EVALUATING SUSTAINABILITY OF ENDANGERED SPECIES VIA SIMULATION: A CASE STUDY OF THE ATTWATER'S PRAIRIE CHICKEN *(TYMPANUCHUS CUPIDO ATTWATERI)*

A Dissertation

by

TULIA I. DEFEX CUERVO

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2008

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

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ABSTRACT

Evaluating Sustainability of Endangered Species via Simulation: A Case Study of the Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*).

(December 2008)

Tulia I. Defex Cuervo, D.V.M, La Salle University;

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Dr. Roel R. Lopez

Once abundant in the Texas and Louisiana coastal prairie, currently the Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*, APC) is close to extinction. Efforts to increase the size of the remaining populations at the Attwater Prairie Chicken National Wildlife Refuge (APCNWR) and the Galveston Bay Prairie Preserve (GBPP) with releases of captive-reared individuals are part of the APC captive- breeding initiative. However, after a decade of yearly releases, the populations are not reaching viable sizes.

I analyzed post-release survival data of individuals released at the APCNWR from 1996 to 2005. Results suggest that age at release or date of release had little influence on survival of captive-breed APC. At two weeks post-release, survival estimates (SE) were 0.76 (0.03) for females and 0.82 (0.04) for males. Approximately 50% of the females and 33% of the males died within the first 60 days post-release.

Survivorship during the breeding season showed that male survival (0.36) was higher than female survival (0.23). Survivorship from the median release date to beginning of the breeding season was 52% for males and 39% for females. Mean female survival was 155 days, while median survival was 94 days. For males, mean survival was 135 days and the median was 81 days.

Results from a stochastic simulation model, which was developed based on the survival analysis of APC on the APCNWR, confirmed that releasing individuals closer to the beginning of the breeding season and sex ratio at release had little effect on population growth. Regardless of the number of individuals released annually, population sizes immediately prior to the release dates were only 11–12% of the population sizes immediately after the release dates. At current mortality rates, simulated APC populations could not sustain themselves even if reproductive parameters were increased to the maximum rates reported for APC, or to the maximum rates reported for the closely related Greater prairie chicken. Based on these results, the APC may face extinction within the next decade unless conservation efforts succeed on increasing reproductive success and greatly reducing mortality rates.

ACKNOWLEDGMENTS

This has been a fantastic journey and as every chapter in my life, it would not be the same without many amazing people with whom I shared laughs and dreams, silliness and frustrations, and much more from the beautiful simplicity of the day to day; to all of them my most sincere appreciation and love.

My committee members played a major role in making this time very satisfyingly productive: Bill Grant, Roel Lopez, Robert Coulson, and Dough Loh. Thanks to all of them for always being available for me, for countless hours of brain-storming and work, and for being brilliant and modest at the same time. Thanks also to Bret Collier for making the survival analyses a reality, and to Dr. N. Silvy for his precious expertise and advice. Thanks to my main sources of funding, three years from the U.S. National Park Service and one year from the U.S. Fish and Wildlife Service. I meet lovely people during these years, Maria Tchakerian, Lilly Sanchez, Dr. Robert Stanton, etc, thanks to all of them for their invaluable friendship. Thanks to my lab mates and friends from College Station, the ones that are still around and the ones that already left, including the Aggiñoles clan. Special thanks to Todd S. for priceless advice and making this trip a lot more fun with his inimitable combination of good sense of humor and bad jokes. Thanks also to Dusty D. and Abraham H. for coming into my life at the perfect moment. Thanks to my dear friends in Colombia and Houston for their encouragement and contagious optimism. Lastly, my deepest appreciation is to my family for their love, cheerfulness, inspiration, and for walking every step with me as always has been.

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CHAPTER I

INTRODUCTION

1.1 CONSERVATION EFFORTS

In many cases, severe declines in species abundance and distribution have required that conservation projects apply drastic measures to increase the probability of species survival. These measures may include *ex-situ* (= off-site) conservation, involving captive breeding, gene banks, zoos, and aquaria (Primack, R., 2000), *in-situ* (= on-site) conservation, including the establishment and management of protected areas (Primack, R., 2000; Soulé, 1991). One of the most common components of conservation projects involving captive breeding programs are translocation of individuals (Tenhumberg et al., 2004). Translocations are defined as the intentional release of individuals into the wild to establish, reestablish, or augment a population (Griffith et al., 1989; Snyder et al., 1999; Tenhumberg et al., 2004), and can include movement of wild animals among natural populations or into captive populations (capture or collection), and / or movement of captive animals into wild populations (reintroduction or release) (Tenhumberg et al., 2004).

The majority of recovery plans for endangered species in the United States have identified re-introductions as part of specific tasks to recover species to a stage where they can be down listed from endangered to threatened or removed from threatened

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This dissertation follows the style of Ecological Modelling.

status (delisted) (Tear et al., 1993). However, only a small number of all attempts at reintroductions in the United States have been successful (Beck et al., 1994; Earnhardt, 1999). Frequently, information that can enlighten the causes for failure of these projects is not well documented. Failure to document procedures, monitor released animals (Beck et al., 1994; Ostermann et al., 2001), and publish findings in easily-accessible sources of literature (Scott and Carpenter, 1987; Griffith et al., 1989; Beck et al., 1994; Sarrazin and Barbault, 1996), in addition to political, social, and economic biases (Tear et al., 1993), are common.

A successful reintroduction has been defined as the establishment of a self sustainable population (Griffith et al., 1989; Kleiman et al., 1994; Ebenhard, 1995), and as indicated by the World Conservation Union (IUCN) in 1987, these efforts are aimed at enhancing the long-term survival of a species in an ecosystem and maintaining and/or restoring natural biodiversity. For conservation efforts that include the release of individuals, it is paramount to evaluate post-release factors to determine whether criteria for success have been attained (Stanley Price, 1991). In fact, the ultimate goal of a species recovery plan is "to restore the listed species to a point where they are viable, self-sustaining components of their ecosystem" (U.S. Fish and Wildlife Service, 1990).

Since translocations are expensive enterprises in terms of funds, time and human involvement (Clark et al., 2002), it is imperative to take into consideration multiple factors that maximize the chances of success. Rout et al., (2007), summarized several key factors previously identified that influence the establishing of self-sustaining populations, including (1) the number of individuals released (Griffith et al., 1989;

Veltman et al., 1996; Wolf et al., 1996, 1998; Fisher and Lindenmayer, 2000; Matson et al., 2004), (2) the habitat quality of the release area (Griffith et al., 1989; Wolf et al., 1996, 1998), (3) the duration of the translocation project (Griffith et al., 1989), (4) the location of the release area in relation to the historical range of the species (Griffith et al., 1989; Wolf et al., 1996, 1998), (5) the type of the source population used (Griffith et al., 1989; Wolf et al., 1996; Fisher and Lindenmayer, 2000), (6) the diet and reproductive traits of the species (Griffith et al., 1989; Wolf et al., 1996, 1998), and (7) persistence or removal of the original cause of decline (Fisher and Lindenmayer, 2000).

Indeed, there has been tangible emphasis on the use of simulation models to determine the optimal number of released individuals to reach the establishment of a viable population (World Conservation Union, 1987, 1998; Tenhumberg et al., 2004), and to evaluate the possible effect of alternative translocation strategies (Haig et al., 1993; Lubow, 1996; Haight et al., 2000). Thus, including some of the aforementioned factors, I examined through the use of a quantitative simulation model, several releases strategies varying the number of individuals released, reproductive traits of the endangered Attwater's prairie chicken, and mortality rates.

1.2 ATTWATER'S PRAIRIE CHICKEN

1.2.1 SPECIES BACKGROUND

Throughout North America, populations of endemic prairie grouse (*Tympanuchus spp.*) have undergone large decreases in size since the early 20th century (Peterson et al., 1998; Silvy and Hagen, 2004). The strict habitat requirements of these species, coupled with the rapid urbanization and the resulting habitat loss during the latter half of the last century, have been identified as the main factors for these declines. One of these species, the Attwater's prairie chicken (*Tympanuchus cupido attwateri,* APC), a close relative of the extinct Heath hen (*T. c. cupido*) and the vulnerable Greater prairie-chicken (*T. c. pinnatus*), is currently one of the most endangered species in the United States (Lockwood et al., 2005*a*).

1.2.2 Brief Life History

The APC is a non-migratory medium-sized grouse with a mean weight of 745 and 982 g for females and males, respectively (Lehmann, 1941; Peterson, 1994). Generation time previously reported for prairie chickens is about 2 years (Bellinger et al., 2003). APC are lek-breeding species that use communal display areas known as booming grounds. Booming grounds are crucial for their breeding (Hamerstrom et al., 1957; Toepfer, 2003) and usually vary in size from approximately one-eighth an acre to several acres (Jurries, 1979). A typical booming season starts in late January to early February and ends by the third week in May (Lehmann, 1941; Jurries, 1979). Breeding behavior is typically initiated with males gathering and displaying at the booming ground throughout the morning and afternoon to attract females (Schwartz, 1945). Males exhibit a characteristic booming behavior which mainly consists of strong vocalizations, snapping of their tails, and inflation of air sacs, and females choose their mates based on the male's display ability. After mating, females move to establish the nest within one mile of the booming ground (Lehmann, 1941; Horckel, 1979), and in cases where the first nest is unsuccessful a re-nesting attempt will occur. Once the chicks hatch, they remain with the mother until brood breakup occurs at approximately 12 weeks of age (Peterson and Silvy, 1996).

1.2.3 DISTRIBUTION AND ABUNDANCE

Historically, the APC inhabited the coastal prairies of Texas and Louisiana, with estimated abundances reaching approximately 1 million individuals on an estimated 2.4 million hectares (ha) prior to European settlement (Lehmann, 1941; Peterson, 1994; Morrow et al., 2004; Silvy et al., 2004). However, populations of APC have steadily declined in numbers since 1935 reaching critical levels (Lehmann, 1941; Peterson et al., 1998; Silvy et al., 2004). APC decline is mainly due to habitat lost and fragmentation (Lawrence and Silvy, 1980; Morrow et al., 1996; Morrow et al., 2004; Silvy et al., 2004), and it has been estimated that less than 1% of coastal prairie ecosystem remains (Smeins et al., 1991). As a result of both range-wide depletion of habitat and critically low numbers on the populations, the APC was one of the first species to be listed as federally endangered under The Endangered Species Conservation Act of 1966, when its numbers were approximately 1,070 individuals throughout its entire range (Lawrence and Silvy, 1980; Morrow et al., 2004).

Currently, there are less than fifty (50) free-ranging individuals remaining in two isolated populations (Fig. 1.1) (Preisser and Yelin, 1999; Silvy et al., 1999; Morrow et al., 2004).

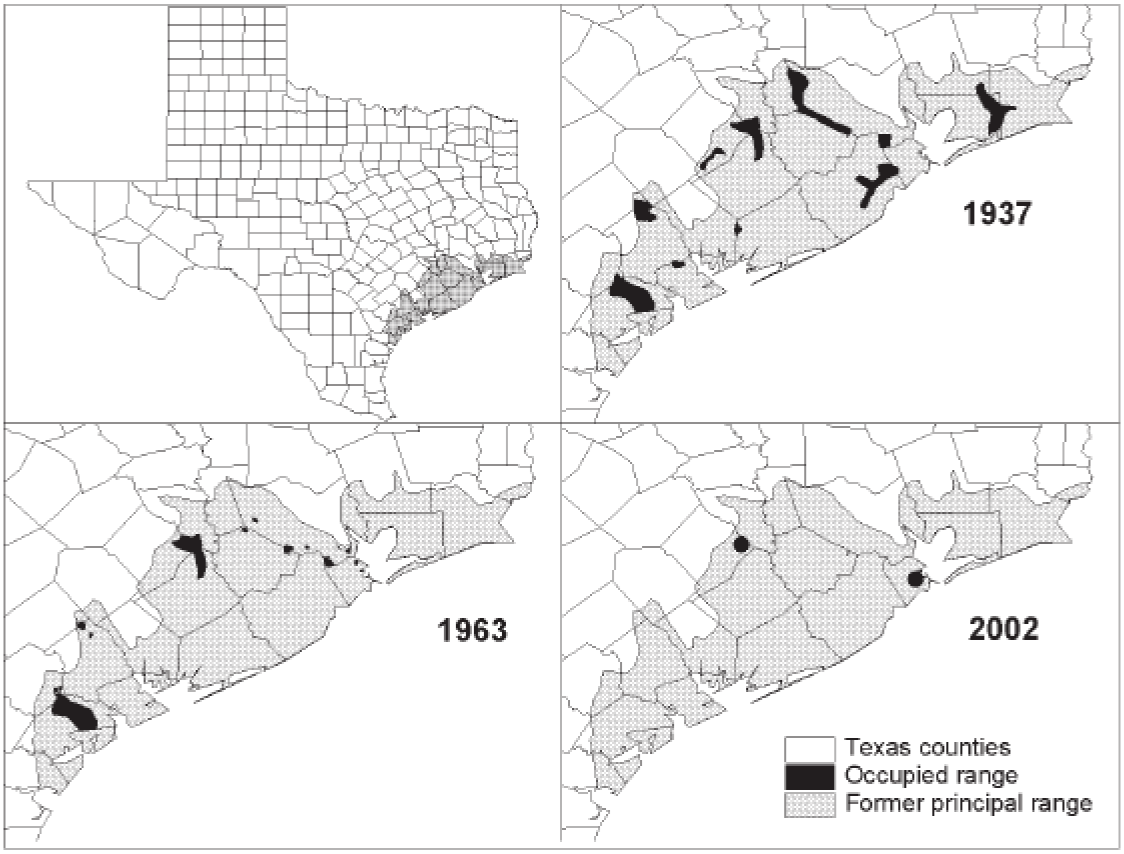


Figure 1.1. Approximately historical geographic distribution of Attwater's prairie-chicken in southeast Texas, USA, 1937 (Lehmann 1941), 1963 (Lehmann and Mauermann 1963), and 2002. Figure from Morrow et al.; 2004.

These individuals are kept at two wildlife reserves dedicated to the APC conservation and together they represent approximately > 0.2% of the APC historical habitat: the Attwater Prairie Chicken National Wildlife Refuge (APCNWR), located in Colorado County with 10,538 acres, and (2) Galveston Bay Prairie Preserve (GBPP) in Galveston County, Texas with 2,303 acres (Fig. 1.1). Neither population is self-sustainable (Silvy et al., 1999) and must be supplemented with yearly releases of individuals currently bred at seven (7) breeding and research facilities: Fossil Rim Wildlife Center at Glen Rose, TX, Sea Word San Antonio, Texas A&M University at College Station, and the Abilene, Caldwell, Houston, and San Antonio Zoos (Hess et al., 2005, U.S. Fish and Wildlife Service, 2007).

1.2.4 Research Status

Previous studies on APC have focused on ecology and life history (Lehmann, 1941; Horkel, 1979; Jurries, 1979; Cogar, 1980; Horkel and Silvy, 1980), periodic population surveys (Lehmann, 1941; Lehmann and Mauermann, 1963) habitat management (Chamrad and Dodd, 1972; Kessler, 1978; Morrow, 1986; Morrow et al., 1996), predator management (Lawrence, 1982), parasites and infectious diseases (Peterson, 2004 and references cited therein), influence of insects availability (Griffon et al., 1997), breeding and release techniques (Watkins, 1971; Drake, 1994; Griffin, 1998; Hess et al., 2005; Lockwood et al., 2005*a*), genetics (Ellsworth et al., 1994; Osterndorff, 1995; Stoley 2002), and the impact of stochastic precipitation events (Peterson and Silvy 1994, Morrow et al. 1996) on population dynamics, among many more.

Various early attempts to successfully maintain individuals in captivity were ineffectual (Watkins, 1971; Lawrence and Silvy, 1980). However, efforts were re-initiated in 1992 when the remaining APC populations reached 456 birds (U. S. Fish and Wildlife Service, 2007), and a assessment by the Captive Breeding Specialist Group of the International Union for Conservation of Nature predicted extinction of the species by 2000 if supplementation was not initiated (Seal, 1994). A pilot release program of captive-bred APC was achieved in 1995 (Lockwood et al., 2005*a*; U. S. Fish and Wildlife Service, 2007), and over the last decade, intense conservation efforts have supplemented the two remaining free-ranging APC populations with captive-reared individuals (Silvy et al., 1999; Silvy et al., 2004; Lockwood et al., 2005*a*). Indeed, the restoration program for Attwater's prairie chickens hinges on survival and reproduction of released birds (Lockwood et al. 2005*a*).

1.3 RESEARCH OBJECTIVES

My dissertation research focuses on:

(1) estimating the effects of day of release (calendar day), age at release (age in days since hatch), gender, and year on post-release survival of pen-reared, radio-tagged APC released on the APCNWR from 1996 to 2005,

(2) developing a stochastic simulation model to project population trends for the APC on the APCNWR based on the survival estimates of Objective (1), and

(3) using the model developed in Objective (2) to examine population-level responses to hypothesized changes in rates of natural recruitment and mortality, and to changes in the number of captive-reared birds released annually.

CHAPTER II

POST-RELEASE SURVIVAL OF CAPTIVE-REARED TYMPANUCHUS CUPIDO ATTWATERY AT THE ATTWATER PRAIRIE CHICKEN NATIONAL WILDLIFE REFUGE

2.1 INTRODUCTION

The Attwater's prairie-chicken (*Tympanuchus cupido attwateri*, APC), a close relative of the extinct Heath hen (*T. c. cupido*), is one of the most endangered avian species in North America. Wild populations of APC once numbered nearly 1 million individuals on 2.4 million ha of coastal prairie in Texas and Louisiana (Lehmann, 1941). However, conversion to agriculture, overgrazing, and invasion of woody species, as well as increased urbanization along the coastal plain, has extirpated the APC from Louisiana and drastically reduced populations in Texas (Lehmann, 1941; Lawrence and Silvy, 1980; Morrow et al., 1996; Morrow et al., 2004; Silvy et al., 2004). Populations of APC have declined steadily since 1935, and as a result the APC was one of the first species listed under The Endangered Species Conservation Act of 1966 (Morrow et al., 2004). By 1967 APC numbers had decreased to approximately 1,070 individuals (U. S. Fish and Wildlife Service, 2007), which stimulated the first efforts to supplement existing wild APC populations through a captive breeding program (Watkins, 1971; Lawrence and Silvy, 1980). The last free-ranging Attwater's populations are on the Attwater Prairie Chicken National Wildlife Refuge (APCNWR), located in eastern Colorado

County, Texas, and the Texas City Prairie Preserve (TCPP) in Galveston County, Texas (Morrow et al., 2004; Silvy et al., 2004; Lockwood et al., 2005*a*). By 1992, approximately 432 wild APC remained, at which time a captive breeding program was again attempted to supplement the remaining populations and preserve genetic variation (Lockwood et al., 2005*a*). As part of the APC recovery strategy, 7 breeding and research facilities collectively have produced >700 birds (through 2005, Attwater Prairie Chicken National Wildlife Refuge, unpublished data), which have been released at both areas. These releases are the main source of recruitment for both populations (Silvy et al., 1999; Silvy et al., 2004).

Because long-term sustainability of APC populations relies on the survival and subsequent reproduction of pen-reared individuals (Lutz et al., 1994; Peterson and Silvy, 1996; Lockwood et al., 2005*a*), knowledge of potential factors causing variation in survival is paramount to long-term population conservation. Using data from the APCNWR for 10 years (from 1996 to 2005) of radio-tagged APC that were kept in acclimation pens for approximately 14 days prior to release, I evaluated their post-release survival examining the effects of day of release (calendar day), age at release (age in days since hatch), gender, and year. I estimated survival of males and females for several periods post-release for comparison with previous studies. Further, due to the mating behavior of the species, I evaluated post-release survival from the median release date to the initiation of the breeding season, and between breeding and non-breeding seasons.

2.1.1 STUDY AREA

Data for this research has been collected by the APCNWR during a period of ten years (1996 – 2005) and has not been analyzed previously. The refuge is located in eastern Colorado County, Texas, on the border of the Gulf Prairies and Marshes and Post Oak Savannah ecoregions (Gould, 1975), and currently contains 10,538 ac (4,265 ha) (U. S. Fish and Wildlife Service, 2007). The refuge is mainly (71%) open mid-grass prairie (Morrow et al., 1996), which is maintained by an intensive program of prescribed burning, controlled grazing, herbicide application, and seeding of native grasses (Horkel, 1979; Lockwood et al., 2005*b*).

2.2 METHODS

I evaluated post-release survival of 562 (293 males and 269 females) captive-bred APC released on the APCNWR from 1996 to 2005; excluding 19 individuals because sex was unknown. Data consisted of birds that were kept in acclimation pens at the release site for approximately 14 days (range 10-20 days). Upon release, pen gates were opened allowing individuals to leave freely. Food and water were provided outside acclimation pens for approximately 30 days post-release. All released individuals were equipped with mortality-sensitive radio transmitters (<3% body mass) before placement in acclimation pens, and were monitored daily after release (M. Morrow, APCNWR, personal communication). Data on each individual included gender, date of hatching (19 April 1996 to 20 May 2005), day of release (calendar day; 48 to 351), age at release (83 to 970 days), last day observed alive, date found, and bird status. Mortality date was estimated as the mid-point between last day observed alive and date found.

Survival and mortality hazard of captive-bred APC were estimated as a function of age at release (in days), day of release (day of year), as well as within and between genders and years using a Cox proportional hazard modeling approach implemented in the program R (R Core Development Team, 2006) using packages Survival, Design, and MASS (Venables and Ripley, 2002; Lumley, 2003; Harrell, 2006). Data consisted of both left-truncated and right censored information, thus I followed standard survival analysis assumptions described by Pollock et al., (1989). I checked the proportionality of hazards goodness of fit assumption by evaluating the scaled Schoenfeld residuals (Grambsch and Therneau, 1994; Venables and Ripley, 2002). Based on the predicted Cox model, I estimated survival for each year of the study, and for comparison to previous studies I evaluated survival for males and females at 14 days, 28 days, and 60 days post-release.

In order to evaluate seasonal survival (breeding and non-breeding seasons) in Attwater's prairie chickens, I used the known fate design in program MARK (White and Burnham, 1999). I defined encounter occasions weekly, using 1 September as the initial date individuals entered the survival dataset. I chose 1 September each year for entry as this represented the median release date for captive-bred APC with a 14 days acclimation period pre-release and released between 1996 and 2005. I defined the breeding season from 1 February (week 5) to 31 May (week 22) as in Lockwood et al., 2005*a*, and the non-breeding season from 1 June (week 22) to 31 January (week 4).

2.3 RESULTS

I found no evidence of an interaction between gender of individuals released and year of release, thus I combined genders when evaluating year to year variation (Fig. 2.1). Using the 1996 cohort (survival was high in 1996, Lockwood et al., 2005*a*) as the baseline for the ten years of this study (from 1996 to 2005), estimated hazard ratios ranged from 0.31 (in 2004) to 3.42 (in 2000) (Table 2.1). I found no evidence the proportional hazards assumptions for gender of individuals released (ρ= 0.002, P =0.962), age at release (ρ= 0.03, P =0.50), day of year of release (calendar day) (ρ= 0.03, P =0.71), or across years ($-0.03 \leq \rho_t \leq -0.007$; P >0.15) were violated. I estimated survival (SE) for released captive-bred females during three (3) periods from 0–14, 15–28, and 29–60 days after release as 0.76 (0.03), 0.70 (0.03), 0.58 (0.03), respectively, whereas male post-release survival estimates were 0.82 (0.04), 0.77 (0.04), 0.67 (0.04), respectively.

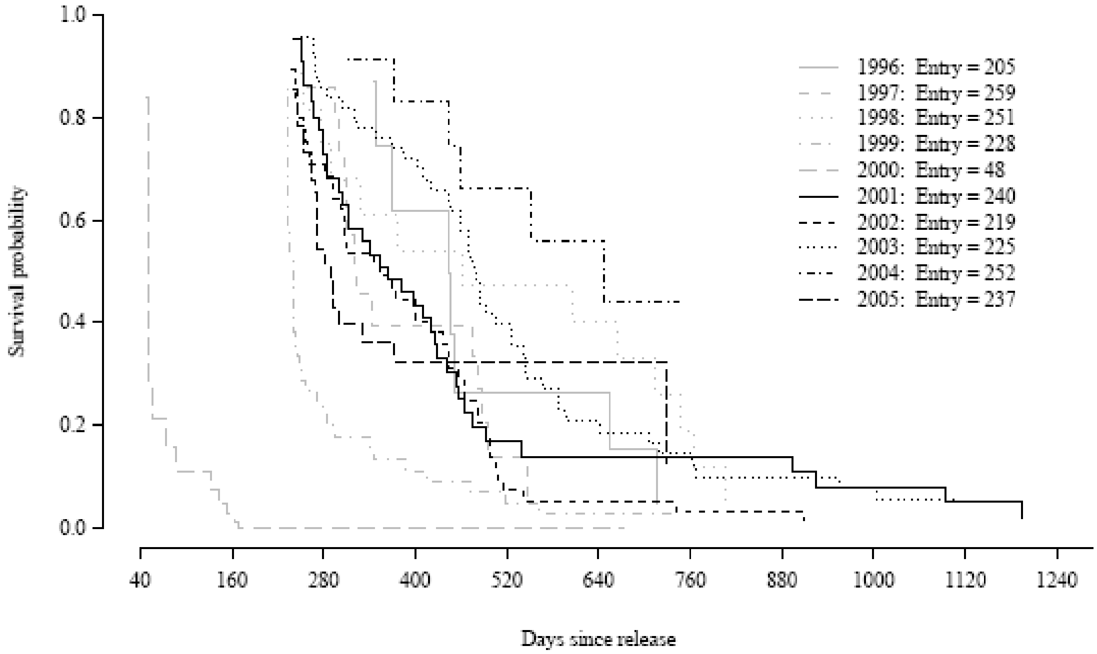


Figure 2.1. Estimated yearly post-release survival curves for captive-bred Attwater's prairie chickens released on the Attwater Prairie Chicken National Wildlife Refuge from 1996 to 2005. Entry is defined as the first day of each year in which an individual was released.

Table 2.1. Estimates of mortality hazards (β), standard errors (se(β)), and associated hazard ratios (exp(β)) for Attwater's prairie-chickens released on the Attwater Prairie Chicken National Wildlife Refuge between 1997 and 2005; 1996 (a high survival year) was used as the baseline for hazard rate estimation.

Year	β	se(β)	exp(β)
1997	0.48	0.36	1.16
1998	0.08	0.34	1.10
1999	0.99	0.30	2.70
2000	1.23	0.38	3.42
2001	0.39	0.29	1.48
2002	0.34	0.28	1.41
2003	-0.45	0.29	0.64
2004	-1.17	0.48	0.31
2005	0.70	0.31	2.01

Mortality hazard of females (β = - 0.346) was significantly higher than that of males, with an associated hazard ratio for males of 0.70 (SE=0.10). Mortality hazard was statistically significant for both day of year of release (β_j = 0.0094; P<0.001) and age at release (β_i =0.0005; p=0.05), however, the associated hazard ratios (1.01 and 1.00, respectively) suggested these differences were of no biological significance.

Median release date was about 1 September and showed little variation except during 2000 (Fig. 2.2). Weekly survival during the breeding season was slighter high for males (0.965, SE= 0.002) than for females (0.963, SE= 0.003). Non-breeding season survival followed the same pattern, with male survival (0.969, SE=0.002) exceeding female survival (0.958, SE= 0.003). Based on weekly survival estimates, the likelihood of females surviving the non-breeding season (1 June to 31 January) was approximately 13% lower than that of males (0.23 versus 0.36) (Fig. 2.3A). Based on median release date, 52% of the males would survive to the beginning of their first breeding season while only 39% of the females would survive the same period (Fig. 2.3B). The likelihood of surviving the period of the breeding season (1 February to 31 May) was essentially the same for both males (0.50) and females (0.49).

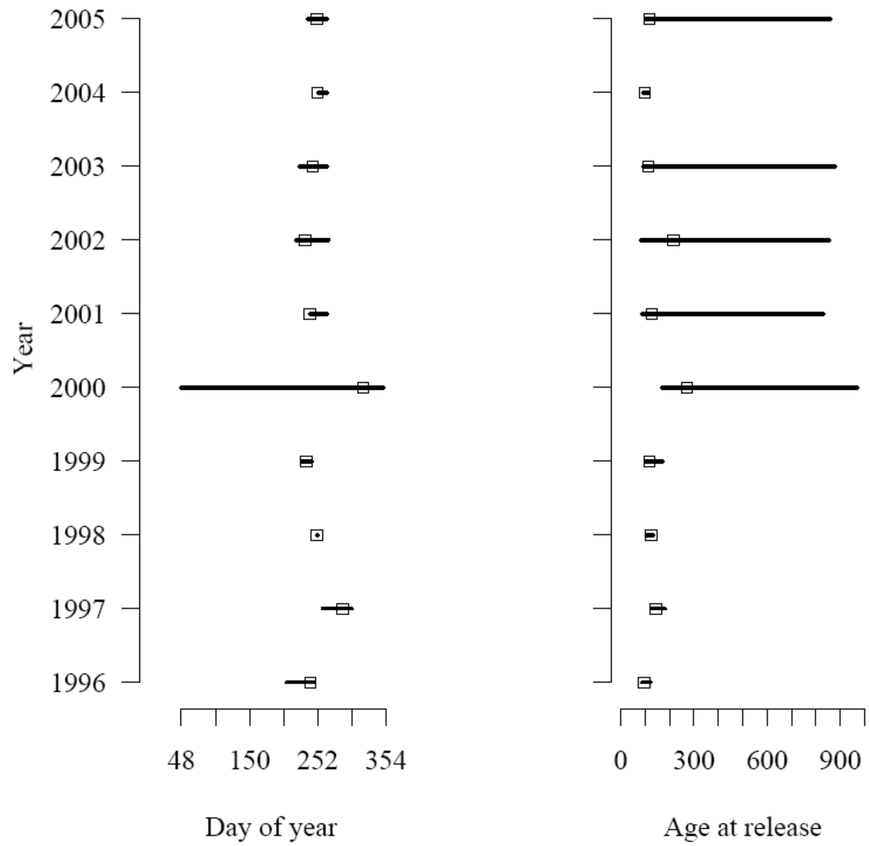
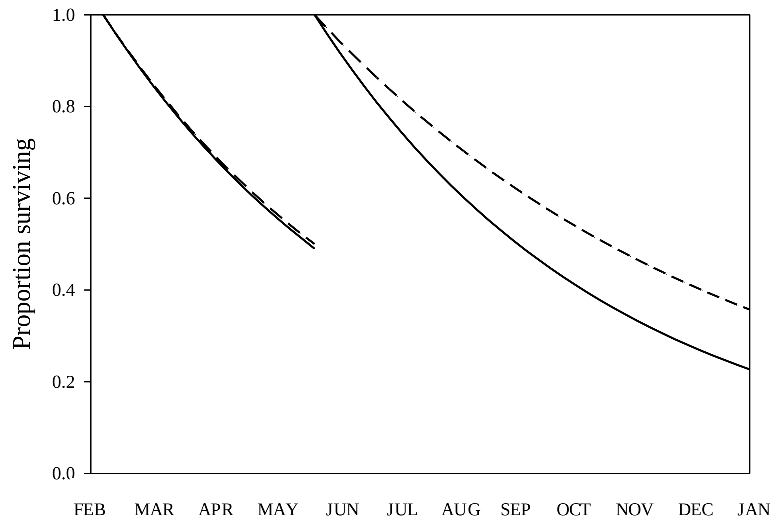


Figure 2.2. Medians (indicated by boxes) and ranges for day of year of release and age at release (in days) of Attwater’s prairie-chickens on the Attwater Prairie Chicken National Wildlife Refuge from 1996 to 2005.

A



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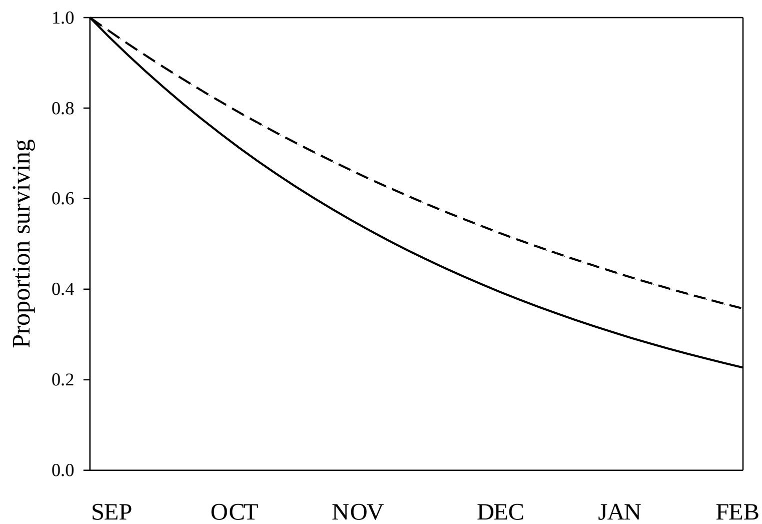


Figure 2.3. Weekly survivorship for males (dotted lines) and females (solid lines) Attwater's prairie chickens at the Attwater Prairie Chicken National Wildlife Refuge (A) during the breeding season (February 1 to May 31), and during the non-breeding season (June 1 to January 31), and (B) from release to the first breeding season (September 1 to January 31).

2.4 DISCUSSION

Survival of APC steadily declined post release, and approximately 50% of the females and 33% of the males died within the first 60 days post-release. Gender-specific differences in survival have been reported previously for other species of prairie grouse (Hamerstrom and Hamerstrom, 1973). As expected, survival of APC showed considerable year-to-year variation during the study period (1996-2005). At two weeks post-release, survival estimates (SE) were higher in pen-reared APC (0.76 (0.03) for females and 0.82 (0.04) for males) than those reported for translocated birds from wild populations (0.64 (Lawrence and Silvy, 1987) and 0.737 (Lockwood et al., 2005*a*). However, Lockwood et al., 2005*a* found higher survival estimates (SE) at two weeks post-release for pen-reared birds with a 14-day acclimation period (0.961 (0.027)). Results showed that survival during the first two weeks post-release was higher than during the second two weeks, indicating that, at least for pen-reared birds, the second two weeks post-release is more critical.

I found little evidence that age at release or date of release influenced survival of pen-reared Attwater's prairie-chickens. The earliest age at release was 83 days and 75% of releases occurred before birds had reached 210 days of age. However, age of release frequently was tied to a minimal mass, typically 500g, thus age of release may be confounded with one or several factors (e.g., physiological condition) which it was not evaluated in this study. This analysis, tended to concur with results from Lockwood et al., (2005*a*) which indicated survival was not influenced by date of release.

Assuming that reproduction is initiated in February and extends through May (Lockwood et al., 2005*a*), survival estimates indicate Attwater's prairie-chickens must survive, on average, 5 months from the median release date (1 September, Fig. 2.2) to reach the beginning of the breeding period (1 February). They then must survive an additional 1-4 months (February–May), depending on timing of breeding and nest success, to produce offspring. Mean female survival was 155 days (about 5.5 months), while median survival was 94 days. For males, mean survival was 135 days (about 4.8 months) and the median was 81 days. The results of this study are more optimistic that Toepfer (1988:139) which reported that 90% of released pen-reared Greater prairie chickens were dead within 90 days, and none survived longer than 120 days. While estimates of other production characteristics are available for wild and released pen-reared Attwater's prairie-chickens (Lutz et al., 1994; Peterson and Silvy, 1996; Peterson et al., 1998; Lockwood et al., 2005*a*), I am unaware of other estimates of breeding season survival or survival from release date to breeding season initiation (but see Lockwood et al., 2005*a* for estimates to 1 January).

Management of endangered species requires that conservation biologists determine which factors contribute to variation in life-history parameters and which of those parameters most likely constrain populations. Given the results of this analysis, concerns regarding effects of age at release and date of release on survival of pen-raised APC released on the APCNWR are unwarranted, but results also indicate that survival steadily declined after release with female survival lower than male survival. My future research includes using these findings and daily post-release survival estimates for the endangered APC to build a stochastic simulation model representing the population dynamics of the APC released at the APCNWR. Therefore, these results are a step forward towards learning about the post-release dynamics affecting the captive-rear APC and contribute to maximize conservation strategies for recovery of the species.

CHAPTER III

PROJECTING POPULATION DYNAMICS OF THE ATTWATER'S PRAIRIE CHICKEN: SIMULATING EFFECTS OF NATURAL RECRUITMENT, MORTALITY, AND RELEASE OF CAPTIVE-REARED BIRDS

3.1 INTRODUCTION

The Attwater's Prairie-chicken (*Tympanuchus cupido attwateri,* APC) is one of the three subspecies of prairie chickens currently existing in North America and it represents the southernmost extension of the genus *Tympanuchus*, historically existing in the prairies of Texas and Louisiana where it reached 1 million individuals prior to European settlement (Lehmann, 1941). The APC was one of the first species to be listed under the Federal Endangered Species List (Lawrence and Silvy, 1980; Morrow et al., 2004) when numbers were reduced to 1,070 individuals in 1967. Its dramatic decline has continued with approximately 99% of its suitable habitat lost mostly due to land fragmentation, and destruction of its native habitat (Lehmann, 1941; Jurries, 1979; Lawrence and Silvy, 1980; McKinney, 1996; Silvy et al., 2004). Only two isolated populations remain at: (1) Attwater Prairie Chicken National Wildlife Refuge (APCNWR), located in Colorado County, Texas and (2) Galveston Bay Prairie Preserve (GBPP) in Galveston County, Texas (Morrow et al., 2004; Silvy et al., 2004; Lockwood et al., 2005*a*). Intensive conservation efforts have supplemented these last free-ranging

Attwater's prairie chicken populations with captive-reared individuals during the last decade, yet the populations have not reached self-sustainable levels (Silvy et al., 1999).

The vulnerability of small populations and the lack of available time prevent field experimentation with endangered species, so simulation models have proved to be useful to project future dynamics of populations of threatened and endangered species (Vos et al., 2001; Mooij and DeAngelis, 2003). Simulation models have been used under various assumptions regarding potential changes in demographic parameters (Peterson et al., 1998; Lopez et al., 2000; Wisdom et al., 2000), and to estimate risk of population extinction (Boyce, 1992; Krebs, 2001). A previous study simulated the relative importance of three reproductive parameters on the APC population and found that an increasing population could be generated only if nesting success, brood survival, and number of chicks per brood all increased to within 10 percent of the corresponding values for the non-endangered Greater prairie chicken (*T. c. pinnatus*) (Peterson et al., 1998). However, in the absence of demographic data for APC, it was assumed that APC mortality rates were the same as those of the Greater prairie chicken (Peterson et al., 1998). In addition, effects of population supplementation via the release of captive-reared birds, which currently is the main source of new recruits into the population have not been investigated.

In this chapter, I present a stochastic simulation model developed to project population trends for the Attwater's prairie-chicken at the APCNWR based on estimates of natural mortality (Chapter II). I first describe the model (Section 3.2), and then verify its ability to simulate observed population trends at the APCNWR and to exhibit the expected sensitivities to changes in model parameters (Section 3.3). I then use the model to examine population-level responses to hypothesized changes in rates of natural recruitment and mortality, and to changes in the number of captive-reared birds released annually (Section 3.4).

3.2 Model Description

3.2.1 Overview of Model Structure

The model is formulated as an age- and sex-structured compartment model based on difference equations (Δt = 1 day), programmed in STELLA® 7 (High Performance Systems, 2001).

It consist of 2 sub-models representing the dynamics of naturally-recruited (Fig. 3.1A) and captive-reared released individuals (Fig. 3.1B). Each of four sets of state variable equations (naturally-recruited males, naturally-recruited females, captive-reared and released males, captive-reared and released females) takes the following general form:

$$N_{i,t+1} = N_{i,t} + (n_{i,t} - m_{i,t} - s_{i,t}) * \Delta t, \text{ for } i = 0 \quad (1)$$

$$N_{i,t+1} = N_{i,t} + (s_{i-1,t} - m_{i,t} - s_{i,t}) * \Delta t, \text{ for } i > 0 \quad (2)$$

where $N_{i,t}$ represents the number of individuals in age class i at the beginning of time t, $n_{i,t}$ represents the number of individuals recruited into age class i during time t, $m_{i,t}$ represents the number of individuals in age class i dying during time t, and $s_{i,t}$ represents the number of individuals surviving to age class $i + 1$ during time t.

3.2.2 Recruitment

Natural recruitment is calculated as:

$n_{83,t}$ = k1 + (1 - k1) * k2) * (k3 / 2) * $NR_{i,t}$ if *day-of-year = 120* (3)

$n_{83,t}$ = 0 if *day-of-year ≠ 120* (4)

where $NR_{i,t}$ represents the number of females in the population that have attained reproductive age ($i \geq 365$), *k*1 represents the proportion of first nests that are successful, *k*2 represents the proportion of second nests that are successful (renesting success), and *k*3 represents the number of chicks per brood prior to brood breakup (at 83 days of age) (Fig. 3.1A). Individuals are recruited into the simulated population at an age of 83 days, which is the approximate age of chicks at brood breakup reported by Peterson and Silvy (1996; these authors reported an age at brood breakup of approximately 12 weeks of age). The baselines values of *k*1, *k*2, and *k*3 reported by Peterson and Silvy (1996) and summarized in Peterson et al., (1998, Table 1) were 0.342, 0.241, and 4.3, respectively, for Attwater's prairie-chickens and 0.495, 0.495, and 6.0 respectively, for greater prairie chickens. Individuals are recruited as males or females depending on sex rate (*k*4, Fig. 3.1).

Recruitment of released captive-reared individuals into the population is represented as a management variable, and depends on number of individuals released (*k*5), the day-of-year of their release (*k*6), and the proportion of females released (*k*7) (Fig. 3.1B). Since age-at-release does not affect survivorship (Chapter II), all captive-reared individuals are released at one year of age ($i = 365$).

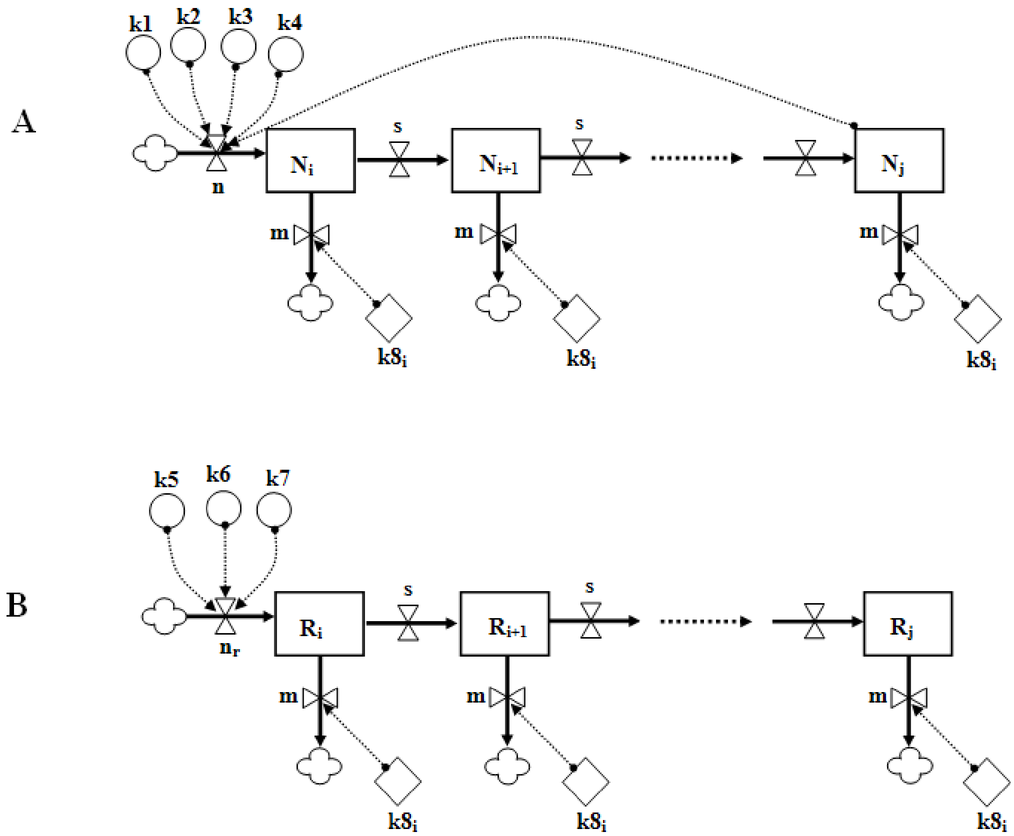


Figure 3.1. Conceptual model of population dynamics of the endangered Attwater's prairie chicken population at the Attwater's Prairie Chicken National Wildlife Refuge, consisting of sub-models representing dynamics of naturally-recruited (N) and captive-reared and released (R) individuals. Natural mortality (m) and survival (s) rates (k8i) are age- and sex-specific, but are the same for N and R. (A) Initial nesting success, renesting success, number of chicks per brood prior to brood breakup, and sex ratio are represented by k1 - k4, respectively, and n represents natural recruitment. (B) Number released, day-of-year of release, and proportion of females released, are represented by k5 – k7, respectively, and nr represents recruitment of captive-reared birds. See text for details.

3.2.3 Natural Mortality

Natural mortality is calculated as:

$$m_{i,t} = k8_i * N_{i,t} \quad (5)$$

where $k8_i$ represents the proportion of individuals in age class i that die during time t. I parameterized $k8_i$ separately for males and females based on results of the survival analysis for Attwater's prairie-chickens at the APCNWR described in Chapter II. Mortality rates were treated as stochastic variables and were drawn from a normal distribution created from the mean mortality rates and the associate standard deviation for each age class i.

Survival from age class i to age class $i + 1$ is calculated as:

$$s_{i,t} = N_{i,t} – m_{i,t}. \quad (6)$$

3.3 Model Verification

Before using the model, I verified that model behavior was consistent with general observations of APC population dynamics at the APCNWR during the study period (from 1996 – 2005), and with results of survival analyses based on data collected on the Refuge, over the last decade (Chapter II).

If the model was performing appropriately, (1) simulated population sizes should exhibit relatively stable annual fluctuations, with minimums and maximums occurring immediately pre- and post-release events, respectively, (2) population sizes should be significantly affected by changing the number of captive-reared individuals released annually, but (3) changing the day-of-year that birds were released and the proportion of females released should not have a significant effect on population size (Chapter II).

I ran eighteen (18) sets of simulations with the model parameterized to represent general conditions on the APCNWR over the past decade. I initialized each simulation with a population of 30 adults (1:1 sex ratio), set the natural recruitment parameters (*k*1 - *k*4) equal to zero (natural recruitment on the Refuge has been negligible), and used the mortality estimates ($k8_i$) calculated from data collected on the Refuge (see Chapter II). Each of the 18 sets of simulations represented a different combination of the number of captive-reared individuals released each year (*k*5 = 60, 100, or 200), the day-of-year (calendar day) that birds were released (*k*6 = 1, 244, or 305) and the proportion of females released (*k*7 = 0.48 or 0.7). I chose the values of *k*5 because, on average, 60 captive-reared birds have been released annually on the Refuge, the most recent species recovery plan suggested an annual release of 100 birds (U.S. Fish and Wildlife Service, 2007), and Toefler et al. (2003) suggested that for grouse populations with displaying males (such as the Attwater's prairie chicken) at least 200 individuals should be maintained in the population. I chose the values of *k*6 and *k*7 to encompass a wide range of plausible release dates and proportions of females released to give these factors a reasonable opportunity to affect population size.

For each set of simulations, I ran twenty (20), ten (10)-year, Monte Carlo (replicate stochastic) simulations, and monitored changes in simulated population size. Twenty Monte Carlo simulations allowed detection of a difference in population sizes of two (2) individuals (a breeding pair) with type I and II errors of $\alpha < 0.05$ and $\beta < 0.80$, respectively (Ott & Longnecker, 2001).

Results of the simulations verified that (1) simulated population sizes exhibited relatively stable annual fluctuations, with minimums and maximums occurring immediately pre- and post-release event, respectively (Fig. 3.2), (2) population sizes were significantly affected by changing the number of individuals (captive-reared) released annually, but (3) population sizes were not significantly affected by changing the day-of-year (calendar day) that individuals were released and the proportion of females released (Table 3.1, Figure 3.3). Also, not surprisingly, but importantly, although changing the number of individuals released annually affected population size, it did not qualitatively affect population dynamics, that is, population sizes immediately pre-release events were consistently about 11 or 12% of population sizes immediately post-release event (Fig. 3.2).

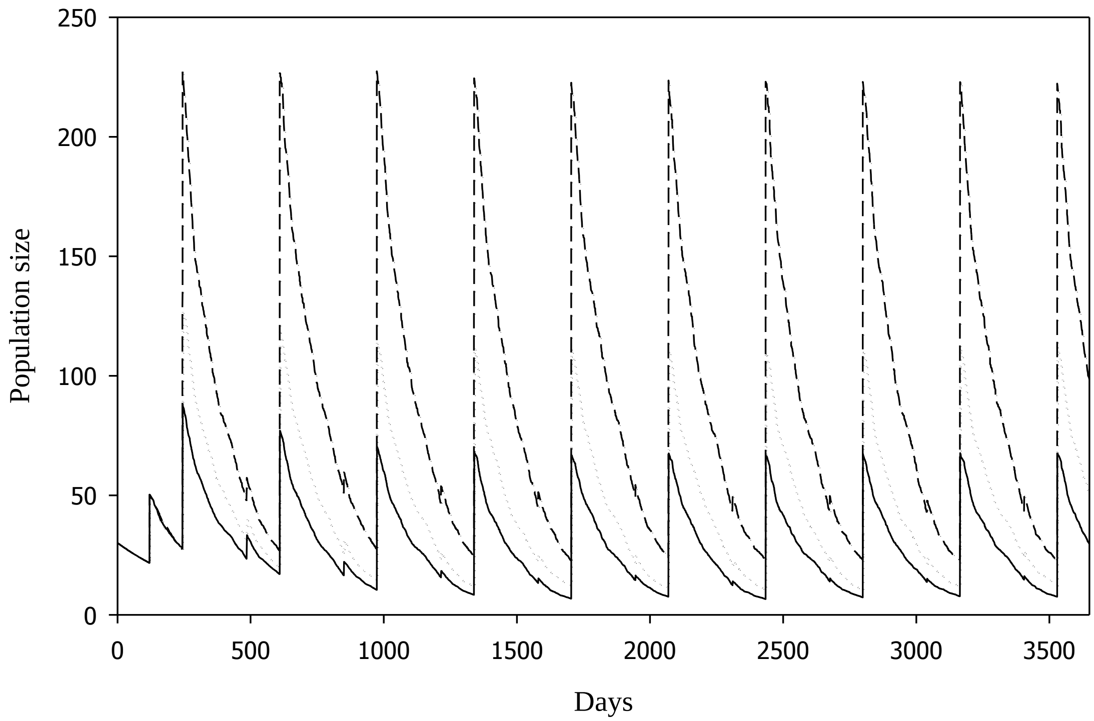


Figure 3.2. Representative results of simulations verifying that model behavior is consistent with general observations made on the Attwater's Prairie Chicken National Wildlife Refuge over the last decade. Lines represent typical Monte Carlo simulations in which either 60 (solid line), 100 (dotted line), or 200 (dash line) captive-reared birds were released annually. Refer to text for details.

Table 3.1 Results of ANOVA of effect of number of birds released (*k*5), proportion of females released (*k*6), and day-of-year that birds were released (*k*7) on simulated population size after 10 years. Results are based on 18 sets of 20, 10-year Monte Carlo simulations. Refer to text for details.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	2607(a)	5	521	455	< 0.001
Intercept	10485	1	10485	9150	< 0.001
*k*5	2607	2	1304	1138	< 0.001
*k*6	0.046	1	0.046	0.040	0.843
*k*7	0.013	2	0.007	0.006	0.994
Error	55.008	48	1.146		
Total	13148	54			
Corrected Total	2662	53			

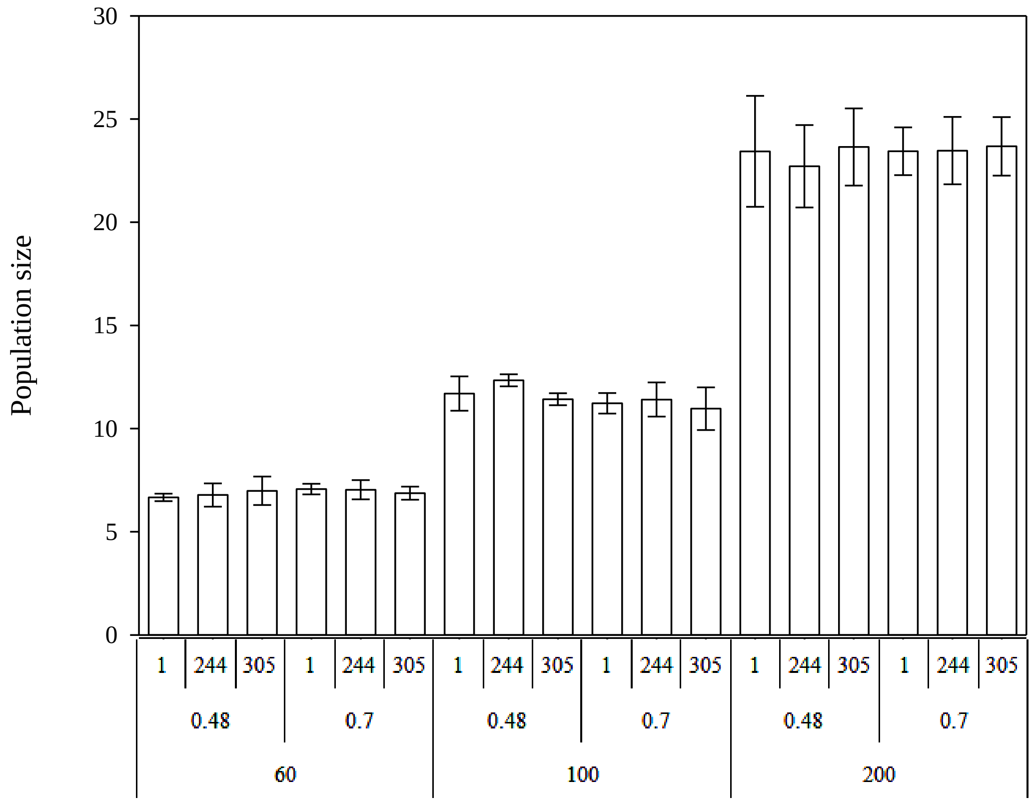


Figure 3.3 Results of 18 sets of 20, 10-year Monte Carlo simulations representing parameter combinations of number of birds released (*k*5 = 60, 100, 200), proportion of females released (*k*6 = 0.48, 0.7), and day-of-year that birds were released (*k*7 = 1, 244, 305). Mean minimum population sizes at year 10 (±SD) are shown.

3.4 Simulated Effects of Changes in Rate of Natural Recruitment, Mortality, and Release of Captive-reared Attwater's Prairie Chickens

3.4.1 Natural Recruitment and Mortality

To examine population-level responses to changes in rates of natural recruitment and mortality, I assumed that no captive-reared individuals were released and hypothesized thirty (30) scenarios with different natural recruitment rates based on those reported for other APC populations, and for the closely-related and vulnerable Greater prairie-chicken (*T. c. pinnatus*, GPC) (Table 3.2). Lutz et al., (1994) reported that initial nest success ($k1$) for APC populations ranged from 19 to 64% annually, and renesting success ($k2$) ranged from 0 to 51%. Peterson et al., (1998) reported baselines values of 0.342 (SE=0.047) for initial nest success ($k1$) and 0.241 (SE=0.073) for renesting success ($k2$) for APC populations, and 0.495 (SE=0.021) and 0.495 (SE=0.021) for GPC populations, respectively.

To facilitate comparisons among the 30 scenarios, I combined success of first nests ($k1$) and renesting success ($k2$) into a single parameter, total nest success (tn):

$$tn = (k1 * \mathrm{IC}) + ((k2 * (1 - k1)) * \mathrm{RC}) \qquad (7)$$

where IC represents initial clutch size and RC represents renesting clutch size, using the values for IC (12.1 for both APC and GPC), and RC (9.5 for APC and 10.3 for GPC) reported by Peterson et al., (1998. Table 1). Maximum values for tn were 9.51 for APC and 8.62 for GPC.

Table 3.2. Reproductive parameters (± standard error) reported for populations of Attwater's prairie-chickens and Greater prairie-chickens, representing ranges of values for success of first nests (k1, proportion), re-nesting success (k2, proportion), and number of chicks per brood surviving to brood breakup (k3).

Species	*k* 1	*k* 2	*k* 3	Source
GPC	0.495 (± 0.021)	0.495 (±0.021)	6	Peterson et al., 1998
APC	0.342 (±0.047)	0.241 (±0.073)	4.3	Peterson et al., 1998
APC	0.19 to 0.64	0 to 0.51	Not reported	Lutz et al., 1994

I then determined for each scenario, by trial and error, the proportional reduction ($k8_{adj}$) in current natural mortality ($k8_{\mathrm{i}}$, Appendix A) required for the population to sustain itself (Table 3.3).

I defined a self-sustaining population as one that exhibited stable annual fluctuations, with annual minimums equal to or slightly greater than the initial population size. As before, I initialized the population with 30 adults (1:1 sex ratio), and ran a set of 20, 10-year, Monte Carlo (replicate stochastic) simulations for each of the 30 scenarios.

Simulation results indicate that, even if I assume the highest natural recruitment rates reported for APC, current natural mortality rates would need to be reduced by at least 70% for the population to sustain itself (Table 3.3, Fig. 3.4). If I assume the highest natural recruitment rates reported for GPC, current natural mortality rates would need to be reduced by at least 65%. Assuming the lowest natural recruitment rates reported for APC and GPC, current mortality rates would need to be reduced by at least 83% and 78%, respectively.

Table 3.3. Thirty hypothesized reproductive parameter combinations for Attwater's prairie-chicken, representing different combinations of number of chicks per brood surviving to brood breakup (*k*3) and total nest success (*tn*), and the associated estimated proportional reductions ($k8_{adj}$) in current natural mortality required for the population to sustain itself at the indicated mean (SD) minimum annual population sizes (MMAP). Refer to text for details associated with parameters estimates.

Hypothesis	***k*3**	***tn***	**$k8_{adj}$**	**MMAP (SD)**
1	4.3	4.15	0.83	39.90 (± 0.92)
2	4.3	5.64	0.78	35.94 (± 1.34)
3	4.3	6.11	0.76	33.00 (± 1.010
4	4.3	6.27	0.75	33.10 (± 0.84)
5	4.3	7.15	0.75	29.57 (± 1.16)
6	4.3	7.23	0.73	32.06 (±0.93)
7	4.3	7.35	0.74	33.74 (± 0.94)
8	4.3	7.36	0.73	34.38 (±1.24)
9	4.3	8.36	0.72	35.82 (±1.15)
10	4.3	8.47	0.72	30.92 (±0.89)
11	4.3	8.52	0.72	35.66 (±1.12)
12	4.3	8.57	0.72	36.78 (±1.20)
13	4.3	8.62	0.72	31.88 (± 1.23)
14	4.3	9.44	0.70	31.15 (±1.17)
15	4.3	9.51	0.70	32.1 (±1.19)
16	6	4.15	0.78	40.08 (±1.08)
17	6	5.64	0.73	31.85 (±1.23)
18	6	6.11	0.70	35.28 (±1.36)
19	6	6.27	0.70	34.09 (±1.1)
20	6	7.15	0.70	32.61 (±1.1)
21	6	7.23	0.68	35.01 (1.51)
22	6	7.35	0.69	36.53 (1.68)
23	6	7.36	0.68	37.19 (±1.44)
24	6	8.36	0.67	33.01 (±1.93)
25	6	8.47	0.66	33.94 (±0.39)
26	6	8.52	0.66	33.45 (±2.1)
27	6	8.57	0.67	33.86 (±1.18)
28	6	8.62	0.66	35.18 (±2.10)
29	6	9.44	0.65	35.16 (±2.15)
30	6	9.51	0.65	36.06 (±2.01)

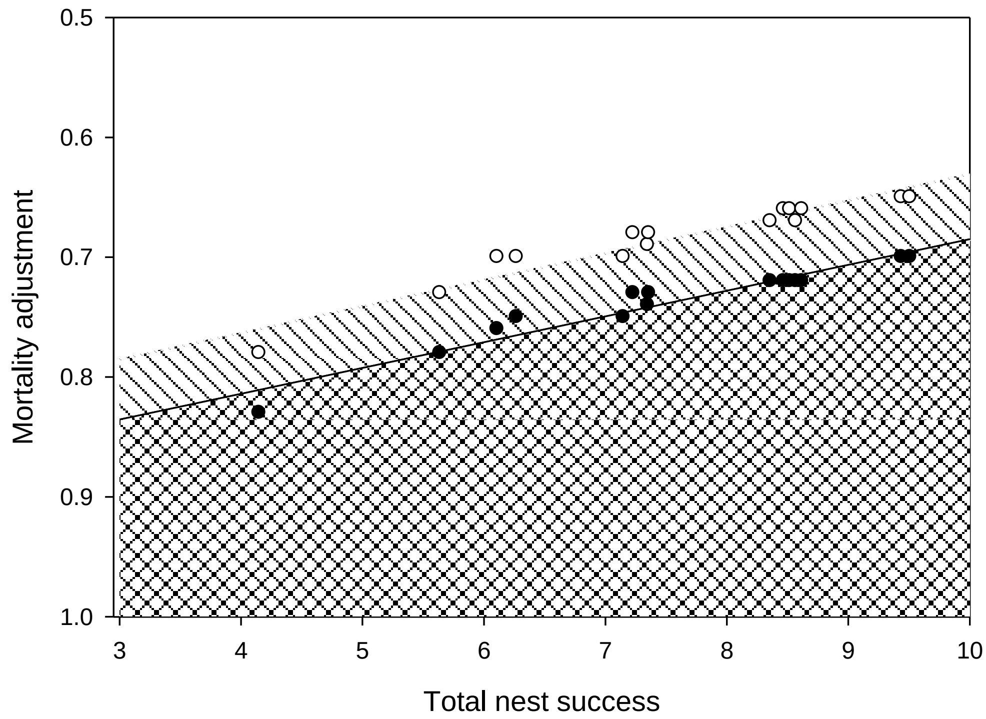


Figure 3.4. Trend lines calculated via linear regression passing through points representing the estimated proportional reductions ($k8_{adj}$, Table 3.3) in current natural mortality ($k8_i$) required for the Attwater's prairie-chicken population to sustain itself under each of the 30 hypothesized natural recruitment rates (Table 3.3). Total nest success (*tn*) includes both initial (*k*1) and re-nesting (*k*2) success (see text for details). Solid and open circles represent hypotheses based on 4.3 and 6 chicks per brood surviving to brood breakup, respectively. Cross-hatched area beneath the lines represents parameter combinations that yield a self- sustaining population. Note the inverted scale on the Y axis.

3.4.2 Release of Captive-reared Individuals

To state the obvious, a population cannot sustain itself if natural recruitment is not large enough to offset mortality. The periodic release of captive-reared individuals can replenish population numbers, but population trends between release events will continue to reflect the difference between natural recruitment and mortality. For small populations that have to become self-sustaining, the relevant question regarding the release of captive-reared individuals becomes: What is the relationship between the number of individuals released and the rate of population increase? This question often is stated in terms of the length of time it will take for the population to reach some target size.

To examine population-level responses to changes in the number of captive-reared APCs released, I simulated population growth assuming that either 60, 100, or 200 birds were released annually under each of four combinations of population parameters. I selected from the parameter combinations that yielded a self-sustaining population (Table 3.3) those that required either the largest (hypotheses 1 and 16) or smallest (hypotheses 15 and 30) adjustments to mortality rates ($k8_{adj}$), assuming the number of chicks per brood surviving to brood breakup ($k3$) was representative of either APC ($k3 = 4.3$) or GPC ($k3 = 6.0$). I again initialized the population with 30 adults (1:1 sex ratio), and ran a set of 20, 10-year, Monte Carlo simulations for each of the 12 scenarios (4 combinations of population parameters x 3 release rates).

To facilitate comparisons among growth rates, I also calculated the population doubling time (d, in years) for each of the 12 scenarios, following Krebs (2001, p. 160):

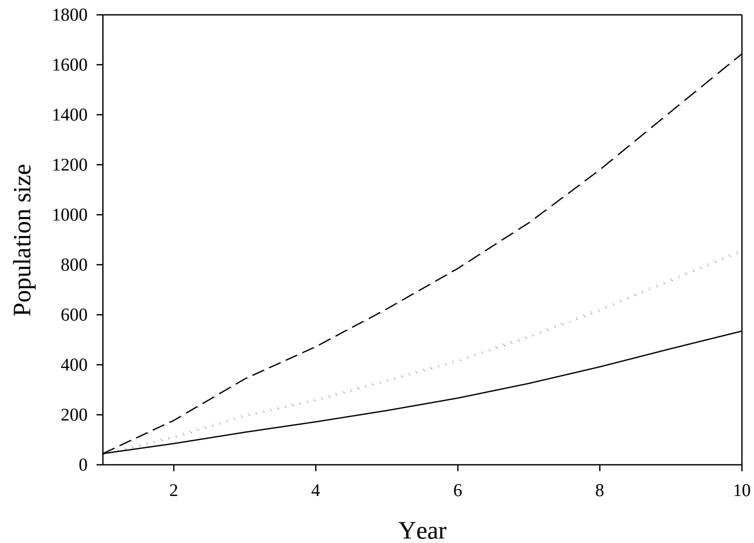
$$N_d / N_0 = 2 = e^{rd} \qquad (8)$$

$$\text{or, } d = \log_e (2) / r \qquad (9)$$

where N_t is population size at time *t*, and *r* is the realized, *per capita*, instantaneous population growth rate. I estimated *r* by calculating the mean annual growth rate ($\lambda = N_{t+1} / N_t$) during years 6 through 10 and then converting λ to an instantaneous rate ($r = \log_e \lambda$). I based my estimate of *r* on population growth rate during years 6 through 10 to avoid an inappropriate interpretation of the initial phase of model behavior (Grant and Swannack, 2008, p. 101), which in this case took the form of small irregularities in growth rate during the first few years of simulation due to differences between the initial age-class distribution and the age-class distributions generated by the particular parameter combinations in the different versions of the model.

Simulation results indicated that mean pre-release population sizes in year 10 after releasing 200 birds annually were approximately 3 times larger than populations into which 60 birds had been released annually, and populations into which 100 birds had been released annually were somewhat less than 2 times larger than populations into which 60 birds had been released annually (Fig. 3.5).

A



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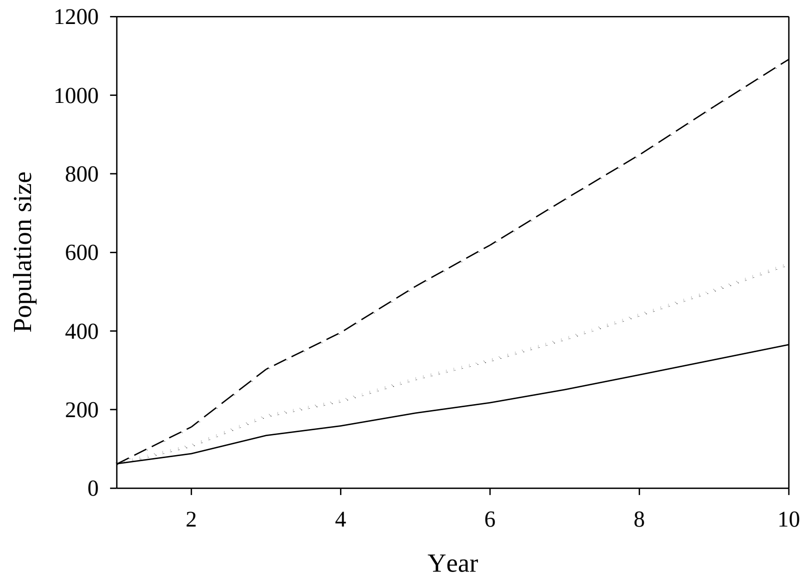
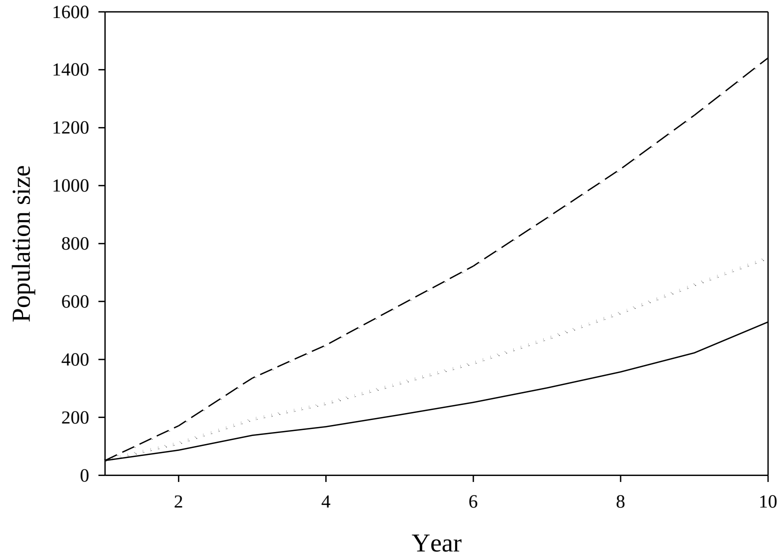


Figure 3.5. Simulated growth of an Attwater's prairie chicken population under each of four hypothesized parameter combinations that yielded a self-sustaining population (A, B, C, and D represent hypotheses 1, 15, 16, and 30, respectively, in Table 3.3), assuming that 60 (solid lines), 100 (dotted lines), or 200 (dashed lines) captive-reared birds were released annually.

C



D

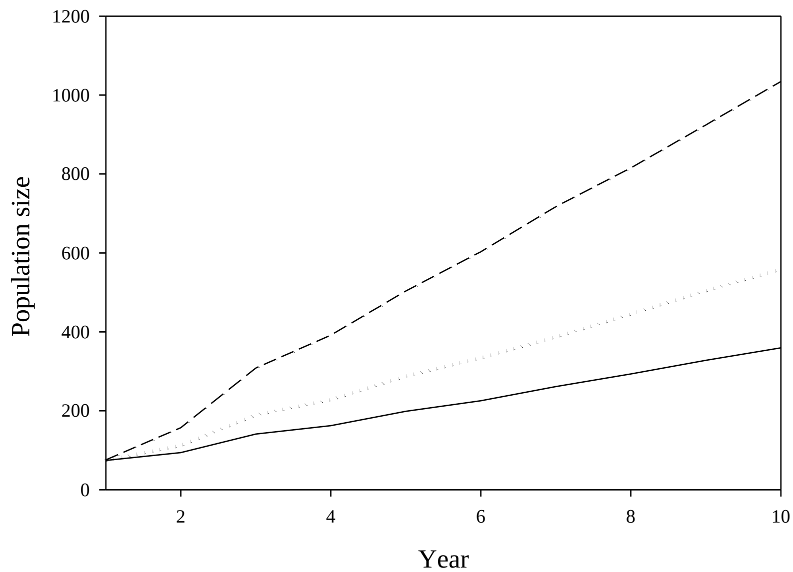


Figure 3.5. con’t.

Reductions in population doubling times attained by increasing from 60 to 200 the number of individuals released annually ranged from 7 to 18%, with greater reductions attained by populations characterized by higher rates of natural reproduction and mortality (hypotheses 15 and 30, Table 3.3), that is, by populations with higher turnover rates (Table 3.4). Reductions in population doubling times attained by increasing from 60 to 100 the number of birds released annually ranged from 3 to 10%, with greater reductions once again attained by populations with higher turnover rates.

3.4.3 Relationship between Population Turnover Rate and Effect of Number of Individuals Released

To examine the relationship between population turnover rate and the effect on population growth of the number of birds released, I conducted a two-factor ANOVA of mean pre-release population sizes in year 10 simulated under the 12 treatments (the 12 scenarios representing 4 hypothesized combinations of population parameters x 3 annual release rates) described in Section 3.4.2. I used Bonferroni post-hoc tests to identify significant differences among treatment groups.

Results of ANOVA indicated that both hypothesized parameter combination and annual release rate had a significant effect on pre-release population sizes in year 10 ($F_{\text{hypothesis, df = 36}} = 43.73$, $p < 0.001$; $F_{\text{AnRelRate, df=36}} = 361.399$, $p < 0.001$). Since there was no significant difference between hypotheses 1 and 16 ($p > 0.05$) or between hypotheses 15 and 30 ($p > 0.05$), I aggregated these pairs of hypotheses into two groups. Group A represented lower population turnover rates (lower natality and mortality) and Group B represented higher population turnover rates (higher natality and mortality).

Table 3.4. Estimated population doubling times (in years) under each of four combinations of reproductive parameters that yielded a self-sustaining population (hypotheses 1, 15, 16, and 30 in Table 3.3), assuming, for each parameter combination, that 60, 100, or 200 captive-reared birds were released annually (k5). See text for details.

	Number of Birds Released Annually (*k*5)		
Hypothesis	60	100	200
1	3.84	3.72	3.57
15	5.35	4.82	4.59
16	4.16	4.02	3.85
30	5.83	5.22	4.80

Results of ANOVA with hypotheses aggregated into two groups again indicated that both hypothesized parameter combination and annual release rate had a significant effect on pre-release population sizes in year 10 (Table 3.5). Changes in annual release rates had a greater effect on growth of populations with lower turnover rates (Group A) than on populations with higher turnover rates (Group B) (Fig. 3.6).

3.5 DISCUSSION

Projecting future trends for the endangered APC population at the APCNWR in the face of great uncertainly involving small populations is a very challenging task. The stochastic model developed for this study allowed analysis at a fine temporal scale, and as a result, it was possible to evaluate effects of release strategies, reproductive parameters, and mortality rates on Attwater's prairie chicken population dynamics.

Regardless of the number of individuals released annually, population size immediately pre-release decreased to 11 – 12% of population size immediately post-release. That is, if 60 birds were released during a given year, then only 6-7 of these birds would remain a year after the release event. Therefore, management strategies involving larger numbers of releases can increase population size in the short term, but these efforts cannot produce a self-sustaining population. One advantage of increasing population sizes, even temporarily, is the influx of new genetic variation the population will receive (Soulé, 1986). Suggested minimum population sizes for this purpose are at least 500 individuals (Lande and Barrowclough, 1987), but this scenario is very unlikely in the near future because the required number of yearly releases will be un reachable

Table 3.5. Results of a two-factor ANOVA of mean pre-release Attwater's prairie chicken population sizes in year 10 simulated under the 12 treatments (the 12 scenarios representing 4 hypothesized combinations of population parameters x 3 annual release rates) described in Section 3.4.2. The four hypotheses were aggregated into two groups (Group A included hypotheses 1 and 16, Group B included hypotheses 15 and 30). See text for details.

Source	Type III Sum of Squares	df	Mean Square	F	p
Corrected Model	5460740.366	3	1820246.789	239.089	< 0.001
Intercept	23722452.125	1	23722452.125	3115.937	< 0.001
Ann. Release Rate	4664201.966	2	2332100.983	306.321	< 0.001
Hypothesis Group	796538.400	1	796538.400	104.625	< 0.001
Error	243624.490	32	7613.265		
Total	29426816.981	36			
Corrected Total	5704364.856	35			

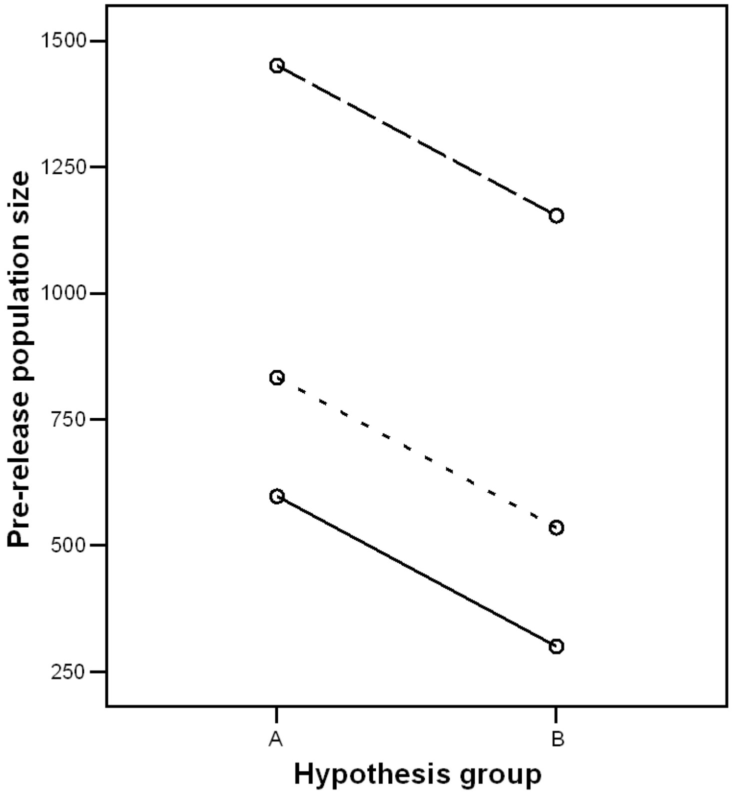


Figure 3.6. Effects of changes in the number of captive-reared APCs released annually on pre-release population sizes in year 10 for simulated populations with lower turnover rates (lower natality and mortality, Hypothesis Group A), and higher turnover rates (higher natality and mortality, Hypothesis Group B). See text for details about hypothesis groups. Solid, sort-dashed, and long-dashed lines represent simulations in which 60, 100, and 200 captive-reared birds, respectively, were released annually.

(around 4,500 individuals released per year to maintain minimum population sizes over 500 individuals) with current mortality rates. Additional factors involving release strategies, such day-of-year of releases and sex ratio of the individuals released, did not show a significant effect on population growth.

At current mortality rates the Attwater's prairie chicken population cannot be self-sustainable even if reproductive parameters are increased to maximum rates previously reported for populations of both the endangered Attwater's and the closely related vulnerable greater prairie chicken. With the most favorable reproductive success scenarios, mortality rates must decrease by approximately 65 – 70% of their current values for the population to reach self-sustainable levels. Even larger decreases in mortality will be necessary for the population to grow. At lower values of reproductive success, mortality rates must be reduced even more, by approximately 78 – 83% of their current values, for the population to be self-sustainable.

If management actions can decrease mortality by the required level for self-sustainability and birds are continued to be released, the population, unsurprisingly exhibits exponential growth, regardless of the initial size of the population (Fig. 3.5). While these results seem promising, management efforts must reduce current mortality rates by at least 65% in order for the population to be self-sustainable. Calculations for population doubling time showed that number of individuals released every year had a small effect on the reduction on the doubling time. Hypotheses with lower turnover rates had shorter doubling times; likewise, population doubling time decreased for parameter combinations that had higher turnover rates (Table 3.4). Populations with higher turnover rates benefits more from the release of more individuals, whether as population with low turnover rates benefit less from releases. Attwater's prairie chicken populations could have a higher probability of recovery only if management strategies achieve turnover rates that can self-sustain the population, which in general terms imply great increases in natality rates and decreases in current mortality rates for the captive-bred individuals.

CHAPTER IV

CONCLUSIONS

There was little evidence that variables such as age at release or date of release influenced survival of captive-reared Attwater's prairie-chickens. This analysis, which included 8 more years of data than previously analyzed, agreed with results from Lockwood et al. (2005*a*) which indicated post-release survival of captive-reared APC was not influenced by date of release. Results indicated that survival of APC steadily declined post-release, and approximately 50% of the females and 33% of the males died within the first 60 days post-release. Mean female survival was 155 days (about 5.5 months), while median survival was 94 days. For males, mean survival was 135 days (about 4.8 months) and the median was 81 days. If birds are released on or about the median release day (1 Sept.), then they must survive, on average, about 150 days to reach the beginning of the breeding season, and probably at least an additional 4 months to complete breeding, nesting, and the rearing of offspring until brood break up (when chicks are approximately at 12 weeks of age). The post-release survival estimates obtained from this study indicate that few birds will survive the necessary time to successfully breed and rear young, however, the aforementioned results are actually more optimistic than those reported for released pen-reared Greater prairie-chickens, in which 90% of released pen-reared Greater prairie-chickens were dead within 90 days, and none survived longer than 120 days (Toepfer, 1988:139).

The stochastic model developed for this research allowed projection of future trends for the APC population and it was possible to evaluate effects of release strategies, reproductive parameters, and mortality on APC population dynamics. Increasing the number of individuals released annually to 100 individuals is one of the recovery objectives of the Attwater's Prairie chicken recovery plan (U.S. Fish and Wildlife, 2007). However, regardless of the number of individuals released annually, population sizes immediately prior to the release dates were only 11 – 12% of the population sizes immediately after the release dates. Therefore, for the Attwater's prairie chicken, management strategies involving increasing the number of individuals released annually can increase population size in the short term, but cannot produce a self-sustaining population, which is the overall goal of any species conservation project (World Conservation Union, 1987; Griffith et al., 1989; U.S. Fish and Wildlife Service, 1990; Tear et al., 1993).

At current mortality rates, simulated APC populations could not sustain themselves even if reproductive parameters were increased to the maximum rates reported for APC, or to the maximum rates reported for the closely related Greater prairie chicken. With the most favorable reproductive parameter combinations, mortality rates must decrease by approximately 65 – 70% of their current values for the population to be self-sustaining.

Despite massive conservation efforts involving long-term captive breeding and annual supplementation with captive-bred individuals, the APC population at the

APCNWR is not self-sustaining, with population replenishment depending on released of captive-reared birds.

There are several factors that could influence the success of captive breeding and re-introduction programs that were not analyzed in this study, such as behavior, social interaction, and level of human imprint on captive individuals, in addition to physiological condition of the individuals at released. Individuals raised in captivity usually required special care and extensive training so the skills needed to survive in their natural environment are not lost. Indeed, successful re-introduction programs in other species, such as the California condor and Whooping crane, have heavily included these components. Therefore, I recommend that future work focus on maintaining untamed behavior and social interactions of individuals during captivity, along with restricted human interaction.

REFERENCES

Beck, B.B., Rapaport, L.G., Stanley Price, M.R., Wilson, A.C., 1994. Reintroduction of captive-born animals. In: Olney, P.J.S., Mace, G.M., Feistner, A.T.C. (Eds.), Creative Conservation: Interactive Management of Wild and Captive Animals. Chapman and Hall, London, pp. 265–286.

Bellinger, J.A., Toepfer, J.E., Dunn, P., 2003. Loss of genetic variation in greater prairie chickens following a population bottleneck in Wisconsin, USA. Conservation Biology 17, 717–724.

Boyce, M.S., 1992. Population viability analysis. Annual Review of Ecology and Systematics 23, 481–506.

Chamrad, A.D., Dodd, J.D., 1972. Prescribed burning and grazing for prairie chicken habitat manipulation in the Texas coastal prairie. In: Proceedings of Annual Tall Timbers Fire Ecology Conference, Lubbock, Texas, USA. 12, 257–276.

Clark, J.D., Huber, D., Serveen, C., 2002. Bear reintroduction: lessons and challenges. Ursus 13, 153–163.

Cogar, V.F., 1980. Food habits of Attwater's prairie chicken in Refugio County, Texas. Dissertation, Texas A&M University, College Station, Texas, USA.

Drake, D., 1994. Captive propagation and brood behavior of greater prairie chickens. Thesis, Texas A&M University, College Station, Texas, USA.

Earnhardt, J.M., 1999. Reintroduction programmes: genetic trade-offs for populations. Animal Conservation 2, 179–286.

Ebenhard, T., 1995. Conservation breeding as a tool for saving animal species from extinction. Trends in Ecology & Evolution 10, 438–443.

Ellsworth, D.L., Honeycutt, R.L., Silvy, N.J., Rittenhouse, K.D., Smith, M.H., 1994. Mitochondrial-DNA and nuclear-gene differentiation in North American prairie grouse (genus Tympanuchus). The Auk 111, 661–671.

Fisher, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. Biology Conservation 96, 1–11.

Gould, F.W., 1975. Texas plants - a checklist and ecological summary. Miscellaneous Publication 585, Texas Agricultural Experimentation Station, College Station, Texas, USA.

Grambsch, P., Therneau, T.M., 1994. Proportional hazards tests and diagnostics based on weighted residuals. Biometrika 81, 515–526.

Grant, W. E., Swannack, T. M., 2008. Ecological Modeling: A Common-sense Approach to Theory and Practice. Blackwell Publishing. Malden, Massachusetts, USA. 155 pp.

Griffin, C.P., 1998. Factors affecting captive prairie chicken production. Dissertation, Texas A&M University, College Station, Texas, USA.

Griffith, B., Scott, M.J., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool: status and strategy. Science 245, 477–480.

Griffon, C.P., Morrow, M.E., Silvy, N.J., 1997. Insects as a possible limiting factor for Attwater's prairie chicken Tympanuchus cupido attwateri. Wildlife Biology 3, 288.

Haig, S.M., Belthoff, J.R., Allen, D.H., 1993. Population viability analysis for a small population of red-cockaded Woodpeckers and an evaluation of enhancement strategies. Conservation Biology 7, 289–301.

Haight, R.G., Ralls, K., Starfield, A.M., 2000. Designing species translocation strategies when population growth and future funding are uncertain. Conservation Biology 14, 1298–1307.

Hamerstrom, F.N.Jr., Hamerstrom, F., 1973. The prairie chicken in Wisconsin. Wisconsin Department of Natural Resources Technical Bulletin No. 64, Madison, Wisconsin, USA.

Hamerstrom, F.N.Jr., Mattson, O.E., Hamerstrom, F., 1957. A guide to prairie chicken management. Wisconsin Conservation Department Technical Wildlife Bulletin No. 15, Madison, Wisconsin, USA.

Harrell, J., 2006. Hmisc: Harrell Miscellaneous. R package version 3.0-10. http://biostat.mc.vanderbilt.edu/s/Hmisc.

Hess, M.F., Silvy, N.J., Griffin, C.P., Lopez, R.R., Davis, D.S., 2005. Differences in flight characteristics of pen-reared and wild prairie-chickens. Journal of Wildlife Management 69, 650–654.

Horkel, J.D., 1979. Cover and space requirements of Attwater's prairie chicken (Tympanuchus cupido attwateri) in Refugio County, Texas. Dissertation, Texas A&M University, College Station, Texas, USA.

Horkel, J.D., Silvy, N.J., 1980. Evolutionary considerations in creating artificial leks for Attwater's prairie chicken. In: Vohs, P.A. Jr., Knopf, F. L. (Eds.), Proceedings of the Prairie Grouse Symposium, Stillwater, Oklahoma, USA, pp. 42−47

Jurries, R.W., 1979. Attwater's prairie chicken. Texas Parks and Wildlife Department, F. A. Series No. 18, Austin, Texas, USA.

Kessler, W.B., 1978. Attwater prairie chicken ecology in relation to agricultural and range management practices. Texas A&M University, College Station, Texas, USA.

Kleiman, D.G., Stanley Price, M.R., Beck, B.B., 1994. Criteria for reintroductions. In: Olney, P.J.S. (Ed.) Creative Conservation: Interactive Management of Wild and Captive Animals. Chapman and Hall, London, pp. 287−303.

Krebs, C.J., 2001. Ecology. Benjamin Cummings, San Francisco, California, USA.

Lande, R., Barrowclough, G.F., 1987. Effective population size, genetic variation, and their use in population management. In: Soulé, M.E. (Ed.), Viable Populations for Conservation. Cambridge University Press, Cambridge, England, UK. pp. 87−123.

Lawrence, J.S., 1982. Effect of predator reduction on the reproductive success of Attwater's prairie chicken. Thesis, Texas A&M University, College Station, Texas, USA.

Lawrence, J.S., Silvy, N.J., 1980. Status of the Attwater's prairie chicken-an update. In: Vohs, P.A. Jr., Knopf, F. L. (Eds.), Proceedings of Prairie Grouse Symposium, Oklahoma State University, Stillwater, Oklahoma, USA, pp. 29−33.

Lawrence, J.S., Silvy, N.J., 1987. Movements and mortality of transplanted Attwater's prairie chicken. Journal of World Pheasant Association 12, 57−65.

Lehmann, V.W., 1941. Attwater's prairie chicken, its life history and management. United States Fish and Wildlife Service, North American Fauna Series 57. United States Government Printing Office, Washington, D. C., USA.

Lehmann, V.W., Mauermann, R.G., 1963. Status of Attwater's prairie chicken. Journal of Wildlife Management 27, 713–725.

Lockwood, M.A., Clifton, C.P., Morrow, M.E., Randel, C.J., Silvy, N.J., 2005a. Survival, movements, and reproduction of released captive-reared Attwater's prairie chicken. Journal of Wildlife and Management 69, 1251–1258.

Lockwood, M.A., Morrow, M.E., Silvy, N.J., Smeins, F.E., 2005b. Spring habitat requirements of captive-reared Attwater's prairie chicken. Rangeland Ecology Management 58, 320–323.

Lopez, R.R., Grant, W.E., Silvy, N.J., Peterson, M.J., Feuerbacher, C.K., Corson, M.S., 2000. Restoration of the wild turkey in east Texas: simulation of alternative restocking strategies. Ecological Modelling 132, 275–285.

Lubow, B.C., 1996. Optimal translocation strategies for enhancing stochastic metapopulation viability. Ecological Applications 6, 1268–1280.

Lumley, T., 2003. Survival analysis, including penalised likelihood. Version 2.21. R package, http://cran.r-project.org .

Lutz, R.S., Lawrence, J.S., Silvy, N.J., 1994. Nesting ecology of Attwater's prairie-chicken. Journal of Wildlife Management 58, 230–233.

Matson, T.K., Goldizen, A.W., Jarman, P.J., 2004. Factors affecting the success of translocations of the black-faced impala in Namibia. Biology Conservation 116, 359–365.

McKinney, L.B., 1996. Forty years of landscape change in Attwater's prairie chicken habitat within the coastal prairie of Texas. Thesis, Texas A&M University, College Station, Texas, USA.

Mooij, W.M., DeAngelis, D.L., 2003. Uncertainty in spatially explicit animal dispersal models. Ecological Applications 13, 794–805.

Morrow, M.E., 1986. Ecology of Attwater's prairie-chicken in relation to land management practices on the Attwater Prairie Chicken National Wildlife Refuge. Dissertation, Texas A&M University, College Station, Texas, USA.

Morrow, M.E., Adamcik, R.S., Friday, J.D., McKinney, L.B., 1996. Factors affecting Attwater's prairie-chicken decline on the Attwater Prairie Chicken National Wildlife Refuge. Wildlife Society Bulletin 34, 593–601.

Morrow, M.E., Rossignol, T.A., Silvy, N.J., 2004. Federal listing of prairie grouse: lessons from the Attwater's prairie-chicken. Wildlife Society Bulletin 32, 112–118.

Ostermann, S.D., Deforge, J.R., Edge, W.D., 2001. Captive breeding and reintroduction evaluation criteria: a case study of Peninsular bighorn sheep. Conservation Biology 15, 749–760.

Osterndorff, E.A., 1995. Conservation genetics of the endangered Attwater's prairie-chicken. Thesis, Texas A&M University, College Station, Texas, USA.

Ott, R.L., Longnecker, M.T., 2001. An introduction to statistical methods and data analysis. Duxbury, Pacific Grove, CA, 1152 p.

Peterson, M.J., 1994. Factors limiting population size of the endangered Attwater's prairie chicken. Dissertation, Texas A&M University, College Station, Texas, USA.

Peterson, M.J., 2004. Parasites and infectious diseases of prairie grouse: should managers be concerned? Wildlife Society Bulletin 34, 35–55.

Peterson, M.J., Grant, W.E., Silvy, N.J., 1998. Simulation of reproductive stages limiting productivity of the endangered Attwater's prairie chicken. Ecological Modeling 111, 283–298.

Peterson, M.J., Silvy, N.J., 1994. Spring precipitation and fluctuations in Attwater's prairie-chicken numbers: hypotheses revisited. Journal of Wildlife and Management 58, 222–229.

Peterson, M.J., Silvy, N.J., 1996. Reproductive stages limiting productivity of the endangered Attwater's prairie chicken. Conservation Biology 10, 1264–1276.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53, 7–15.

Preisser, E.L., Yelin, J.R., 1999. Attwater's prairie chicken : the conservation challenge and recommendations. Endangered Species UPDATE 16 (1).

Primack, R., 2000. Essentials of conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.

R Development Core Team, 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07 0. http://www.R-project.org.

Rout, T.M., Hauser, C.E., Possingham, H.P., 2007. Minimize long-term loss or maximize short-term gain/ optimal translocation strategies for threatened species. Ecological Modelling 201, 67–74.

Sarrazin, F., Barbault, R., 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology & Evolution 11, 474–478.

Schwartz, C.W., 1945. The ecology of the prairie chicken in Missouri. University of Missouri Studies 20, 1–99.

Scott, J.M., Carpenter, W., 1987. The release of captive-reared or translocated endangered birds: what do we need to know. Auk 104, 544–545.

Seal, U.S., 1994. Attwater’s prairie chicken (Tympanuchus cupido attwateri) population and habitat viability assessment. Conservation Breeding Specialist Group, Apple Valley, Minnesota, USA.

Silvy, N.J., Griffin, C.P., Lockwood, M.A., Morrow, M.E., Peterson, M.J., 1999. Attwater's prairie chicken: a lesson in conservation biology research. In: Svedarsky , W.D., Hier , R.H., Silvy , N.J. (Eds), The Greater Prairie Chicken: A National Look. University of Minnesota, St. Paul, Minnesota, USA, pp. 153–162.

Silvy, N.J., Hagen, C.A., 2004. Introduction: management of imperiled prairie grouse species and their habitat. Wildlife Society Bulletin 32, 2–5.

Silvy, N.J., Peterson, M.J., Lopez, R.R., 2004. The cause of the decline of pinnated grouse: the Texas example. Wildlife Society Bulletin 32, 16–21.

Smeins, F.E., Diamond, D.D., Hanselka, C.W., 1991. Coastal prairie. In: Coupland, R.T. (Ed.), Ecosystems of the world 8A-natural grasslands-introduction and western hemisphere. Elsevier Press, New York, New York, USA, pp. 269–290.

Snyder, J.W., Pelren, E.C., Crawford, J.A., 1999. Translocation histories of prairie grouse in the United States. Wildlife Society Bulletin 27, 428–432.

Soulé, M.E., 1986. Conservation biology: the science and scarcity of diversity. Sinauer, Sunderland, Massachusetts, USA.

Soulé, M.E., 1991. Conservation: tactics for a constant crisis. Science 253, 744–749.

Stanley Price, M.R., 1991. A review of mammal re-introductions, and the role of the Re-Introduction Specialist Group of IUCN/SSC. In: Gipps , J.H.W. (Ed.), Beyond captive breeding: re-introducing endangered mammals to the wild. Clarendon Press, Oxford, England, pp. 9–25.

Stoley, M.M., 2002. Microsatellite analyses of genetic variability in historic and extant populations of Attwater's prairie chicken Tympanuchus cupido attwateri. Thesis, Tarlenton State University, Stephenville, Texas, USA.

Tear, T.H., Scott, J.M., Hayward, P., Griffith, B., 1993. Status and prospects for the Endangered Species Act: a look at recovery plans. Science 262, 976–977.

Tenhumberg, B., Tyre, A.J., Shea, K., Possingham, H.P., 2004. Linking wild and captive populations to maximize species persistence: optimal translocation strategies. Conservation Biology 18, 1304–1314.

Toepfer, J.E., 1988. The ecology of the greater prairie chicken as related to reintroductions. Dissertation, University of Montana, Bozeman, Montana, USA.

Toepfer, J.E., 2003. Prairie chickens & grasslands: 2000 and beyond. Report to the Council of Chiefs, Society of Tympanuchus Cupido Pinnatus, Ltd., Elm Grove, Wisconsin, USA.

U. S. Fish and Wildlife Service, 1990. Report to congress: endangered and threatened species recovery program. Government Printing Office, Washington D.C., USA.

U. S. Fish and Wildlife Service, 2007. Attwater's prairie chicken draft recovery plan. United States Fish and Wildlife Service, Albuquerque, New Mexico, USA. http://www.fws.gov/southwest/es/Documents/R2ES/Draft_Revised_APC_Recovery_Plan_11-19-07.pdf.

Veltman, C.J., Nee, S., Crawley, M.J., 1996. Correlates of introduction success in exotic New Zealand birds. The American Naturalist 147, 542–557.

Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S. Springer-Verlag, New York, New York, USA.

Vos, C.C., Verboom, J., Opdam, P.F.M., Ter Braak, C.J.F., 2001. Toward ecologically scaled landscape indices. The American Naturalist 183, 24–41.

Watkins, R.M., 1971. The propagation of the Attwater's prairie chicken in captivity. Thesis, Texas A&M University, College Station, Texas, USA.

Wisdom, M.J., Mills, L.S., Doak, D.F., 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology 3, 628–641.

Wolf, C.M., Garland Jr, T., Griffith, B., 1998. Predictions of avian and mammalian translocations success; reanalysis with phylogenetically independent contrasts. Biology Conservation 86, 243–255.

Wolf, C.M., Griffith, B., Reed, C., Temple, S.A., 1996. Avian and mammalian translocations: update and re-analysis of 1987 survey data. Conservation Biology 10, 1142–1154.

World Conservation Union (IUCN), 1987. IUCN position statement on the translocation of living organisms: introductions, re-introductions, and re-stocking. World Conservation Union (IUCN), Gland, Switzerland.

World Conservation Union (IUCN), 1998. IUCN species survival commission guidelines for re-introductions. World Conservation Union (IUCN), Gland, Switzerland.

APPENDIX A

Daily mortality rates ($k8_i$) for captive-reared Attwater's prairie chicken males. Estimates are based on results of the survival analysis for the Attwater's prairie chicken population at the Attwater's Prairie Chicken National Wildlife Refuge described in Chapter II.

Age Class	DMM	Age Class	DMM	Age Class	DMM
0	0.002483	32	0.009667	64	0.002652
1	0.00249	33	0.00914	65	0.002659
2	0.002496	34	0.009224	66	0.002667
3	0.002502	35	0.00836	67	0.002204
4	0.002508	36	0.004215	68	0.002208
5	0.002515	37	0.004233	69	0.002213
6	0.002521	38	0.008373	70	0.003253
7	0.002527	39	0.008184	71	0.003264
8	0.002534	40	0.008251	72	0.003275
9	0.00254	41	0.008056	73	0.003286
10	0.002547	42	0.007855	74	0.006593
11	0.002553	43	0.007582	75	0.006637
12	0.008246	44	0.00764	76	0.001306
13	0.008314	45	0.007494	77	0.001308
14	0.008384	46	0.003638	78	0.001309
15	0.024096	47	0.003651	79	0.001311
16	0.022525	48	0.003526	80	0.001313
17	0.021493	49	0.003539	81	0.002242
18	0.010303	50	0.006894	82	0.002247
19	0.010411	51	0.006942	83	0.002252
20	0.004133	52	0.002212	84	0.010232
21	0.00415	53	0.002217	85	0.010338
22	0.004167	54	0.002222	86	0.002639
23	0.004185	55	0.001308	87	0.002646
24	0.015282	56	0.00131	88	0.002653
25	0.002125	57	0.001311	89	0.00266
26	0.002129	58	0.001313	90	0.002667
27	0.002134	59	0.001315	91	0.013531
28	0.002138	60	0.00644	92	0.013716
29	0.002143	61	0.006481	93	0.004636
30	0.010738	62	0.002638	94	0.004657
31	0.009574	63	0.002645	95	0.004679

Age Class	DMM	Age Class	DMM	Age Class	DMM
96	0.003484	140	0.001595	184	0.001948
97	0.003497	141	0.001598	185	0.009757
98	0.007185	142	0.0016	186	0.004927
99	0.005343	143	0.001603	187	0.004951
100	0.005372	144	0.001606	188	0.009951
101	0.005401	145	0.001005	189	0.010051
102	0.00543	146	0.001006	190	0.004959
103	0.007223	147	0.001007	191	0.004983
104	0.007362	148	0.001008	192	0.003339
105	0.007416	149	0.001009	193	0.00335
106	0.004923	150	0.00101	194	0.003361
107	0.004947	151	0.001011	195	0.010118
108	0.004972	152	0.001012	196	0.010221
109	0.007673	153	0.001621	197	0.010327
110	0.002518	154	0.001624	198	0.003395
111	0.002524	155	0.001626	199	0.003407
112	0.00253	156	0.001629	200	0.003419
113	0.022649	157	0.001632	201	0.010291
114	0.003801	158	0.001634	202	0.010145
115	0.003815	159	0.001637	203	0.010505
116	0.001915	160	0.00164	204	0.010357
117	0.001918	161	0.001642	205	0.021455
118	0.001922	162	0.001645	206	0.010963
119	0.001926	163	0.008673	207	0.011084
120	0.007718	164	0.001706	208	0.011208
121	0.007589	165	0.001709	209	0.011335
122	0.007647	166	0.001712	210	0.011186
123	0.007706	167	0.001715	211	0.003865
124	0.003786	168	0.001718	212	0.00388
125	0.0038	169	0.001471	213	0.003895
126	0.005086	170	0.001473	214	0.011731
127	0.005112	171	0.001475	215	0.004053
128	0.005138	172	0.001477	216	0.00407
129	0.007747	173	0.001479	217	0.004086
130	0.015616	174	0.001482	218	0.003077
131	0.007932	175	0.001914	219	0.003087
132	0.001558	176	0.001918	220	0.003096
133	0.00156	177	0.001921	221	0.003106
134	0.001563	178	0.001925	222	0.00638
135	0.001565	179	0.001929	223	0.006421
136	0.001568	180	0.001933	224	0.006613
137	0.007851	181	0.001936	225	0.006657
138	0.003957	182	0.00194	226	0.006701
139	0.003972	183	0.001944	227	0.006746

Age Class	DMM	Age Class	DMM	Age Class	DMM
228	0.027169	272	0.002594	316	0.000785
229	0.007141	273	0.002601	317	0.000785
230	0.007192	274	0.002608	318	0.000786
231	0.014971	275	0.006645	319	0.000787
232	0.015199	276	0.006689	320	0.000787
233	0.0078	277	0.006734	321	0.000788
234	0.007861	278	0.00678	322	0.000788
235	0.03203	279	0.002731	323	0.000789
236	0.008185	280	0.002738	324	0.00079
237	0.008253	281	0.002746	325	0.00079
238	0.016997	282	0.002753	326	0.000791
239	0.008646	283	0.002761	327	0.000792
240	0.008721	284	0.002768	328	0.000792
241	0.006109	285	0.002776	329	0.000793
242	0.006147	286	0.002784	330	0.000794
243	0.006185	287	0.002792	331	0.000794
244	0.019417	288	0.002799	332	0.000795
245	0.019802	289	0.001754	333	0.000795
246	0.020202	290	0.001758	334	0.000796
247	0.003002	291	0.001761	335	0.000797
248	0.003011	292	0.001764	336	0.000797
249	0.00302	293	0.001767	337	0.000798
250	0.003029	294	0.00177	338	0.000799
251	0.003039	295	0.001773	339	0.000799
252	0.003048	296	0.001776	340	0.0008
253	0.003057	297	0.001779	341	0.0008
254	0.010936	298	0.001783	342	0.000801
255	0.011057	299	0.001786	343	0.000802
256	0.002761	300	0.001789	344	0.000802
257	0.002768	301	0.001792	345	0.000803
258	0.002776	302	0.001795	346	0.000804
259	0.002784	303	0.001799	347	0.000804
260	0.002791	304	0.001802	348	0.000805
261	0.002799	305	0.007221	349	0.000806
262	0.002807	306	0.007273	350	0.000806
263	0.002815	307	0.007326	351	0.000807
264	0.002823	308	0.007381	352	0.000808
265	0.002548	309	0.005201	353	0.000808
266	0.002554	310	0.005228	354	0.000809
267	0.002561	311	0.005255	355	0.00081
268	0.002567	312	0.005283	356	0.00081
269	0.002574	313	0.005311	357	0.000811
270	0.002581	314	0.00534	358	0.003385
271	0.002587	315	0.000784	359	0.003397

Age Class	DMM	Age Class	DMM	Age Class	DMM
360	0.003408	404	0.002386	448	0.012718
361	0.00342	405	0.002391	449	0.002034
362	0.003432	406	0.002504	450	0.002038
363	0.003444	407	0.00251	451	0.002042
364	0.003456	408	0.002516	452	0.002046
365	0.003468	409	0.002523	453	0.002051
366	0.00348	410	0.002529	454	0.002055
367	0.003492	411	0.002535	455	0.002059
368	0.002695	412	0.002542	456	0.002063
369	0.002703	413	0.002548	457	0.002068
370	0.00271	414	0.002555	458	0.002072
371	0.002717	415	0.002561	459	0.002076
372	0.002725	416	0.002568	460	0.00208
373	0.002732	417	0.001169	461	0.012856
374	0.00274	418	0.00117	462	0.013024
375	0.002747	419	0.001171	463	0.004398
376	0.002755	420	0.001173	464	0.004418
377	0.002762	421	0.001174	465	0.004438
378	0.00277	422	0.001176	466	0.004457
379	0.002778	423	0.001177	467	0.004477
380	0.002786	424	0.001178	468	0.004497
381	0.004549	425	0.00118	469	0.005421
382	0.00457	426	0.001181	470	0.005451
383	0.004591	427	0.001183	471	0.005481
384	0.004612	428	0.001184	472	0.005511
385	0.004633	429	0.001185	473	0.005541
386	0.004655	430	0.001187	474	0.004644
387	0.004677	431	0.001188	475	0.004665
388	0.005001	432	0.00119	476	0.004687
389	0.005026	433	0.001191	477	0.004709
390	0.005051	434	0.001192	478	0.004731
391	0.005077	435	0.001194	479	0.004754
392	0.005103	436	0.001195	480	0.002866
393	0.005129	437	0.001197	481	0.002874
394	0.00233	438	0.002652	482	0.002883
395	0.002335	439	0.002659	483	0.002891
396	0.002341	440	0.002666	484	0.002899
397	0.002346	441	0.002674	485	0.002908
398	0.002352	442	0.002681	486	0.002916
399	0.002357	443	0.002688	487	0.002925
400	0.002363	444	0.002695	488	0.002933
401	0.002369	445	0.002703	489	0.002942
402	0.002374	446	0.00271	490	0.001876
403	0.00238	447	0.012558	491	0.00188

Age Class	DMM	Age Class	DMM	Age Class	DMM
492	0.001883	536	0.003707	580	0.010368
493	0.001887	537	0.003721	581	0.010476
494	0.001891	538	0.003735	582	0.010587
495	0.001894	539	0.003749	583	0.0107
496	0.001898	540	0.003763	584	0.010816
497	0.001901	541	0.003777	585	0.010934
498	0.001905	542	0.003791	586	0.011055
499	0.001909	543	0.003806	587	0.011179
500	0.001912	544	0.00382	588	0.011305
501	0.001916	545	0.003835	589	0.07371
502	0.00192	546	0.002231	590	0.010942
503	0.001923	547	0.002236	591	0.011063
504	0.001927	548	0.002241	592	0.011186
505	0.001931	549	0.002246	593	0.011313
506	0.001934	550	0.002251	594	0.011442
507	0.002084	551	0.002256	595	0.011575
508	0.002088	552	0.002261	596	0.01171
509	0.002092	553	0.002267	597	0.011849
510	0.002097	554	0.002272	598	0.008818
511	0.002101	555	0.002277	599	0.008896
512	0.002105	556	0.002282	600	0.008976
513	0.00211	557	0.002287	601	0.009057
514	0.002114	558	0.002293	602	0.00914
515	0.002119	559	0.002298	603	0.009225
516	0.002123	560	0.002303	604	0.00931
517	0.002128	561	0.002308	605	0.009398
518	0.002132	562	0.002314	606	0.009487
519	0.002137	563	0.002319	607	0.009578
520	0.002142	564	0.002325	608	0.009671
521	0.002146	565	0.00233	609	0.009765
522	0.002151	566	0.002335	610	0.009861
523	0.002155	567	0.002341	611	0.00996
524	0.005368	568	0.006705	612	0.01006
525	0.005397	569	0.006751	613	0.030821
526	0.005426	570	0.006797	614	0.031801
527	0.005456	571	0.006843	615	0.032845
528	0.005486	572	0.00689	616	0.033961
529	0.005516	573	0.006938	617	0.035155
530	0.005546	574	0.006987	618	0.016382
531	0.00976	575	0.007036	619	0.016654
532	0.009857	576	0.009955	620	0.016937
533	0.009955	577	0.010055	621	0.017228
534	0.010055	578	0.010157	622	0.01753
535	0.003693	579	0.010261	623	0.017843

Age Class	DMM	Age Class	DMM	Age Class	DMM
624	0.018167	668	0.000971	712	0.001014
625	0.018503	669	0.000972	713	0.001015
626	0.018852	670	0.000973	714	0.001016
627	0.019215	671	0.000974	715	0.001017
628	0.019591	672	0.000975	716	0.001018
629	0.000936	673	0.000976	717	0.00102
630	0.000936	674	0.000977	718	0.001021
631	0.000937	675	0.000978	719	0.001022
632	0.000938	676	0.000979	720	0.001023
633	0.000939	677	0.00098	721	0.001024
634	0.00094	678	0.000981	722	0.001025
635	0.000941	679	0.000981	723	0.001026
636	0.000942	680	0.000982	724	0.001027
637	0.000943	681	0.000983	725	0.001028
638	0.000944	682	0.000984	726	0.001029
639	0.000944	683	0.000985	727	0.00103
640	0.000945	684	0.000986	728	0.001031
641	0.000946	685	0.000987	729	0.001032
642	0.000947	686	0.000988	730	0.001033
643	0.000948	687	0.000989	731	0.001034
644	0.000949	688	0.00099	732	0.001035
645	0.00095	689	0.000991	733	0.001036
646	0.000951	690	0.000992	734	0.001037
647	0.000952	691	0.000993	735	0.001039
648	0.000952	692	0.000994	736	0.00104
649	0.000953	693	0.000995	737	0.001041
650	0.000954	694	0.000996	738	0.001042
651	0.000955	695	0.000997	739	0.001043
652	0.000956	696	0.000998	740	0.001044
653	0.000957	697	0.000999	741	0.001045
654	0.000958	698	0.001	742	0.001046
655	0.000959	699	0.001001	743	0.001047
656	0.00096	700	0.001002	744	0.001048
657	0.000961	701	0.001003	745	0.001049
658	0.000962	702	0.001004	746	0.001051
659	0.000963	703	0.001005	747	0.001052
660	0.000964	704	0.001006	748	0.001053
661	0.000964	705	0.001007	749	0.001054
662	0.000965	706	0.001008	750	0.001055
663	0.000966	707	0.001009	751	0.001056
664	0.000967	708	0.00101	752	0.001057
665	0.000968	709	0.001011	753	0.001058
666	0.000969	710	0.001012	754	0.001059
667	0.00097	711	0.001013	755	0.001061

Age Class	DMM	Age Class	DMM	Age Class	DMM
756	0.001062	800	0.001843	844	0.002005
757	0.001063	801	0.001846	845	0.002009
758	0.001064	802	0.00185	846	0.002013
759	0.001065	803	0.001853	847	0.002017
760	0.001066	804	0.001856	848	0.002022
761	0.001067	805	0.00186	849	0.002026
762	0.001069	806	0.001863	850	0.00203
763	0.00107	807	0.001867	851	0.002034
764	0.001071	808	0.00187	852	0.002038
765	0.001072	809	0.001874	853	0.002042
766	0.001073	810	0.001877	854	0.002046
767	0.001074	811	0.001881	855	0.002051
768	0.001075	812	0.001884	856	0.002055
769	0.001077	813	0.001888	857	0.002059
770	0.001078	814	0.001892	858	0.002063
771	0.00955	815	0.001895	859	0.004545
772	0.009642	816	0.001899	860	0.004565
773	0.009736	817	0.001902	861	0.004586
774	0.009832	818	0.001906	862	0.004607
775	0.00993	819	0.00191	863	0.004629
776	0.010029	820	0.001913	864	0.00465
777	0.010131	821	0.001917	865	0.004672
778	0.010235	822	0.001921	866	0.004694
779	0.01034	823	0.001924	867	0.004716
780	0.010448	824	0.001928	868	0.004738
781	0.010559	825	0.001932	869	0.004761
782	0.010671	826	0.001935	870	0.004784
783	0.010787	827	0.001939	871	0.004807
784	0.010904	828	0.001943	872	0.00483
785	0.012277	829	0.001947	873	0.004853
786	0.01243	830	0.001951	874	0.004877
787	0.012586	831	0.001954	875	0.004901
788	0.012747	832	0.001958	876	0.004925
789	0.012911	833	0.001962	877	0.00495
790	0.01308	834	0.001966	878	0.004974
791	0.013253	835	0.00197	879	0.004999
792	0.013431	836	0.001974	880	0.005024
793	0.013614	837	0.001978	881	0.00505
794	0.013802	838	0.001981	882	0.005075
795	0.013995	839	0.001985	883	0.005101
796	0.001829	840	0.001989	884	0.005127
797	0.001833	841	0.001993	885	0.005154
798	0.001836	842	0.001997	886	0.00518
799	0.001839	843	0.002001	887	0.005207

Age Class	DMM	Age Class	DMM	Age Class	DMM
888	0.005235	932	0.061176	976	0.061176
889	0.005262	933	0.061176	977	0.061176
890	0.00529	934	0.061176	978	0.061176
891	0.005318	935	0.061176	979	0.061176
892	0.005347	936	0.061176	980	0.061176
893	0.005375	937	0.061176	981	0.061176
894	0.005404	938	0.061176	982	0.061176
895	0.005434	939	0.061176	983	0.061176
896	0.005463	940	0.061176	984	0.061176
897	0.005493	941	0.061176	985	0.061176
898	0.005524	942	0.061176	986	0.061176
899	0.005554	943	0.061176	987	0.061176
900	0.005585	944	0.061176	988	0.061176
901	0.005617	945	0.061176	989	0.061176
902	0.005649	946	0.061176	990	0.061176
903	0.005681	947	0.061176	991	0.061176
904	0.005713	948	0.061176	992	0.061176
905	0.005746	949	0.061176	993	0.061176
906	0.005779	950	0.061176	994	0.061176
907	0.005813	951	0.061176	995	0.061176
908	0.046847	952	0.061176	996	0.061176
909	0.049149	953	0.061176	997	0.061176
910	0.05169	954	0.061176	998	0.061176
911	0.054507	955	0.061176	999	0.061176
912	0.05765	956	0.061176	1000	0.061176
913	0.061176	957	0.061176	1001	0.061176
914	0.061176	958	0.061176	1002	0.061176
915	0.061176	959	0.061176	1003	0.061176
916	0.061176	960	0.061176	1004	0.061176
917	0.061176	961	0.061176	1005	0.061176
918	0.061176	962	0.061176	1006	0.061176
919	0.061176	963	0.061176	1007	0.061176
920	0.061176	964	0.061176	1008	0.061176
921	0.061176	965	0.061176	1009	0.061176
922	0.061176	966	0.061176	1010	0.061176
923	0.061176	967	0.061176	1011	0.061176
924	0.061176	968	0.061176	1012	0.061176
925	0.061176	969	0.061176	1013	0.061176
926	0.061176	970	0.061176	1014	0.061176
927	0.061176	971	0.061176	1015	0.061176
928	0.061176	972	0.061176	1016	0.061176
929	0.061176	973	0.061176	1017	0.061176
930	0.061176	974	0.061176	1018	0.061176
931	0.061176	975	0.061176	1019	0.061176

Age Class	DMM	Age Class	DMM	Age Class	DMM
1020	0.061176	1064	0.061176	1108	0.061176
1021	0.061176	1065	0.061176	1109	0.061176
1022	0.061176	1066	0.061176	1110	0.061176
1023	0.061176	1067	0.061176	1111	0.061176
1024	0.061176	1068	0.061176	1112	0.061176
1025	0.061176	1069	0.061176	1113	0.061176
1026	0.061176	1070	0.061176	1114	0.061176
1027	0.061176	1071	0.061176	1115	0.061176
1028	0.061176	1072	0.061176	1116	0.061176
1029	0.061176	1073	0.061176	1117	0.061176
1030	0.061176	1074	0.061176	1118	0.061176
1031	0.061176	1075	0.061176	1119	0.061176
1032	0.061176	1076	0.061176	1120	0.061176
1033	0.061176	1077	0.061176	1121	0.061176
1034	0.061176	1078	0.061176	1122	0.061176
1035	0.061176	1079	0.061176	1123	0.061176
1036	0.061176	1080	0.061176	1124	0.061176
1037	0.061176	1081	0.061176	1125	0.061176
1038	0.061176	1082	0.061176	1126	0.061176
1039	0.061176	1083	0.061176	1127	0.061176
1040	0.061176	1084	0.061176	1128	0.061176
1041	0.061176	1085	0.061176	1129	0.061176
1042	0.061176	1086	0.061176	1130	0.061176
1043	0.061176	1087	0.061176	1131	0.061176
1044	0.061176	1088	0.061176	1132	0.061176
1045	0.061176	1089	0.061176	1133	0.061176
1046	0.061176	1090	0.061176	1134	0.061176
1047	0.061176	1091	0.061176	1135	0.061176
1048	0.061176	1092	0.061176	1136	0.061176
1049	0.061176	1093	0.061176	1137	0.061176
1050	0.061176	1094	0.061176	1138	0.061176
1051	0.061176	1095	0.061176	1139	0.061176
1052	0.061176	1096	0.061176	1140	0.061176
1053	0.061176	1097	0.061176	1141	0.061176
1054	0.061176	1098	0.061176	1142	0.061176
1055	0.061176	1099	0.061176	1143	0.061176
1056	0.061176	1100	0.061176	1144	0.061176
1057	0.061176	1101	0.061176	1145	0.061176
1058	0.061176	1102	0.061176	1146	0.061176
1059	0.061176	1103	0.061176	1147	0.061176
1060	0.061176	1104	0.061176	1148	0.061176
1061	0.061176	1105	0.061176	1149	0.061176
1062	0.061176	1106	0.061176	1150	0.061176
1063	0.061176	1107	0.061176	1151	0.061176

Age Class	DMM
1152	0.061176
1153	0.061176
1154	0.061176
1155	0.061176
1156	0.061176
1157	0.061176
1158	0.061176
1159	0.061176
1160	0.061176
1161	0.061176
1162	0.061176
1163	0.061176
1164	0.061176
1165	0.061176
1166	0.061176
1167	0.061176
1168	0.061176
1169	0.061176
1170	0.061176
1171	0.061176
1172	0.061176
1173	0.061176
1174	0.061176
1175	0.061176
1176	0.061176
1177	0.061176
1178	0.061176
1179	0.061176
1180	0.061176
1181	0.061176
1182	0.061176
1183	0.061176
1184	0.061176
1185	0.061176
1186	0.061176
1187	0.061176
1188	0.061176
1189	0.061176
1190	0.061176
1191	0.061176
1192	0.061176
1193	0.061176
1194	0.061176

Age Class	DMM
1195	0.061176
1196	0.061176
1197	0.061176
1198	0.061176
1199	0.061176
1200	0.061176

APPENDIX B

Daily mortality rates ($k8_i$) for captive-reared Attwater's prairie chicken females. Estimates are based on results of the survival analysis for the Attwater's prairie chicken population at the Attwater's Prairie Chicken National Wildlife Refuge described in Chapter II.

Age Class	DFM	Age Class	DFM	Age Class	DFM
0	0.002597	31	0.007105	62	0.007326
1	0.002604	32	0.007156	63	0.001805
2	0.002611	33	0.021622	64	0.001808
3	0.002618	34	0.010929	65	0.001811
4	0.002624	35	0.010049	66	0.001815
5	0.002631	36	0.009479	67	0.003585
6	0.002638	37	0.018779	68	0.003598
7	0.002645	38	0.027397	69	0.01444
8	0.002652	39	0.009132	70	0.003663
9	0.002659	40	0.00905	71	0.003676
10	0.002666	41	0.004255	72	0.01476
11	0.002674	42	0.004273	73	0.00369
12	0.002681	43	0.008298	74	0.003704
13	0.002688	44	0.016462	75	0.007435
14	0.004819	45	0.008031	76	0.007435
15	0.004842	46	0.003891	77	0.00749
16	0.004866	47	0.003906	78	0.003745
17	0.00489	48	0.003746	79	0.003759
18	0.004914	49	0.00376	80	0.007548
19	0.011494	50	0.007491	81	0.007605
20	0.011627	51	0.007435	82	0.007662
21	0.010526	52	0.00738	83	0.002535
22	0.010638	53	0.007435	84	0.002541
23	0.003876	54	0.007326	85	0.002548
24	0.003891	55	0.014545	86	0.002497
25	0.003906	56	0.002407	87	0.002503
26	0.003922	57	0.002413	88	0.002509
27	0.014598	58	0.002418	89	0.003718
28	0.013422	59	0.004814	90	0.003732
29	0.01227	60	0.004837	91	0.007435
30	0.007055	61	0.00486	92	0.015093

Age Class	DFM	Age Class	DFM	Age Class	DFM
93	0.003832	140	0.002945	187	0.010695
94	0.003846	141	0.002954	188	0.003564
95	0.007722	142	0.008811	189	0.003577
96	0.023346	143	0.002963	190	0.00359
97	0.007967	144	0.002972	191	0.010472
98	0.002008	145	0.002981	192	0.010582
99	0.002012	146	0.001762	193	0.005235
100	0.002016	147	0.001765	194	0.005263
101	0.00202	148	0.001768	195	0.010473
102	0.00135	149	0.001771	196	0.00529
103	0.001351	150	0.001775	197	0.005318
104	0.001353	151	0.008889	198	0.006091
105	0.001355	152	0.008968	199	0.006129
106	0.001357	153	0.00905	200	0.006166
107	0.001359	154	0.009132	201	0.006205
108	0.008096	155	0.001536	202	0.006243
109	0.004049	156	0.001538	203	0.010472
110	0.004065	157	0.001541	204	0.003528
111	0.008164	158	0.001543	205	0.00354
112	0.016326	159	0.001546	206	0.003553
113	0.008299	160	0.001548	207	0.005346
114	0.004183	161	0.004739	208	0.005375
115	0.004201	162	0.004761	209	0.010812
116	0.016879	163	0.009571	210	0.01093
117	0.001716	164	0.00322	211	0.001381
118	0.001719	165	0.003231	212	0.001383
119	0.001722	166	0.003241	213	0.001385
120	0.001725	167	0.001626	214	0.001387
121	0.001728	168	0.001629	215	0.001389
122	0.002886	169	0.001632	216	0.001391
123	0.002895	170	0.001634	217	0.001392
124	0.002903	171	0.001637	218	0.001394
125	0.008658	172	0.00164	219	0.022348
126	0.008659	173	0.003284	220	0.003809
127	0.004292	174	0.003295	221	0.003823
128	0.00431	175	0.003305	222	0.003838
129	0.004255	176	0.010049	223	0.011562
130	0.004273	177	0.002538	224	0.002924
131	0.004291	178	0.002545	225	0.002933
132	0.00431	179	0.002551	226	0.002941
133	0.008659	180	0.002558	227	0.00295
134	0.008733	181	0.010363	228	0.002958
135	0.00881	182	0.00349	229	0.002967
136	0.00889	183	0.003503	230	0.002976
137	0.004444	184	0.003515	231	0.002984
138	0.004464	185	0.005291	232	0.005918
139	0.002937	186	0.005319	233	0.005953

Age Class	DFM	Age Class	DFM	Age Class	DFM
234	0.023952	283	0.018021	330	0.001863
235	0.006134	284	0.03738	331	0.001866
236	0.006172	285	0.019416	332	0.00187
237	0.004141	286	0.001414	333	0.001873
238	0.004159	287	0.001416	334	0.001877
239	0.004176	288	0.001418	335	0.00188
240	0.004192	289	0.00142	336	0.001884
241	0.00421	290	0.001422	337	0.001887
242	0.004228	291	0.001424	338	0.001891
243	0.012741	292	0.001426	339	0.001894
244	0.003225	293	0.001428	340	0.001898
245	0.003236	294	0.00143	341	0.001902
246	0.003246	295	0.001433	342	0.026664
247	0.003257	296	0.001435	343	0.002283
248	0.008715	297	0.001437	344	0.002288
249	0.008791	298	0.001439	345	0.002293
250	0.008869	299	0.001441	346	0.002299
251	0.013421	300	0.004041	347	0.002304
252	0.004536	301	0.004058	348	0.002309
253	0.004556	302	0.004074	349	0.002315
254	0.004577	303	0.004091	350	0.00232
255	0.013791	304	0.004108	351	0.002325
256	0.013988	305	0.041233	352	0.002331
257	0.014182	306	0.003072	353	0.002336
258	0.028777	307	0.003081	354	0.002342
259	0.014815	308	0.003091	355	0.028166
260	0.015038	309	0.0031	356	0.003623
261	0.007632	310	0.00311	357	0.003636
262	0.007691	311	0.00312	358	0.003649
263	0.015506	312	0.00313	359	0.003663
264	0.007873	313	0.007325	360	0.003676
265	0.007935	314	0.007379	361	0.00369
266	0.016002	315	0.007434	362	0.003703
267	0.048778	316	0.02247	363	0.003717
268	0.001709	317	0.011495	364	0.003419
269	0.001712	318	0.011628	365	0.003431
270	0.001715	319	0.011765	366	0.003443
271	0.001718	320	0.011905	367	0.003455
272	0.001721	321	0.024094	368	0.003467
273	0.001724	322	0.024689	369	0.003479
274	0.001727	323	0.005063	370	0.003491
275	0.00173	324	0.005089	371	0.003503
276	0.001733	325	0.005115	372	0.003515
277	0.001736	326	0.005141	373	0.005968
278	0.017394	327	0.005167	374	0.006004
281	0.008848	328	0.001856	375	0.00604
282	0.008927	329	0.001859	376	0.006077

Age Class	DFM	Age Class	DFM	Age Class	DFM
377	0.006114	424	0.002006	471	0.004048
378	0.002283	425	0.00201	472	0.004064
379	0.002289	426	0.002014	473	0.004081
380	0.002294	427	0.002018	474	0.004098
381	0.002299	428	0.002022	475	0.024701
382	0.002304	429	0.002026	476	0.008437
383	0.00231	430	0.00203	477	0.008509
384	0.002315	431	0.002034	478	0.008582
385	0.002321	432	0.002038	479	0.012652
386	0.002326	433	0.001914	480	0.012814
387	0.002331	434	0.001918	481	0.002165
388	0.002337	435	0.001921	482	0.002169
389	0.002342	436	0.001925	483	0.002174
390	0.003913	437	0.001929	484	0.002179
391	0.003928	438	0.001932	485	0.002184
392	0.003944	439	0.001936	486	0.002188
393	0.003959	440	0.00194	487	0.002193
394	0.003975	441	0.001944	488	0.002198
395	0.003991	442	0.001947	489	0.002203
396	0.004007	443	0.001951	490	0.002208
397	0.027398	444	0.021505	491	0.002213
398	0.005479	445	0.0043	492	0.002217
399	0.005509	446	0.004319	493	0.026669
400	0.005539	447	0.004338	494	0.0137
401	0.00557	448	0.004357	495	0.01389
402	0.005601	449	0.004376	496	0.009388
403	0.006849	450	0.010987	497	0.009477
404	0.006897	451	0.011109	498	0.009567
405	0.006944	452	0.022481	499	0.00966
406	0.006993	453	0.002298	500	0.009754
407	0.006493	454	0.002304	501	0.00985
408	0.006536	455	0.002309	502	0.010254
409	0.006579	456	0.002314	503	0.010361
410	0.006622	457	0.00232	504	0.010469
411	0.025977	458	0.002325	505	0.005649
412	0.002389	459	0.002331	506	0.005681
413	0.002395	460	0.002336	507	0.005713
414	0.002401	461	0.002342	508	0.005746
415	0.002406	462	0.002347	509	0.00578
416	0.002412	463	0.003921	510	0.005813
417	0.002418	464	0.003936	511	0.035083
418	0.002424	465	0.003952	512	0.005197
419	0.00243	466	0.003968	513	0.005224
420	0.002436	467	0.003983	514	0.005251
421	0.021974	468	0.003999	515	0.005279
422	0.001998	469	0.004015	516	0.005307
423	0.002002	470	0.004032	517	0.005335

Age Class	DFM	Age Class	DFM	Age Class	DFM
518	0.005364	565	0.01408	612	0.001572
519	0.00539	566	0.008161	613	0.001574
520	0.005419	567	0.008228	614	0.001577
521	0.005449	568	0.008296	615	0.001579
522	0.005479	569	0.008366	616	0.001582
523	0.005509	570	0.008436	617	0.001584
524	0.005539	571	0.008508	618	0.001587
525	0.00557	572	0.008581	619	0.001589
526	0.008162	573	0.008655	620	0.001592
527	0.008229	574	0.008731	621	0.001594
528	0.008297	575	0.008808	622	0.001597
529	0.008366	576	0.008886	623	0.001599
530	0.008437	577	0.008966	624	0.001602
531	0.042544	578	0.009047	625	0.001604
532	0.003418	579	0.009129	626	0.001607
533	0.00343	580	0.032247	627	0.00161
534	0.003442	581	0.033322	628	0.001612
535	0.003453	582	0.00383	629	0.001615
536	0.003465	583	0.003845	630	0.001617
537	0.003477	584	0.00386	631	0.00162
538	0.00349	585	0.003875	632	0.001623
539	0.003502	586	0.00389	633	0.001625
540	0.003514	587	0.003905	634	0.001628
541	0.003526	588	0.00392	635	0.001631
542	0.003539	589	0.003936	636	0.001633
543	0.003552	590	0.003951	637	0.001636
544	0.003564	591	0.003967	638	0.001639
545	0.02325	592	0.003983	639	0.001641
546	0.023804	593	0.003998	640	0.001644
547	0.006502	594	0.004015	641	0.001647
548	0.006545	595	0.004031	642	0.001649
549	0.006588	596	0.004047	643	0.001652
550	0.006632	597	0.004063	644	0.001655
551	0.006676	598	0.00408	645	0.001658
552	0.006721	599	0.004097	646	0.00166
553	0.006766	600	0.001543	647	0.001663
554	0.006812	601	0.001545	648	0.004704
555	0.006859	602	0.001547	649	0.004726
556	0.006907	603	0.00155	650	0.004749
557	0.006955	604	0.001552	651	0.004771
558	0.007003	605	0.001555	652	0.004794
559	0.007053	606	0.001557	653	0.004817
560	0.007103	607	0.001559	654	0.004841
561	0.007154	608	0.001562	655	0.004864
562	0.01351	609	0.001564	656	0.004888
563	0.013695	610	0.001567	657	0.004912
564	0.013885	611	0.001569	658	0.004936

Age Class	DFM	Age Class	DFM	Age Class	DFM
659	0.004961	706	0.003924	753	0.00328
660	0.004985	707	0.00394	754	0.003291
661	0.00501	708	0.003956	755	0.003302
662	0.005036	709	0.003971	756	0.003312
663	0.005061	710	0.003987	757	0.003323
664	0.005087	711	0.004003	758	0.003335
665	0.008687	712	0.004019	759	0.003346
666	0.008763	713	0.004035	760	0.003357
667	0.008841	714	0.009792	761	0.003368
668	0.00892	715	0.009888	762	0.00338
669	0.009	716	0.009987	763	0.005305
670	0.009082	717	0.010088	764	0.005333
671	0.009165	718	0.010191	765	0.005361
672	0.00925	719	0.010296	766	0.00539
673	0.009336	720	0.010403	767	0.00542
674	0.009424	721	0.010512	768	0.005449
675	0.009519	722	0.010624	769	0.005479
676	0.00961	723	0.010738	770	0.005509
677	0.009703	724	0.010854	771	0.00554
678	0.009798	725	0.010974	772	0.005571
679	0.009895	726	0.022191	773	0.005602
680	0.009994	727	0.022694	774	0.005633
681	0.010095	728	0.023221	775	0.005665
682	0.010198	729	0.023773	776	0.014813
683	0.010303	730	0.024352	777	0.015036
684	0.01041	731	0.02496	778	0.015266
685	0.003626	732	0.003069	779	0.015502
686	0.003639	733	0.003078	780	0.015746
687	0.003652	734	0.003087	781	0.004921
688	0.003666	735	0.003097	782	0.004945
689	0.003679	736	0.003107	783	0.004969
690	0.003693	737	0.003116	784	0.004994
691	0.003706	738	0.003126	785	0.005019
692	0.00372	739	0.003136	786	0.005045
693	0.003734	740	0.003146	787	0.00507
694	0.003748	741	0.003156	788	0.005096
695	0.003762	742	0.003166	789	0.005122
696	0.003776	743	0.003176	790	0.005149
697	0.003791	744	0.003186	791	0.005175
698	0.003805	745	0.003196	792	0.005202
699	0.00382	746	0.003206	793	0.005229
700	0.003834	747	0.003217	794	0.005257
701	0.003849	748	0.003227	795	0.016122
702	0.003864	749	0.003237	796	0.016386
703	0.003879	750	0.003248	797	0.016659
704	0.003894	751	0.003258	798	0.016941
705	0.003909	752	0.003269	799	0.017233

Age Class	DFM	Age Class	DFM	Age Class	DFM
800	0.017535	847	0.002606	894	0.012906
801	0.017848	848	0.002613	895	0.019008
802	0.018173	849	0.00262	896	0.019376
803	0.037018	850	0.002627	897	0.019759
804	0.038441	851	0.002634	898	0.020158
805	0.008884	852	0.002641	899	0.020572
806	0.008964	853	0.002648	900	0.021004
807	0.009045	854	0.002655	901	0.021455
808	0.009127	855	0.002662	902	0.153478
809	0.009211	856	0.002669	903	0.030217
810	0.009297	857	0.002676	904	0.031159
811	0.009384	858	0.002683	905	0.032161
812	0.009473	859	0.00269	906	0.03323
813	0.009564	860	0.002698	907	0.034372
814	0.010863	861	0.002705	908	0.035595
815	0.010982	862	0.002712	909	0.013003
816	0.011104	863	0.004572	910	0.013174
817	0.011229	864	0.004593	911	0.01335
818	0.011357	865	0.004614	912	0.013531
819	0.011487	866	0.004636	913	0.013716
820	0.011621	867	0.004657	914	0.013907
821	0.011757	868	0.004679	915	0.014103
822	0.014477	869	0.004701	916	0.014305
823	0.01469	870	0.004723	917	0.014512
824	0.014909	871	0.004746	918	0.014726
825	0.015135	872	0.004768	919	0.014946
826	0.015367	873	0.004791	920	0.015173
827	0.015607	874	0.004814	921	0.015407
828	0.002483	875	0.004838	922	0.015648
829	0.00249	876	0.004861	923	0.015897
830	0.002496	877	0.004885	924	0.016153
831	0.002502	878	0.004909	925	0.016419
832	0.002508	879	0.004933	926	0.014936
833	0.002515	880	0.004958	927	0.015162
834	0.002521	881	0.004982	928	0.015396
835	0.002527	882	0.005007	929	0.015636
836	0.002534	883	0.005032	930	0.015885
837	0.00254	884	0.005058	931	0.016141
838	0.002547	885	0.005084	932	0.016406
839	0.002553	886	0.011698	933	0.016679
840	0.00256	887	0.011837	934	0.016962
841	0.002566	888	0.011979	935	0.017255
842	0.002573	889	0.012124	936	0.017558
843	0.002579	890	0.012273	937	0.017872
844	0.002586	891	0.012425	938	0.018197
845	0.002593	892	0.012582	939	0.018534
846	0.0026	893	0.012742	940	0.018884

Age Class	DFM	Age Class	DFM	Age Class	DFM
941	0.019248	988	0.004465	1035	0.005651
942	0.019626	989	0.004485	1036	0.005683
943	0.020018	990	0.004505	1037	0.005715
944	0.020427	991	0.004525	1038	0.005748
945	0.003746	992	0.004546	1039	0.005781
946	0.00376	993	0.004567	1040	0.005815
947	0.003774	994	0.004588	1041	0.005849
948	0.003788	995	0.004609	1042	0.005883
949	0.003803	996	0.00463	1043	0.005918
950	0.003817	997	0.004652	1044	0.005953
951	0.003832	998	0.004674	1045	0.005989
952	0.003847	999	0.004695	1046	0.006025
953	0.003861	1000	0.004718	1047	0.006062
954	0.003876	1001	0.00474	1048	0.006099
955	0.003891	1002	0.004763	1049	0.006136
956	0.003907	1003	0.004785	1050	0.002088
957	0.003922	1004	0.004808	1051	0.002092
958	0.003937	1005	0.004832	1052	0.002097
959	0.003953	1006	0.004855	1053	0.002101
960	0.003969	1007	0.004879	1054	0.002106
961	0.003985	1008	0.004903	1055	0.00211
962	0.004	1009	0.004927	1056	0.002114
963	0.004017	1010	0.004951	1057	0.002119
964	0.004033	1011	0.004976	1058	0.002123
965	0.004049	1012	0.005001	1059	0.002128
966	0.004065	1013	0.005026	1060	0.002132
967	0.004082	1014	0.005051	1061	0.002137
968	0.004099	1015	0.005077	1062	0.002142
969	0.004116	1016	0.005103	1063	0.002146
970	0.004133	1017	0.005129	1064	0.002151
971	0.00415	1018	0.005155	1065	0.002155
972	0.004167	1019	0.005182	1066	0.00216
973	0.004185	1020	0.005209	1067	0.002165
974	0.004202	1021	0.005236	1068	0.00217
975	0.00422	1022	0.005264	1069	0.002174
976	0.004238	1023	0.005292	1070	0.002179
977	0.004256	1024	0.00532	1071	0.002184
978	0.004274	1025	0.005348	1072	0.002188
979	0.004292	1026	0.005377	1073	0.002193
980	0.004311	1027	0.005406	1074	0.002198
981	0.00433	1028	0.005436	1075	0.002203
982	0.004348	1029	0.005465	1076	0.002208
983	0.004367	1030	0.005495	1077	0.002213
984	0.004386	1031	0.005526	1078	0.002218
985	0.004406	1032	0.005556	1079	0.002223
986	0.004425	1033	0.005587	1080	0.002227
987	0.004445	1034	0.005619	1081	0.002232

Age Class	DFM	Age Class	DFM	Age Class	DFM
1082	0.002237	1129	0.0025	1176	0.002833
1083	0.002242	1130	0.002507	1177	0.002841
1084	0.002248	1131	0.002513	1178	0.00285
1085	0.002253	1132	0.002519	1179	0.002858
1086	0.002258	1133	0.002526	1180	0.002866
1087	0.002263	1134	0.002532	1181	0.002874
1088	0.002268	1135	0.002538	1182	0.002882
1089	0.002273	1136	0.002545	1183	0.002891
1090	0.002278	1137	0.002551	1184	0.002899
1091	0.002283	1138	0.002558	1185	0.002908
1092	0.002289	1139	0.002565	1186	0.002916
1093	0.002294	1140	0.002571	1187	0.002925
1094	0.002299	1141	0.002578	1188	0.002933
1095	0.002304	1142	0.002584	1189	0.002942
1096	0.00231	1143	0.002591	1190	0.00295
1097	0.002315	1144	0.002598	1191	0.002959
1098	0.002321	1145	0.002605	1192	0.002968
1099	0.002326	1146	0.002611	1193	0.002977
1100	0.002331	1147	0.002618	1194	0.002986
1101	0.002337	1148	0.002625	1195	0.002995
1102	0.002342	1149	0.002632	1196	0.003004
1103	0.002348	1150	0.002639	1197	0.003013
1104	0.002353	1151	0.002646	1198	0.003022
1105	0.002359	1152	0.002653	1199	0.003031
1106	0.002364	1153	0.00266	1200	0.00304
1107	0.00237	1154	0.002667	1201	0.003049
1108	0.002376	1155	0.002674	1202	0.003059
1109	0.002381	1156	0.002681	1203	0.003068
1110	0.002387	1157	0.002689	1204	0.003078
1111	0.002393	1158	0.002696	1205	0.003087
1112	0.002398	1159	0.002703	1206	0.003097
1113	0.002404	1160	0.002711	1207	0.003106
1114	0.00241	1161	0.002718	1208	0.003116
1115	0.002416	1162	0.002725	1209	0.003126
1116	0.002422	1163	0.002733	1210	0.003135
1117	0.002428	1164	0.00274	1211	0.003145
1118	0.002433	1165	0.002748	1212	0.003155
1119	0.002439	1166	0.002755	1213	0.003165
1120	0.002445	1167	0.002763	1214	0.003175
1121	0.002451	1168	0.002771	1215	0.003185
1122	0.002457	1169	0.002778	1216	0.003196
1123	0.002463	1170	0.002786	1217	0.003206
1124	0.00247	1171	0.002794	1218	0.003216
1125	0.002476	1172	0.002802	1219	0.003226
1126	0.002482	1173	0.002809	1220	0.003237
1127	0.002488	1174	0.002817	1221	0.003247
1128	0.002494	1175	0.002825	1222	0.003258

Age Class	DFM	Age Class	DFM	Age Class	DFM
1223	0.003269	1268	0.003832	1313	0.004631
1224	0.003279	1269	0.003847	1314	0.004653
1225	0.00329	1270	0.003862	1315	0.004674
1226	0.003301	1271	0.003877	1316	0.004696
1227	0.003312	1272	0.003892	1317	0.004718
1228	0.003323	1273	0.003907	1318	0.004741
1229	0.003334	1274	0.003923	1319	0.004763
1230	0.003345	1275	0.003938	1320	0.004786
1231	0.003356	1276	0.003954	1321	0.004809
1232	0.003368	1277	0.003969	1322	0.004832
1233	0.003379	1278	0.003985	1323	0.004856
1234	0.003391	1279	0.004001	1324	0.00488
1235	0.003402	1280	0.004017	1325	0.004904
1236	0.003414	1281	0.004033	1326	0.004928
1237	0.003425	1282	0.00405	1327	0.004952
1238	0.003437	1283	0.004066	1328	0.004977
1239	0.003449	1284	0.004083	1329	0.005002
1240	0.003461	1285	0.004099	1330	0.005027
1241	0.003473	1286	0.004116	1331	0.005052
1242	0.003485	1287	0.004133	1332	0.005078
1243	0.003497	1288	0.00415	1333	0.005104
1244	0.00351	1289	0.004168	1334	0.00513
1245	0.003522	1290	0.004185	1335	0.005156
1246	0.003534	1291	0.004203	1336	0.005183
1247	0.003547	1292	0.004221	1337	0.00521
1248	0.00356	1293	0.004238	1338	0.005237
1249	0.003572	1294	0.004256	1339	0.005265
1250	0.003585	1295	0.004275	1340	0.005293
1251	0.003598	1296	0.004293	1341	0.005321
1252	0.003611	1297	0.004312	1342	0.005349
1253	0.003624	1298	0.00433	1343	0.005378
1254	0.003637	1299	0.004349	1344	0.005407
1255	0.00365	1300	0.004368	1345	0.005437
1256	0.003664	1301	0.004387	1346	0.005466
1257	0.003677	1302	0.004407	1347	0.005496
1258	0.003691	1303	0.004426	1348	0.005527
1259	0.003705	1304	0.004446	1349	0.005558
1260	0.003718	1305	0.004466	1350	0.005589
1261	0.003732	1306	0.004486	1351	0.00562
1262	0.003746	1307	0.004506	1352	0.005652
1263	0.00376	1308	0.004526	1353	0.005652
1264	0.003775	1309	0.004547		
1265	0.003789	1310	0.004568		
1266	0.003803	1311	0.004589		
1267	0.003818	1312	0.00461		

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