS grid using the NS method in Spring 2000. Minimum population abundance on SMI apparently does not reach the same low levels as seen on SBI; on SMI the number of instances when fewer than 10 individuals were caught was only 1 (< 2 %), compared to 9 instances on SBI (15
%). The data also show that the response of mouse populations to predator removal was strong in all habitats. All methods showed the highest densities yet recorded for SMI in the fall of 1998 on all grids, and on the WC grid densities increased to even greater levels in the fall of 2001. Unlike SBI there were no instances on SMI where densities declined from spring to fall.

Estimator Selection - The Jackknife estimator was selected approximately 80% of the time by the selection procedure in CAPTURE (Table 3.1). Given the preponderance of this estimator in the dataset, we did not conduct a separate analysis substituting the Jackknife for the selected estimator in the remaining 20% of the datasets.

Method Selection - Models failed to provide a reasonable estimate in approximately 8% of the cases, with the IP method failing most often. We did not attempt to investigate the reasons for individual failures, though plausible causes include inadequate recaptures and non-random distribution of animals across the grid (Efford et al. 2004).

Overall the NS method resulted in the highest density estimates. The IP and ML methods produced very similar results, and there was only one instance where the difference between these two was >100. The index density value generally tracked between the NS and the IP and ML methods, but was often lower than all models on SBI. Differences between estimator and index values were greatest when populations were at peak levels and minimal at very low abundances. In only two
instances (F96 and F98 on the TG grid) did the index provide a density value indicating a trend different than all of the estimation methods (the index suggested a density decline while the estimators indicated an increase). Because differences are greatest when densities are higher, we calculated differences for fall trapping sessions on SMI when data from all methods were available for comparison (Figure 3.3). For all cases where estimates could be calculated by all four methods (n = 82), the NS estimate was highest in 48 % of the cases, the IP in 13%, and the ML in 6%, and the index in 33%.

**Capture probabilities**

Estimated capture probabilities (\( \hat{p} \)) ranged from 0.10 to 0.78 (Table 3.1). The highest average \( \hat{p} \) was on the AS grid (0.48, se = 0.02), and the lowest was on the TG grid (0.35, se = 0.04). The AS and NC grids each had significantly higher capture probabilities than the TG grid (\( P = 0.003 \) and 0.004, respectively), and the WC and TC grids were not significantly different from the others. On both islands \( \hat{p} \) was significantly higher in the spring than in the fall (SBI: \( F = 7.34, P = 0.0094, n = 49 \); SMI: \( F = 28.2, P < 0.0001, n = 74 \)). Of the 16 sessions with the highest \( \hat{p} \) (\( \geq 0.60 \)), 13 occurred in the spring. Estimated capture probabilities were negatively correlated with \( M_{t+1} \) on SMI (\( F = 22.39, P < 0.0001, R^2 = 0.23 \)), but not on SBI (\( F = 0.36, P = 0.54 \)). In some cases capture probabilities correlated with the differences
in estimates provided by each method, suggesting conditions where abundance or behavior may determine the effectiveness of a particular method (Table 3.3).

Discussion

Method selection

When a simple density index was applied to all datasets, a coarse interpretation of general population trends emerged that reasonably suggested periods of population peaks and declines. Using indices to make inferences about comparable changes in population values over time, however, requires that there be a consistent relationship between the calculated index value of interest and the true value (Nichols and Pollock 1983, Slade and Blair 2000, MacKenzie and Kendall 2002), a criterion that was not met with our data (nor likely is in any animal population). Consequently we cannot assume that there is any proportional relationship between these indices and true abundance or density measures in these populations. Indices may serve as a general indicator of high vs. low numbers, but they are a poor choice for understanding details of population dynamics, or for relating small mammal numbers to community function.

Statistical estimation models do incorporate heterogeneity and behavioral variation in capture probabilities and provide what we believe is a much more accurate depiction of true population and density variability. Several studies have
criticized the NS approach (Wilson and Anderson 1985, Parmenter et al. 2003), and do not recommend using it for small mammal density estimation, while other field assessments have shown good agreement between NS and other estimators (Jett and Nichols 1987). The successful use of the NS method depends on adequate sample size and capture probabilities throughout the grid (Jett and Nichols 1987), conditions that were often met with our data, however low captures or spatial inconsistencies likely affected the utility of the method in some cases. For example while the TG grid is homogenous with respect to habitat structure, the TC grid is less so, with a higher density of Coreopsis shrubs on the south portion of the grid. In several instances observers cursorily noted more captures in some portions of a grid over others, and a convenient utility included in program DENSITY that provides a visual representation of capture locations confirmed this observation for several sessions. (We did not attempt to identify the specific cases where spatial heterogeneity may have affected the NS analysis.)

The most striking example of data that were inappropriate for NS analysis was from the fall of 1995 on the TC grid, where 31 individuals were captured with only one recapture, resulting in a capture probability value of 0.03. In this extreme case the NS method was unable to calculate animal movement or effective grid size, even though $M_{t+1}$ was not particularly low. Conversely, heterogeneity caused by spatial access of an individual to a trap and negative bias associated with small sample sizes are automatically down-weighted by IP and ML procedures, and
density estimates could be nearly unbiased despite biased population estimates suggesting that model selection with this method may be less critical (Efford 2004).

Large discrepancies between the estimates provided by different methods for one dataset could usually be explained by a subjective examination of the data. For example the estimates provided for the TG grid in S02 by the IP method were greater by a factor of 3 than those provided by the NS method, resulting in a value for density that was several hundred mice/ha greater than that for the TC grid during the same period. Given historic observations of consistently higher densities on the TC grid, it seemed unlikely that this result represented real differences in population abundance between the sites. Instead, given a relatively large difference in capture probabilities for the populations and selection by CAPTURE of different models for the two datasets, it is more likely that the results represented substantial differences in animal behavior that lead to variable capture results.

Similarly, in the spring of 2007 there was a reasonable number of captures and recaptures on the AS grid, but both the IP and ML methods resulted in unlikely estimates of density. A visual examination of capture locations in DENSITY showed a highly clumped distribution of animals and large travel distances between traps. Consequently the spatial detection models were less applicable and the NS method and the index provided the most realistic density estimates.
Estimator selection

We suggest that the extreme variation in capture probabilities, and the differences in the strengths and mechanisms of the processes that contribute to that variation, argue against the consistent application of a single estimation model to long-term datasets over time. Variable factors that affect mouse abundance, primarily the availability of food resources and levels of predation, likely have significant effects on the behavioral characteristics that underlie capture probabilities and movements, so that capture results represent a changing suite of existing ecological conditions acting on the population at a particular time. For example, in the spring of 2002, owl abundance on SBI was extremely high; on one night more than 12 barn and short-eared owls (*Asio flammeus*) were counted simultaneously at one location (CS personal observation.). While the number of individual mice captured during sampling on the two grids was similar (40 and 44 on the TG and TC grids respectively), the capture probabilities were quite different (0.10 and 0.58). Grassland habitats provide less cover in general than do stands of *Coreopsis*, so we suspect that mice either forage less in the grassland when owls are present, or that very low survival rates during these times actually affect recapture rates. (This condition would clearly nullify the assumption of closure, a possibility that should be pursued further in future studies.) On SMI the absence of foxes almost certainly decreased the perception of risk by mice, a condition that leads to changes in foraging behavior (Orrock in prep.). Analysis that incorporates
behavioral differences within populations is best expressed using model selection procedures and applying models based on population behavior.

Significantly higher capture probabilities in the spring may suggest especially strong effects of trap attraction; food resources in late winter and early spring are generally scarce, and traps containing fresh oats as bait are likely more appealing than at other times when natural food sources are more plentiful. Moreover, because mouse abundance in the spring is generally low, trap saturation effects are negligible. Conversely, reduced capture success during fall trapping suggests related effects of trap saturation and competition on capture potential; higher densities mean more traps are filled more quickly (Hanski et al. 1994). Temporal niche separation may also prevent all animals from foraging each night during a trapping session (Hill 1977). Cumulatively our results illustrate important intraspecific variability in numerical and behavioral factors operating within island deer mouse populations, and the importance of integrating these factors into analysis of monitoring data.

Summary

We suggest that population density analysis methods for mark-recapture data that incorporate temporal changes in animal behavior should be applied whenever possible, but that there will likely be cases within a long-term study when these methods are not appropriate and index values will be required to best quantify
abundance (Parmenter et al. 2003, Bart et al. 2004). This approach is in contrast to that suggested by McKelvey and Pearson (2001) who posit that estimators and indices should not be ‘mixed’ within a study. They rightly assert that this method will result in differential bias, and suggest that one method, either indices or estimators, be applied in all cases, and the decision of which method to use be based on whichever method is applicable to the weakest compared dataset (McKelvey and Pearson 2001). While this approach makes intuitive sense, if we applied it to our mouse populations we would be forced to employ indices in all cases. We suggest that in contrast, the observed variation in abundance and related capture probabilities among sessions persuades us to take advantage of the power of modeling to interpret these dynamics and to acknowledge possible bias when simple estimators or indices are employed for low populations.

Highly variable populations may indicate instability in natural systems, or they may be an important process for sustaining diversity (Laudres et al. 1999). Focused research studies do not always encompass temporal scales large enough to assure detection of the complete range of population values, and long-term monitoring programs remain one of the most valuable tools available for this task (Franklin 1989, Sauer et al. 2003). The goal and utility of long-term population studies lies not only in their ability to document real changes in the dynamics of focal species but to collect data and provide analysis relevant to larger system studies (Brown et al. 2001, Noon 2003, Sauer et al. 2003). To best describe the dynamics of
these populations we determined that a selected estimator applied using the IP or ML method in most cases, and a simple density index applied when numbers are very low, provided an interpretation of the changing dynamics of these two populations in which we had the most confidence.

We suggest that the data presented here also lend themselves to future quantitative analysis that may allow combining data from multiple times or sites to better estimate capture probability, population size, and effective sample size (Converse et al. 2005, Conn et al. 2006). Because mouse dynamics within these island systems are likely indicative of changes in resource condition and possibly predictive of potential impacts by mice on other resources (Ernest et al. 2000, Jaksic et al. 1997), many ongoing and future studies of island ecology would benefit greatly from as accurate a quantification of mouse population trends as we can provide.
### Table 3.1.A - Results of grid trapping and data analysis for mark-recapture sampling of *Peromyscus maniculatus elusus*, Terrace Coreopsis grid (TC), Santa Barbara Island, California, 1989 – 2008

<table>
<thead>
<tr>
<th>Trapping Session</th>
<th>Site</th>
<th>Individuals</th>
<th>Recaptures</th>
<th>Capture probability</th>
<th>Selected estimator</th>
<th>Nested subgrid estimate</th>
<th>Inverse prediction estimate</th>
<th>Maximum likelihood estimate</th>
<th>Index of density/ha</th>
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</thead>
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<td>S91 TC 37</td>
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<td>0.74</td>
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<td>2217</td>
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Table 3.1.B. Results of grid trapping and data analysis for mark-recapture sampling of *P. m. elusus*, Terrace Grassland grid (TG), Santa Barbara Island, California, 1989 – 2008

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Table 3.1.D. Results of grid trapping and data analysis for mark-recapture sampling of *P. m. streatori*, Airstrip grid (AS), San Miguel Island, California, 1993 – 2008

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Table 3.1.E. Results of grid trapping and data analysis for mark-recapture sampling of *P. m. streatori*, Willow Canyon grid (WC), San Miguel Island, California, 1993 – 2008

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Table 3.2. Regressions of estimate differences and capture probabilities, San Miguel and Santa Barbara islands, California.

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Figure 3.1a. Deer mouse densities using four data analysis methods, Terrace Coreopsis grid, Santa Barbara Island

Figure 3.1b. Deer mouse densities using four data analysis methods, Terrace Grassland grid, Santa Barbara Island
Figure 3.2a Deer mouse densities using four data analysis methods, Willow Canyon grid, San Miguel Island

Figure 3.2b. Deer mouse densities using four data analysis methods, Airstrip grid, San Miguel Island
Figure 3.2c. Deer mouse densities using four data analysis methods, Nidever Canyon grid, San Miguel Island
Figure 3.3a. Estimation differences among four methods, Nidever Canyon grid, SMI

Figure 3.3b. Estimation differences among four methods, Willow Canyon grid, SMI

Figure 3.3c. Estimation differences among four methods, Airstrip grid, SMI
CHAPTER 4

Integrated effects of rainfall, consumers and competition on reestablishment and succession of *Coreopsis gigantea* on the California Channel Islands

Introduction

Distributions of plant populations across landscapes result from the interaction of many factors including seed abundance (Eriksson and Jakobsson 1998), seed dispersal (Primack and Miao 2002), competitive and consumer interactions (Huston and Smith 1987), abiotic factors (Dunson and Travis 1991), and density dependence (Antonovics and Levin 1980). Community interactions are also affected by human impacts at landscape scales, including past land uses that have influenced existing community structure and that can affect ecosystem processes far into the future (Fleischner 1994, Bonet 2004, Vellend 2005). Natural succession in particular may be affected if human impacts influence dominant plant species that structure communities (Simberloff 1988). Connecting historic disturbances, such as grazing, with existing plant distributions will aid in understanding active community processes as well as help bolster predictions of future succession (Fleischner 1994).

*Coreopsis gigantea* is a dominant shrub in several coastal scrub communities on the California Channel Islands (Junak et al. 2007). In the absence of tree species on smaller islands, mature stands of *C. gigantea* provide critical habitat for birds and
small vertebrates. Populations of *C. gigantea* were severely impacted by grazing activities that began in the 1860s, to the point that by the 1960s only remnant populations remained in many areas. Following grazing there was substantial recovery of *C. gigantea* in some areas, but in many places *C. gigantea* is absent, and stand replacement by exotic annual grasses and invasion by other non-native species, such as crystalline iceplant (*Mesembryanthemum crystallinum*), has occurred (Halvorson et al. 1988, D’Antonio and Vitousek 1992, Corry 2006).

Mortality factors for established individuals are minimal, and previous investigations suggest that dynamics of *C. gigantea* populations are determined by the interactive effects of consumers, competitors, rainfall, and conspecific inhibition on early life stages (Chapters 1 & 2). This paper has three objectives: 1) summarize long-term consumer and rainfall data to compare trends of these factors to existing *C. gigantea* age structures, 2) compare the relatively small temporal and spatial scale experimental results previously observed in this study on San Miguel Island to Santa Barbara Island, where impacts to *C. gigantea* populations were even more severe (Hulme 1996), and 3) develop management approaches based on these results that will accelerate native shrub community recovery on the Channel Islands.

Identifying the processes that currently facilitate or inhibit growth of *C. gigantea* is important for two reasons. First, reestablishment of *C. gigantea* into many areas within its historic range has been slow or has not occurred at all, even after nearly three decades without direct grazing impacts. Areas where *C. gigantea* is still
absent are largely dominated by invasive species, and human input will be necessary to overcome strong inhibitory processes acting on native species at these sites (Corbin et al. 2007). Understanding limiting processes and ways in which they interact to influence populations of C. gigantea will aid managers working to increase shrub abundance and reduce the influence of invasive species such as exotic annual grasses (Cione et al. 2002).

Secondly, mature stands of C. gigantea appear to represent the climax successional stage in island shrub communities. Very little is known about shrub community processes on the islands prior to grazing, so the future of mature C. gigantea communities is unclear. The majority of mature C. gigantea populations now present on the islands established at the end of the grazing period, approximately 20-25 years ago. The maximum life span of C. gigantea is not known, but is assumed to be less than 30 years (Salas 1990). Consequently, the oldest cohorts of C. gigantea will reach the end of their life span within the next decade, and eventually either disturbance that acts selectively on older individuals (for example high winds) or simple age-driven mortality will create gaps in existing stands within which secondary succession will likely occur.

Many studies have demonstrated that successional dynamics are often determined by the interaction of factors that influence plant establishment immediately following disturbance (Bishop and Schemske 1990, Hulme 1996, Morin 1999, Fagan and Bishop 2000). In shrub communities on the Channel Islands I
suggest that these factors include weather, consumer abundance (in turn influenced by weather and predator abundance), and seed bank dynamics of both native and invasive species. A focused examination of the existing strengths of limiting factors will help predict potential community-assembly processes in *C. gigantea*-dominated ecosystems following disturbance. Understanding *C. gigantea* community dynamics (and maintaining community monitoring programs) will allow managers to determine the likelihood that invasive species will dominate during early succession so that action can be taken if needed to promote the persistence of native species and communities (Ehrenfeld and Toth 1997, Morin 1999, Suding and Gross 2006).

*Santa Barbara and San Miguel Islands*

San Miguel Island was described in detail (Chapter 1). Santa Barbara Island (SBI) is approximately 138 km to the southeast of SMI and is much smaller (2.6 km² vs. 37.7 km²). Vegetation composition on the two islands is similar in many ways, with the majority of each landscape comprised of mixed shrub and exotic annual grassland communities. SMI has a more diverse shrub community than SBI (Johnson and Rodriguez 2001) as well as additional communities, including coastal dune and perennial stream habitats, which SBI lacks. On both islands, grazing and human land-use impacts severely reduced *C. gigantea* abundance; on SMI the primary impacts came from sheep (*Ovis aries*), while on SBI grazing by rabbits (*Oryctolagus cuniculus*) and mechanical removal of *C. gigantea* stands resulted in the loss of nearly
all the *C. gigantea* stands on that island (Philbrick 1972). Consumer diversity is low on both islands, with only one native rodent (*Peromyscus maniculatus*, deer mice), and no large herbivores in either system. Island foxes (*Urocyon littoralis*) are the primary predator of deer mice on SMI but are absent from SBI, where barn owls (*Tyto alba*) strongly influence deer mouse population dynamics (Drost and Fellers 1991).

Methods

*C. gigantea* Demography and Range Expansion

Age distributions were estimated at the Mature and the Transition sites on SMI described in detail in Chapters 1 and 2. The Mature site was situated within a *C. gigantea* population at high density (9.3 m$^2$) with low growth, and the Transition site was in a *C. gigantea* population with moderate densities (4.7 m$^2$) and relatively high growth. Each study site was 2000 m$^2$. Age data were collected in February 2008 by sampling 18, 1-m$^2$ plots along 3 transects at each site (9% of the study area). Six plots were located 10 m apart along each transect, and the transects were also 10 m apart. All *C. gigantea* individuals in each plot were sampled up to a maximum of 15; (total n = 52 at the Transition site and 157 at the Mature site). Plants were aged by counting annual rings produced at the end of each growing season. Rings are present on both the main trunk and on branches, so total age was determined by counting trunk rings to the point of first branching, and then continuing to the end of the longest branch.
The last ring represents the end of the last growing season, so the total number of rings was increased by one to incorporate the present year (in this case 2008).

Four sets of aerial photos (1997, 1994, 1988 and 1983) were examined in an effort to better understand the spatial dynamics of the two populations over the last several decades. Photos were obtained from the National Park Service and scanned at 1200 dpi. The 1997 and 1998 photos were true color and the 1994 and 1983 photos were infrared. ArcGIS (® ESRI, Redlands, CA) was used to register the photos to each other and estimate relative changes in the extent of *C. gigantea* populations. Shrub species could not be identified with certainty based on photo interpretation. Instead, known locations of *C. gigantea* stands were identified on the most recent photos, and the progression of these stands examined in an inverse chronological manner (i.e., determining at what point the stands first established).

*Rainfall*

A greenhouse experiment was conducted to estimate the minimum amount of spring rainfall needed to sustain *C. gigantea* seedlings. Seeds were collected from SMI in early summer 2007, stored in paper envelopes at room temperature, and planted under greenhouse conditions in February 2008. Seeds were planted in a standard 3:1 potting soil/perlite mix, and following germination all surviving seedlings were allowed to grow in the greenhouse for two weeks. Seedlings were then transplanted to growing trays (170 cm²) with 9 seedlings in each tray and placed
outside for the remainder of the experiment. Trays were watered consistently using automatic sprinklers in the greenhouse, and the seedlings allowed to acclimate for 2 more weeks (no additional mortality was noted during the acclimation period). Four trays of seedlings were then randomly assigned to each treatment.

Five watering treatments were applied that encompassed the recorded range of average weekly spring (Feb – Apr) rainfall on SMI between 1992 and 2007 (0.25, 0.65, 1.0, 1.25 and 2.5 cm/week). Depth measurements were converted to volume based on tray area, and this amount of tap water applied as evenly as possible to each tray once per week for 8 weeks. Weekly sampling was conducted to record the number of healthy, stressed, and dead seedlings. Healthy seedlings were completely green, stressed seedlings were either partially brown or wilting, and dead seedlings were completely brown. Seedlings were deemed to have survived if they were alive and without signs of stress. The proportion of surviving seedlings in each treatment was arc-sine transformed, and compared using one-way ANOVA.

Rainfall data for SMI were summarized from weather records collected by the National Park Service. Data are collected daily when personnel are present on the island, and precipitation is recorded at 8:00 am for the previous 24 hours. Prior to 1999 daily records were not always available due to staffing constraints. If a rainfall measure was not available for the last day of a particular month and the first observation of the following month included measurable rainfall, that amount was split between the two months; (i.e. water in the rain gauge in the second month could
have fallen during the last days of the prior month). Consistent monthly totals were available for SMI beginning in mid-1999. Records from SBI were more sporadic due to similar but more severe staffing shortages, and instead, rainfall records from Catalina Island were used. Catalina is approximately 20 km to the east of SBI at the same latitude, and rainfall amounts available on the Catalina Island Conservancy website for the town of Avalon (www.catalinaconservancy.org/ecology/weather/index.htm) were used as a proxy for SBI rainfall. Annual precipitation averages for 1961 – 1990 published online by the Western Regional Climate Center (www.wrcc.dri.edu/precip.html) classify Santa Barbara, Catalina and San Miguel islands in precipitation categories that differ by 5 inches (12.7 cm) annually; Santa Barbara is in the 12.7 cm/year (5 inches) bin and Catalina is in the 25.4 cm (10 inches) bin. The actual averages were not available, but this presentation suggests that over time Santa Barbara receives certainly no more, and probably less precipitation on average than does Catalina.

Consumers

Prior results (Chaps. 1 and 2) indicated that seed predation by mice influenced seed abundance and germination rates, but were inconclusive regarding the existence of a relationship between mouse densities and significant reductions in germination rates or seed bank size. To further explore whether mouse impacts are related to mouse abundance, data on long-term deer mouse dynamics on both SMI and SBI
were summarized and discussed in detail in Chapter 3. For this portion of the study I compared fall mouse abundance with annual *C. gigantea* recruitment (reflected in existing *C. gigantea* age structures) on the assumption that if mouse impacts were related to mouse densities, *C. gigantea* recruitment would be inversely related to the number of mice present in the fall just before germination begins. Results are presented as the average off all grids sampled in each year on the two islands.

Results

*C. gigantea* demography

Very different population histories are reflected in the *C. gigantea* age structures at the two SMI sites (Figure 4.1). At the Mature site the population was highly skewed toward older individuals and 68% of the plants were more than 10 years old. Peak recruitment in the Mature population occurred between 1993 and 1998, but there were individuals at the site prior to that period, and 0.7% of the individuals were over 20 years old. Recruitment appears to have increased again in the last few years, largely in gaps being created by the death of the oldest individuals. At the Transition site only 10% of the individuals were over 10 years old, and none were more than 15 years old. Recruitment at the Transition site peaked between 2002 and 2006, but appears to have declined in the last two years.
Examination of the aerial photos confirmed the period of substantial establishment in the Mature site indicated by the age data (Figure 4.2). From 1983 to 1994, the area remained a relatively consistent mosaic of shrubs and grassland dominated by annual grasses and other herbaceous species. By 1997, much of the area previously dominated by exotic annual grasses had filled in with *C. gigantea*. The dynamics at the Transition site are less clear; shrub density appears to have increased between 1983 and 1994, though the study area itself remained relatively clear of shrubs until recently.

_Rainfall_

All seedlings in all treatments survived the first four weeks (Figure 4.3). By the end of the sixth week less than 20% of the seedlings receiving the lowest amount of water (0.25 cm/week) had survived, and by the following week all of those were dead. From week six to week seven there was a substantial decline in the second-lowest treatment (0.65 cm/week), and from week seven to week eight, an additional decline in both the 1.0 cm/week and the 1.25/cm week treatments.

Survival of the seedlings receiving the highest amount of water (2.5 cm/week) declined significantly from week eight to week nine, however, this result was almost certainly due to root constraint in the growing trays; these individuals were the tallest and had the longest roots (examined at the conclusion of the experiment), and after two months the trays were too shallow to allow further root growth. Transplanting the
seedlings at that point would have added considerable variation to the experiment, so all of the seedlings were left in the trays and the experiment ended at eight weeks. At this point the seedlings were ten weeks old, reflecting the natural period from germination to the onset of summer drought (Jan – April).

Average winter (Nov – April) rainfall from 1993 – 2007 was 32.5 cm on SMI and 17.9 cm on Catalina, and spring (Jan – April) rainfall was 25.6 cm on SMI and 17.9 cm on Catalina (Table 4.1). On SMI there were only four years when the average spring rainfall amount was less than 1.0 cm/week, but on Catalina there were eight years when this was true. The lowest total winter (and spring) rainfall on both islands occurred in 2006-2007, and the highest in 1997-1998.

Consumers

Average fall density estimates for deer mice on SBI and SMI are presented in Figures 3.1 and 3.2 and Table 3.1. Mouse abundance on SMI was historically moderated by island foxes (Urocyon littoralis littoralis), but from about 1996-2005 there were no foxes in the wild and mouse dynamics changed dramatically (for example in the fall of 1998 when densities reached record levels for that island; Drost et al. in prep). Fox reintroductions began in the fall of 2004 with the release of 20 animals, and the population increased to approximately 83 individuals in the spring of 2007 (Coonan 2008). Fall mouse numbers on SMI were the lowest ever recorded in 2007, but this condition was almost certainly due to very low rainfall in the previous
spring and not increased fox densities, which in the spring of 2007 were approximately 2.2/km², still far less than pre-decline densities of approximately 11.6/km² (Coonan 2008). On SBI mouse dynamics were characterized by greater variability than seen on SMI, even when foxes were absent from the SMI system. Densities recorded in the fall of 2003 on SBI (750/ha) are higher than previously published for deer mice. This number is an average of the estimate from two sampling grids, and the individual estimate for the grid located in *C. gigantea* habitat was the higher of the two at over 900/ha (Chapter 3).

There were few clear relationships between high mouse densities in the fall and low annual *C. gigantea* recruitment on SMI. The highest mouse densities were noted in 1998 and 2001, and the effects of those conditions, were they important, would have been noted in lower plant recruitment in 1999 and 2002. In 1999 establishment at the Mature site was lower than it had been for several years, which may have resulted from high seed predation, but recruitment at the Transition site that year was higher than the previous year. In 2002 recruitment at the Transition site was very high, and though it was relatively low at the Mature site was higher than the previous year and could have been related to abnormally low rainfall that year. The lowest recruitment year at both sites was 2001, when fall mouse numbers (in 2000) were about average.
Discussion

Population size and extent of *C. gigantea* have varied across the Channel Islands following the cessation of grazing, but overall have increased more on SMI than on SBI (Corry 2006). The comparison of short-term, single-system experiments with long-term trends of possible regulating factors clarifies the impacts of rainfall and consumers, and presents additional information on the processes operating in *C. gigantea* communities on both islands.

Rainfall had strong effects on seedling survival under field conditions during the period of this study. Nearly 100% of the *C. gigantea* seedlings produced during the winter of 2006-2007 died in the spring due to rainfall levels that were far below normal. Results from greenhouse experiments and an examination of the age structure data, though, suggest that *C. gigantea* seedlings are adapted to survive spring rainfall amounts substantially lower than recent averages. For example the lowest recorded rainfall on SMI since 1993 was in 2001-2002, when only 20.4 cm of rain fall over the entire winter, and only 4.5 cm of that fell between January and April (Figure 4.4). Age data, however, show that recruitment at the Transition site in the spring of 2002 was very high. Data also show that there was recruitment in the Mature population in the spring of 2007, the second lowest rainfall year observed during the study.

These results suggest that instead of total rainfall, it may instead be the distribution of rainfall throughout the growing season, that most influences seedling survival. In the greenhouse experiments, individuals receiving the most water were
taller and had longer roots at the end of the trials (unpublished data), while
individuals receiving less water were smaller in size but still survived for many
weeks. The lowest recruitment suggested by the age data (after the Transition
population became established) for both populations occurred in 2001. In that year
rainfall decreased from 12.5 cm in March to 1.5 cm in April. Likewise the absence of
recruitment in the Mature population in 2004 was accompanied by a drop in rainfall
from 12.1 cm in February to 0.0 cm in April.

*C. gigantea* seedlings apparently respond to higher rainfall with increased
growth, but larger individuals may not be able to sustain themselves if rainfall levels
decline significantly as spring progresses. Alternatively, seedlings may be able to
establish even if rainfall amounts are low, as long as the roots have consistent access
to soil moisture until they reach some required, (but at present unknown), depth
(Wilson and Witkowski 2002). Future studies should examine the importance of the
timing of rainfall throughout the germination and seedling establishment periods as
well as rainfall and temperature interactions as important factors for *C. gigantea*
seedling survival and annual establishment rates.

The effects of consumers on annual recruitment are more difficult to interpret.
There was no obvious relationship between deer mouse densities in the fall and *C.
gigantea* age structure on SMI, as would be expected if mouse impacts previously
observed at early stages (Chaps. 1 and 2) were a primary factor acting on *C. gigantea*
populations (Crawley 2000). Mice may have few impacts on *C. gigantea* populations
during early succession when seed diversity is high and there are presumably more
larger-seeded species available (Blaney and Kotanen 2001), but their influence likely
increases as above-ground plant and seed diversity declines and *C. gigantea* becomes
dominant (Hulme 1996). At present it does not appear that deer mice on SMI
influence *C. gigantea* dynamics, though they do impart short-term and local impacts
on seed abundance and germination under some conditions (Chaps. 1 and 2). In the
absence of *C. gigantea* population age data coincident with mouse abundance data for
SBI, no similar conclusions can be drawn for the SBI system. If deer mice have
effects on *C. gigantea* recovery they would almost certainly be noted on SBI where
mouse densities reach such high levels (Schmitz et al. 2000, Ekerholm et al. 2004),
and efforts to collect present-day *C. gigantea* age data on SBI would be very
worthwhile.

Facilitation by existing shrubs and microsite characteristics may in fact be the
most important processes affecting *C. gigantea* establishment (Armesto and Pickett
1986, Callaway 1995, Pugnaier et al. 1996). Experimental data (Chap. 2) showed that
the existing ground cover at both the Transition and Mature sites support germination.
Also, observed recruitment at the Mature site is occurring in areas where mature
individuals have died and are now a component of the ground cover (Peterson and
Haines 2001). Decomposition of adult individuals leads to microsites that are micro-
topographically diverse and likely protect seedlings in several ways (reduce wind,
retain moisture) while allowing sunlight to reach the surface. Many studies have
demonstrated the importance of safe-site facilitation on seedling survival (Peterson
and Haines 2001, Jones and del Moral 2005), and this factor may be especially important in summer drought ecosystems where seedlings must establish quickly (Williams and Hobbs 1989). Microsite limitation on SBI due to lower shrub diversity (Johnson and Rodriguez 1991, Corry 2006) and drier conditions at the surface may be important reason why *C. gigantea* populations on SBI have recovered more slowly.

Finally, extensive seabird nesting colonies on SBI may be an additional factor that reduces *C. gigantea* recruitment there (Maesako 1999). Colonies of western gulls (*Larus occidentalis*) and California brown pelicans (*Pelecanus occidentalis*) cover nearly 50% of the island from late winter until late summer. Pelicans in particular have enormous physical impacts on vegetation, and at the end of the nesting season many acres of the island are covered with old nests, guano, and food material. Impacts from seabirds on the island have been increasing steadily for several decades as pelican populations have increased, and it is highly unlikely that *C. gigantea* seedlings survive such impacts. The relationship between increased seabird populations and shrub recovery on SBI is worth further study.

**Succession**

The age structures of mature *C. gigantea* communities on both SBI (Salas 1991) and SMI indicates that many populations will experience high mortality in the next decade, either from senescence of old individuals or from disturbance. The timing and severity of such events could have substantial impacts on the dynamics of
future succession for several reasons (Hulme 1996). Studies have shown that the composition of seed banks following disturbance is an important factor determining species assembly during early succession (Collins et al. 1995, Morin 1999). There is a relatively low *C. gigantea* seed bank at the Mature site on SMI due to post-dispersal seed predation (Chap. 2), but seed species diversity there is high (unpublished results). The comparative response of seeds within the seed bank to disturbance will depend on which species germinate most quickly and establish most successfully, plant traits that reflect species adaptations to such factors as rainfall, temperature, and competition (van Breugel et al. 2007). Consumer abundance levels at the time may also act on the seed bank, though the strength and direction of such impacts are difficult to predict.

**Implications for shrubland restoration and protection**

I suggest that existing conditions relating to *C. gigantea* and native shrub community dynamics on the Channel Islands present two challenges for resource managers: anticipating community responses to future disturbance and designing actions to guide succession away from trajectories that lead to further establishment of exotic species, and immediately overcoming limitations that prevent shrub reestablishment in exotic annual grasslands.

The future of the existing climax *C. gigantea* communities on Santa Barbara and San Miguel islands is unclear. The large majority of plants that comprise mature
populations will reach the end of their life soon, but there is no existing record of how island ecosystems respond to the large scale loss of *C. gigantea* communities. Exotic species remain dominant in many areas on SMI and SBI, both in the existing vegetation and in the seed bank.

I suggest that a proactive approach be adopted by managers before mature stands are lost that would incorporate results from this study to assure that post-disturbance processes are determined as much as possible by native rather than invasive species dynamics. Such an approach would include: 1) collecting seed bank samples within stands coincident with monitoring so that when disturbance occurs the existing the relative abundance of invasive seeds will be known (Chap. 1); 2) establishing 2-4 vegetation monitoring sites within mature *C. gigantea* stands to collect data prior to, during, and after large scale mortality events to determine temporal and habitat differences in germination and survival rates (Chap. 2); 3) continued monitoring of deer mice to assess possible impacts of seed predation (Chaps. 2 and 3); and 4) ongoing collection of seed from native species adjacent to the site that could be applied quickly during the winter following disturbance if the seed bank indicates high abundance of exotic annual grasses, iceplant, or other invasive species that would impart strong competitive pressures (Chap. 2).

To overcome the strong physical and biotic limitations of annual grasslands, management efforts aimed at active shrub restoration will need to address both *C. gigantea* seed limitation and competitive effects of grasses on shrub germination and
seedling survival (George et al. 1992, Corbin et al. 2007). In such circumstances an approach that transplants established native seedlings may seem intuitively less risky because the young plants have already been ‘assisted’ though their least survivable stages. In locations where the logistical challenges of on-site projects are significant, though, like the Channel Islands, seeding projects may ultimately be much more cost and labor effective than planting (Eliason and Allen 1997, Cione et al. 2002). Results from this study suggest that in the presence of annual grass seeds smaller native seeds should be relatively protected from rodent granivores. An approach that presents a mixture of sterile annual grass seeds (or other large, sterile seeds) and native seeds to the environment, however, might provide native seeds even greater protection (Sullivan and Sullivan 1982). Also, clearing the site of grass litter prior to seed amendment will be necessary to overcome competitive effects of grass litter and seeds, but this activity does not require complete removal of the seed bank, and hand-clearing alone will have significant positive effects (Eliason and Allen 1997, Bakker et al. 2003, this study).

Restoration applications developed on islands, especially protected ones where fewer human-derived impacts might affect the outcome or confound the resulting data, have great potential to provide information transferable to more complex systems (Wardle 2002). With this in mind, and incorporating results from this study, I suggest the following protocol for a management project on Santa Barbara Island to increase abundance of coastal shrub species:
1. Collect seed from shrub species of concern (or management value) for several years prior to project initiation

2. Conduct viability trials (minimal time and personnel required to determine dormancy and viability of seed cohorts)

3. Acquire funding, but with scheduling conditional on winter rain forecasts for 5 years forward

4. Select sites within grasslands, (possibly away from other habitat edges), and if possible hand-remove grasses in those areas prior to seed set in the spring. (This will be challenging, but could be done for several years with minimal volunteer input.)

5. Decide in late fall whether to proceed based on weather predictions, and possibly mouse densities. (Regular vertebrate monitoring should be conducted, and if mouse populations are extremely high, consider postponing.)

6. Hand-clear the site prior to seed broadcast. Include sterile annual grass seed or other large-seeded species to reduce mouse impacts on native seeds

7. Establish a monitoring protocol

8. Broadcast by hand in early winter. Monitor results, but given logistical realities frequent monitoring isn’t necessary

9. Consider volunteer weeding efforts in early spring

10. Supplemental watering is extremely labor-intensive and probably will be insufficient regardless, so consider alternatives if rainfall is low (e.g. a second year of seeding)
Table 4.1. Annual rainfall, San Miguel and Catalina Islands (cm)

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<th>Rainfall Year</th>
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Figure 4.1. Histogram of *C. gigantea* population age structures at two sites on San Miguel Island.
Figure 4.2. Expansion of *C. gigantea* at two sites, San Miguel Island

Figure 4.2a. Mature site, 1997

Figure 4.2b. Mature site, 1994
Figure 4.2c. Mature site, 1988

Figure 4.2d. Transition site, 1997
Figure 4.2e, Transition site, 1994

Figure 4.2f, Transition site, 1988
Figure 4.3. Survival of *C. gigantea* seedlings in response to watering treatments

Figure 4.4. Winter and spring rainfall, San Miguel and Catalina Islands
Figure 4.5. Population densities of deer mice on San Miguel and Santa Barbara
REFERENCES


