THE ROLE OF BIRDS AND MAMMALS IN THE DISPERSAL ECOLOGY OF ASHE JUNIPER (Juniperus ashei Buckh.) IN THE EDWARDS PLATEAU, TEXAS

A Thesis

by

FELIPE CHAVEZ-RAMIREZ

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

MASTER OF SCIENCE

May 1992

Major Subject: Wildlife and Fisheries Sciences

THE ROLE OF BIRDS AND MAMMALS IN THE DISPERSAL ECOLOGY OF ASHE JUNIPER (<u>Juniperus</u> <u>ashei</u> <u>buckh.</u>)IN THE EDWARDS PLATEAU, TEXAS

A Thesis

by

FELIPE CHAVEZ-RAMIREZ

Approved as to style and content by:

R. Douglas Slack
(Chair of Committee)

Fred E. Smeins
(Member)

Ken L. Risenhoover
(Member)

Charles A. Taylor, Jr.
(Member)

William E. Neill
(Head of Department, Interim)

May 1992

ABSTRACT

The Role of Birds and Mammals in the Dispersal Ecology of
Ashe Juniper (Juniperus ashei Buckh.) in the Edwards Plateau, Texas.
(May 1992)

Felipe Chavez-Ramirez, B.S., Sul Ross State University
Chair of Advisory Committee: Dr. R. Douglas Slack

Seed dispersal ecology of Ashe juniper in the Edwards Plateau was investigated at the Texas Agricultural Experiment Station, near Sonora, Texas. Ashe juniper fruiting characteristics and avian and mammalian seed dispersers were studied to evaluate relative seed dispersal potential and dispersal efficiency of different species.

Ashe juniper produced large fruit crops that ripened during the winter months from December through mid-March. Fruit production did not occur every year and observations suggest fruit production occurs only every other year. Fruit crop maturation on individual trees was synchronous, while fruit ripening throughout the population occurred asynchronously. The synchronous tree-asynchronous population fruiting strategy is believed to be an adaptation to seed dispersal by wintering migratory birds.

Cedar waxwings (Bombycilla cedrorum) and American robins (Turdus migratorius) were the principal disperser species among the nineteen avian frugivores wintering in the study area. Differences in foraging and post-foraging behavioral attributes between cedar waxwings and American robins yielded two distinct seed dispersal patterns. The clumped seed dispersal

ACKNOWLEDGEMENTS

First of all I would like to thank my wife, Gennie, for her untiring support and patience as I pursue my graduate studies. She has tolerated and endured my long absences and has made many stressful moments more bearable.

I want to thank my advisor, Dr. R. Douglas Slack, for the opportunity to study at Texas A&M University and for his support during the various aspects of this project. All members of my graduate committee, Drs. Fred Smeins, Ken E. Risenhoover, and Charles A. Taylor, were extremely helpful with advice and input during field work. I thank them all for their critical review and input on previous drafts of this manuscript. The end product is much improved because of their time and effort.

I want to specially thank Dr. Butch Taylor for his support while conducting field work on the Texas Agricultural Experiment Station at Sonora (TAES) and for his interest in my research. Butch along with his staff were always ready to help and support my research activities in any way possible. Two members of the staff, Robert Moen and Benito Magana, were always willing to go out of their way to provide support and assistance to me, gestures I greatly appreciate.

Mr. Jimmy Holleman allowed me unlimited access to his ranch to conduct portions of the field work for which I thank him.

Several fellow graduate students conducting field work at the TAES (Sonora) provided help with various aspects of my research and made my field experience more enjoyable; they are Glenn Stout, J.R Jacobson and Sheryl Robinson. Two other students, Dustin Heitschmidt and Jeff Gunnels, also provided assistance with field work activities.

With out the financial support of Mrs. Evelyn Lineberry and the Scarborough Foundation I would have been unable to study in the United States or pursue a graduate degree. I am greatly indebted to this wonderful lady. This thesis is dedicated her.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

CHAPTER Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Ashe juniper (Juniperus ashei Buckh.) has increased in abundance and extended its range considerably on the Edwards Plateau, Texas. Ashe juniper is a large dioecious evergreen shrub or small tree with a shrubby aspect and can be up to 6 m high. In Texas its center of distribution is on the Edwards Plateau. Historically Ashe juniper was confined to canyons and rocky breaks but in recent years has spread to all ecological sites, many of which originally had little or no juniper present (Bray 1904, Foster 1917, Smeins 1980). The genus Juniperus is well-known for colonizing and invading grasslands and other communities where juniper trees were formerly present in low numbers (Bray 1904, Emerson 1932, Oosting 1942, Bard 1952, Johnson 1962, Blackburn and Tueller 1970, Burkhardt and Tisdale 1976, Young and Evans 1981). In 1948, when grazing studies were initiated at the Texas Agricultural Experiment Station at Sonora, woody cover in all pastures was reduced, by hand cutting juniper, to between 10 and 14% in different pastures. Currently, juniper represents approximately 35% of the woody plant canopy cover composition and total woody cover has increased from about 12% in 1948 to 35% in 1983 (Smeins and Merrill 1988). Throughout the Edwards Plateau Ashe juniper is present in relative densities of between 40 and 69% (Van Auken 1988).

The rate and pattern of juniper increase, as well as the biological and ecological factors that promote its dispersal, ecesis, and growth

---

Format and style follow that of The Journal of Wildlife Management rate are not well understood. It is known that mammals and birds play a major role in the dispersal of other juniper species (Livingstone 1972, McDonnell and Stiles 1983, Holthuijzen 1983, Holthuijzen and Sharik 1984) and there is some indication that birds and mammals may have an important role in the dispersal of Ashe juniper. Knowledge of dispersal mechanisms and dispersal agents together with knowledge of growth rate and ecesis will allow for greater management control over Ashe juniper. Management and control of Ashe juniper is considered by many to be a major ecological/economical problem on the Edwards Plateau (Smeins 1990).

There are some desirable attributes to Ashe juniper. The wood is much valued and used for fence post due to its high persistence and resistance to rotting. The fruit produced by this species is eaten by many species of birds and mammals in addition to providing cover for wildlife and domestic livestock. The fibrous bark found in old-age trees is the essential nesting material required by the endangered Golden-cheeked Warbler (Dendroica chrysoparia) (Kroll 1980). This fibrous bark was also used in the past by indians to make mats, saddles, and other items (Powell 1988). Ashe juniper has some industrial uses as well. Berries of Ashe juniper and other junipers are used as the flavoring agent in gin and harvested for extractable chemicals for production of perfumes, cleansing compounds, and other products (Simpson and Conner-Ogorzaly 1986).

FRUITING PHENOLOGY AND SYNCHRONY

The main adaptation of plants to enhance the dispersal of seeds is to offer the disperser a nutritional reward through fruit production (Pijl

1982). Production of fruit alone, however, will not be sufficient to attract dispersers. Other factors important in determining the type of dispersal agent are: crop size (Howe and De Steven 1979), time and length of fruiting time (Herrera 1982, Stiles 1980), synchrony of fruiting (Thompson and Willson 1979), accessibility of fruit (Moermond and Denslow 1985), fruit size and color (Wheelwright 1985, Janzen 1983, Snow 1971), nutritional quality (Herrera 1982), and scent (Pijl 1982).

The accessibility and color of fruit are important to avian foragers. In manakins (Moermond and Denslow 1985) and tanagers (Levey 1988) small changes in accessibility overrides choice of species or fruit size preferred. Color is important in determining the kind of frugivore that will be attracted. Black, blue, purple and red (Snow 1971, Pijl 1982, Janzen 1983) and bicolored (Willson and Melampy 1983, Wheelwright 1985) fruits are preferred by birds, while fruits preferred by mammals are aromatic and colored green, yellow, or white (Pijl 1982). Wheelwright (1985) has shown that frugivore size is directly correlated with maximum size of fruit consumed. The size of the seed can also be important. Very large and extremely small seeds both provide protection against predation (Snow 1971, 1981, Stiles 1980, Hoppes 1987).

Fruiting phenology and synchrony of fruit crop are important in determining the types of dispersal agents that visit a fruiting plant. The timing of fruit ripening affects the probability of dispersal by birds and mammals. Fruiting phenologies have apparently evolved influenced by the autumn influx of frugivores in temperate forests (Thompson and Willson 1979, Stiles 1980, Herrera 1982, Skeate 1987). In the eastern deciduous forest, peak migration of frugivores coincides with the peak presentation of bird disseminated fruits (Stiles 1980). Fruiting phenology, however, may be keyed not to disperser abundance but to times for optimal germination and establishment for the plant (Izhaki and Safriel 1985).

Plants producing fruit at different times of the year will have fruit of differing nutritional content and quality (Herrera 1982). Fruits produced during the hot mediterranean summer, when vertebrate water requirements are high, are watery fruits produced during the winter have high lipid contents. High quality fruits are presented during fall bird migration (Stiles 1980). The fruits are taken in large numbers but those persistent on trees are subject to rapid invasion by microorganisms. Low quality fruits are present during fall bird migration but achieve only low levels of dispersal because of competition with high quality fruits (Stiles 1980).

Synchronous or asynchronous fruit production are alternative strategies that result in the attraction of different sets of dispersers. In temperate ecosystems there is a tendency for fall- and winter-fruiting plants to ripen fruit crops more synchronously than summer-fruiting species (Thompson and Willson 1979). Summer-fruiting species develop fruit asynchronously, minimizing exposure to invertebrates while producing fruit for a small number of resident birds over a longer period of time (Thompson and Willson 1979). Fruit on fall-fruiting species ripens synchronously at the height of frugivore migration when bird densities are high. Winter-fruiting species that fruit asynchronously appear to rely on the irregular movements of wintering frugivores for seed dispersal (Thompson and Willson 1979).

Size of a fruit crop can influence the number and type of dispersers that visit a fruiting plant. Highly visible displays of abundant fruit attract a great variety of frugivores, omnivores, and herbivores of different efficiencies as dispersal agents (Smythe 1970). Howe and De Steven (1979) report the number of individual visitors, number of visiting species, and number of seeds removed increased linearly with available fruit crop.

There are advantages and disadvantages to large visible fruit crops. Highly visible fruit crops results in the dispersal of seeds to a variety of habitats and distances by a variety of dispersal agents. However, such broad dispersion of seeds may be offset if generalist frugivores are ineffective at removing and dispersing seeds than others (Howe 1981). In addition, large crops encourage sedentary behavior in frugivores which reduces efficiency of dispersal because seeds often are deposited near or under parent plant canopy (Murray 1988).

SEED DISPERSAL

There are three hypotheses of seed dispersal that apply to most fruiting plants (Howe and Smallwood 1982); the Escape, Colonization, and Directed Dispersal Hypotheses. The Escape Hypothesis predicts that there is a selective advantage for seeds deposited longer distances from the parent plant. Density dependent mortality near the plant can be due to several factors including seedling competition, pathogen attack, and predation. Competition is intense between conspecific seedlings of the same cohort (Harper 1977). Pathogens can spread faster if a greater number of seedlings of the same species are present (Antonovics and Levin

1980). Most seedling and seed predators will tend to look under or near parent plant canopies (Janzen 1971).

In the Colonization Hypothesis the seeds are disseminated widely in all possible directions so that some may encounter favorable germination sites (Howe and Smallwood 1982, Murray 1988). Therefore the possibility of occupying favorable but unpredictable sites in space and time is enhanced. Many gap dependent or early successional stage plants rely on vertebrate dispersers to colonize newly available sites. Ashe juniper's large fruit crop and ability to grow in a variety of microhabitats is predicted by the Colonization Hypothesis.

The Directed Dispersal Hypothesis predicts plants with specific edaphic or other substrate requirements will benefit if dispersers deposits their seeds in locations which meet those requirements. The dispersal of mistletoe berries by phainopepla in North America, and flowerpeckers and honeyeaters in Australia (Reid 1989) and nuts cached by birds (Vander Wall and Balda 1977) are examples of Directed Dispersal to specific substrates.

SEED VECTORS AND DISPERSAL QUALITY

Ashe juniper produces large crops of fleshy fruit. The fruit, which is functionally a berry, is a modified staminate cone composed of about 12 overlapping scarious scales, dark-blue in color and 7-8.5 mm long and 6-7.5 mm wide (Correl and Johnston 1970). In the Edwards Plateau several birds including American robins (Turdus migratorius), cedar waxwings (Bombycilla cedrorum), and scrub jays (Aphelocoma coerulescens) consume Ashe juniper fruits (pers. observ.). In addition I have found juniper seeds in scats of several mammals including raccoons (Procyon lotor), ringtails (Bassariscus astutus), black-tailed jack rabbits (Lepus californicus), and cottontail rabbits (Sylvilagus floridanus).

In temperate regions, where fruit is available only part of the year, the principle disperser agents are usually migratory or have a wide range of food preferences enabling them to switch food types between seasons. Totally frugivorous birds generally are found only in the tropics where a diversity of fruits are available most of the year (Snow 1971). In temperate regions few species outside the family Bombycillidae are highly dependant on fruits year-round (Snow 1971). Partial and opportunistic frugivory, however, can be advantageous for birds and mammals. Fruit is often super abundant in some areas for short periods of time (Morton 1973). Species that can take advantage of short periods of fruit abundance will benefit.

In a large assemblage of frugivores, dispersal vectors will differ in quality of seed dispersal offered to a fruiting plant. Two components to the quality of seed dispersal have been recognized by Herrera and Jordano (1981) and Wheelwright and Orians (1982) and defined by Reid (1989). The two components are "disperser efficiency" and "disperser effectiveness". Disperser efficiency is the probability that a seed dispersed by a vector will lodge in a safe site for germination. Disperser effectiveness is the proportion of seedlings in a population that a particular seed vector is responsible for disseminating. Disperser effectiveness is difficult to assess without the benefit of long-term and detailed studies, while disperser efficiency can be more easily determined by the study of frugivore foraging behavior. In the Edwards Plateau there are large numbers of frugivores, resident and migratory, which consume Ashe juniper fruit. All frugivores are potential dispersers of juniper seeds if the seeds are not destroyed during eating or by the digestive process.

To evaluate the efficiency of different frugivores it is necessary to determine certain parameters for each potential disperser species. A minimum criteria for dispersal agent quality is that seeds are moved beyond the canopy of the parent plant and are not destroyed by the digestion process (Stiles 1980, Howe 1981, Smith 1975, Howe and Vande Kerckhove 1979). Among frugivores, differences in disperser efficiencies are a function of speed and distance moved after feeding (Hoppes 1987), the length of time the seed is retained in the gut (Herrera 1984), and seed location after fecal deposition (Murray 1988). Differences in these parameters will contribute to variation in seed shadows generated by different disperser species (Malmborg and Willson 1988, Hoppes 1987).

The site of seed deposition is particularly important for successful germination and establishment (Sorensen 1981, Herrera 1984b, Murray 1988). Seeds deposited on exposed stones are important in the establishment of pasture juniper (<u>Juniperus</u> <u>communis</u>, Livingstone 1972). The speed at which a frugivore moves away from fruiting trees will be significant since most frugivores have very short gut passage times (Herrera 1984, Sorensen 1981). The distance moved from the fruiting tree can influence the probability of establishment at and colonization of new areas.

Behavioral rather than morphological or physiological attributes most influence seed dispersal by birds (Howe and Estabrook 1977, Herrera 1984a, b, c, 1985). Morphological or physiological adaptations of fruit-eating birds in temperate regions seems to be limited to short gut passage time

(Herrera 1984a, Sorensen 1984). Short gut retention time is advantageous because it allows fruits to be passed rapidly through the digestive system permitting birds to return to foraging in a shorter period of time. Rapid gut passage times are characteristics of good disperser species (Herrera 1984a, Howe 1981, Sorensen 1981, Stiles 1980, Howe and Vande Kerckchove 1979). Some birds regurgitate seeds thus allowing individuals to ingest more fruit and obtain more nutrition during each foraging period. A number of birds do not ingest the whole fruit, instead they take pieces of pulp from the fruit thus avoiding the seeds altogether. These species serve as dispersers only if they accidentally swallow seeds.

SEED DISPERSAL AND COMMUNITY COMPOSITION

Some aspects of community composition and structure are influenced at least partially by dispersers. Dispersers influence the colonization of areas in early successional stages by dispersing seeds of fruit producing plants. In forests represented by a mosaic of plant associations, early successional stages are well represented by animal-dispersed plants (Denslow 1980). Plant species diversity potentially can be increased by seed dispersing species. Competition among conspecific seedlings is greater than between seedlings of other species (Harper 1977). Thus, the mixing of seeds and seedling cohorts resulting from animal dispersal can increase plant species diversity (Denslow 1980). Dispersal influences spatial distribution of adults and juveniles and therefore seedlings have a much greater chance of survival if they become established far from adult trees (Janzen 1969, 1970).

In most of the Edwards Plateau region, Ashe juniper is present in high densities in most communities with the exception of riparian habitats (Van Auken 1988). Texas persimmon (Diospyros texana), plateau live oak (Quercus fusiformis), and agarita (Berberis trifoliata) also are present in high densities throughout the Edwards Plateau (Van Auken 1988). Not surprisingly, all these species rely on vertebrates for dispersal of their seeds. Ashe juniper, Texas persimmon, and agarita produce fleshy fruits of varying sizes while live oak produces acorns. Dispersal by vertebrates is believed to increase fitness of fruiting plants (Murray 1988). Germination is increased in many species after passing through animal guts. Treatment in the gut is not necessary for germination in most plants but seedlings from treated seeds gain a competitive advantage through rapid germination (Murray 1988).

GOALS AND OBJECTIVES

The goal of this research was to determine timing and duration of Ashe juniper fruit-ripening and the mechanisms of Ashe juniper dispersal in the Edwards Plateau of Texas. The study sought to ascertain which species of birds and mammals were important dispersal agents and to identify their relative importance in the overall dispersal and establishment process. Specific objectives were:

1. To determine the ripening period and ripening synchrony of Ashe juniper fruit on individual trees and throughout the study area.

Hypotheses

A. The main ripening period of Ashe juniper will be in the fall during the peak of migratory bird movement through the area.

B. Fruit will tend to ripen asynchronously on individual trees.

2. To determine which species of birds and mammals are important dispersal agents of Ashe juniper seeds.

Hypotheses

A. Birds will serve as dispersal agents of Ashe juniper to a greater degree than mammals.

B. Among birds, migrants play a more significant role in the dispersal of Ashe juniper seeds.

3. To determine the relative dispersal efficiency of different dispersal agents.

Hypotheses

A. Birds are more efficient dispersers of Ashe juniper seeds than mammals.

B. Flocking species will be more efficient at removing and dispersing large fruit crops than non-flocking species.

C. Non-flocking species scatter seeds more widely than flocking species and therefore increase dispersal efficiency.

CHAPTER II

STUDY SITE

This research was conducted on the Texas A&M Agricultural Experiment Station at Sonora, Texas. The 1430-ha station is located in the southwestern portion of the Edwards Plateau, 45 km southeast of Sonora at an elevation of approximately 735 m (Fig. 1). The Sonora station is located partially in Sutton and Edwards counties with the majority of the station occurring in the latter. Precipitation in this area averages 580 mm annually with peaks in spring and fall (Taylor 1988). The average frost-free period is 235 days. Average July temperature is 28.5° C and average January temperature is 9.0° C.

The station was established in 1916 to study animal diseases and management of livestock. Early studies conducted at the station included animal health, range management, and animal breeding. In 1948 grazing management studies were initiated to evaluate effects of different stocking rates and complimentary effects of different species of livestock (Taylor 1988).

Vegetation in the area is potentially a midgrass grassland with scattered individuals or mottes of live oak (Quercus virginiana), shin oak (Quercus pungens var. vaseyena) or juniper (Juniperus Ashei and J. pinchotii). Most pastures are in a shortgrass configuration and are primarily dominated by common curlymesquite (Hilaria belangeri), but some pastures, due to deferred grazing systems or elimination of grazing, have returned to midgrass dominance (Smeins and Merrill 1988).

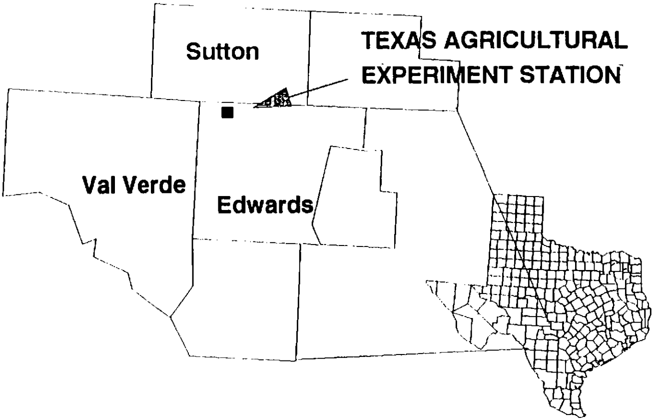

Fig. 1. Location of the Texas Agricultural Experiment Station at Sonora.

The vegetation on the station has experienced some dramatic changes in plant composition and canopy cover by woody species. Due to overgrazing, shortgrasses have replaced midgrasses and palatable forbs (Smeins and Merrill 1988). Junipers have increased from 10% of the woody species composition in 1948 to over 32% by 1985. Increase in woody species canopy cover is mainly a result of increased Ashe juniper density.

Six pastures on the station were used during the study (pastures 4, 5, 13, 14, 15, and 17). All pastures have been under the same grazing regime since 1948. They represent 2 replications of 3 grazing treatments. Pastures 4 and 5 have been under continuous heavy grazing at 0.19 au/ha and pastures 15 and 17 represent moderate deferred rotation at 0.12 au/ha. Pastures 13 and 14 have been excluded from livestock grazing, while pasture 13 also has excluded browsing wildlife by using a 2 m high fence around the pasture. All deer were removed from pasture 13 in 1948. No burning has occurred in these pastures since 1948 and none has had any mechanical or chemical treatment.

CHAPTER III

PHENOLOGY AND FRUIT-RIPENING EFFECTS ON SEED DISPERSAL

INTRODUCTION

Many studies have shown a direct relationship between fruit crop size and fruit removal rates by dispersal agents (Howe and Desteven 1979, Howe and Vande kerckhove 1979, 1981, Howe 1980, Davidar and Morton 1986). Other studies show an increased probability of visitation by frugivores with increased crop size (Jordano 1982, Murray 1987). Several other factors are also important in determining visitation and fruit removal rates in plants by birds. The quality of the fruit (Herrera 1982), the proximity of fruit producing neighbors (Manesse and Howe 1983, Moore and Willson 1982) and type and density of frugivores present in the area are important factors.

The timing of fruit maturation to dispersal by vertebrates is an important adaptation of fruiting plants (Thompson and Willson 1978). Fruiting phenologies of most fruit-producing plants are tuned to that of potential disperser abundance (Levey 1988, Skeate 1987, Herrera 1982, Stiles 1980, Thompson and Willson 1979). In temperate regions the autumn influx of avian migrants is a major selective force influencing fruiting phenology of plants (Thompson and Willson 1979, Stiles 1980, Herrera 1982, Skeate 1987). Fruit maturation periods may also be set in response to other factors, such as avoiding competition for dispersers with other fruiting plants present in the same area (Howe and Smallwood 1982), or to timing for optimal germination and seedling establishment (Izhaaki and

Safriel 1985).

Synchrony versus asynchrony of the fruit crop are believed to be adaptations by plants for the attraction of different sets of dispersers. Asynchronous fruit ripening is believed to occur in plants which rely on a small number of specialized dispersers. This strategy provides fruit for a small number of reliable dispersal agents over a prolonged period of time (McKey 1975, Howe and Estabrook 1977). Synchronous fruit ripening should occur in plants that rely on a high number of opportunistic frugivores to remove the crop in a short period of time. In temperate ecosystems there is a tendency for fall and winter fruiting plants to ripen their crop more synchronously than summer fruiting species (Thompson and Willson 1979). Synchronous fall and winter fruiting may occur because birds are less abundant in the summer and few specialize on fruit because insects are more available and are necessary for feeding the young (Morton 1973).

Synchronized fruiting by species producing large fruit crops is believed to increase the probability of frugivore visitation (Murray 1987, Davidar and Morton 1986) but can potentially satiate dispersers and thus reduce dispersal potential (Howe and Vandekhove 1979, Howe and Estabrook 1977, McKey 1975). In addition synchronous fruiting plants should be found in areas where the density of frugivores is high (Howe and Estabrook 1977, Thompson and Willson 1979, Stapanian 1982) and should have fruit that persists on the plants after ripening (Gorchov 1988, Murray 1987).

I investigated fruiting time, fruiting synchrony and potential dispersal success of Ashe juniper to evaluate the following predictions:

(1) Where large, synchronous fruiting crops satiate dispersers, plants with large fruit crops in areas of high frugivore densities should ripen fruit asynchronously. (2) Where ripening occurs synchronously plants should have highly persistent fruit.

METHODS

Five mature fruit-producing Ashe juniper trees were selected at random for observation on fruit ripening, estimation of fruit crop size and fruit removal rates. A tree was considered mature if it was taller than 3 m and a canopy area greater than 8 m^2. The size of fruit crop was initially estimated using the reference unit method (Carpenter and West 1987, Kimse and Norton 1985). A branch with similar fruit crop to the one to be estimated was selected and used to determine the amount of fruit in 1/8 of the tree canopy. The number obtained was then multiplied by 8 to determine the estimated fruit crop for that tree. The reliability of this method in estimating crop size was determined with a preliminary study where a tree's crop was estimated then actually counted by collecting all fruit on the tree. The results were remarkably similar with the estimated fruit crop (30,888) less than 1,000 berries of the actual fruit crop (31,682). At weekly intervals trees were visited and fruit ripening assessed (see below) and fruit removal rates estimated.

Fruit removal rates were estimated for each tree by counting the berries on 10 previously selected and marked fruit clusters on a branch of each of the five trees. Fruit clusters were marked by tying a wire at the base of stems each with a different color. Two of the selected trees had to be excluded from removal estimates because livestock consumed many berries and broke several of the marked fruit clusters.

Berries were collected each week from marked trees and examined to assess the degree of fruit ripening by measuring length and width of 25 collected berries to the nearest 0.1 mm. The color, texture, and ease of removal of fruit from the peduncle also was noted at each collection time. Number of fruiting trees in a hectare was determined by counting the number of fruit bearing trees of any size in a 100 x 50 m plot and multiplying by 2. The plot, located in a 32 hectare pasture, was selected arbitrarily because it was representative of the surrounding area.

During the summer of 1990, following the 1989-90 winter of high fruit production and dispersal, seed germination was evaluated in the field. The objective was to determine if germination occurs during the spring and summer following dispersal and evaluate germination success at different sites. A 1 x .5 m quadrat was used in defined microhabitats to estimate germination success under selected microhabitats. The microhabitats sampled included observed cedar waxwing perches (N = 5), fruit-producing (N = 6) and nonproducing Ashe juniper trees (N =7), small (N = 11) and large (N = 9) oak-juniper mottes, individual oaks (N = 7), and mesquite trees (N = 6). Since there were great differences in the amount of area sampled per microsite a germination index was used to compare sites. If the density of seedlings was 1 / 1 m^2 the germination index would be 100.

$$\text{germination index} = \# \text{ of seedlings} / \text{area sampled} * 100$$

Three permanent walk-through transects were established within the study pastures for estimation of bird numbers and observations of frugivores feeding on Ashe juniper. The transects were located along the center of the long axis of study pastures since all pastures in the station were rectangular. Transect number 1 was in pasture 4, transect number 2 extended the length of pastures 13 and 14, and the third transect extended through pastures 15 and 17. Individual transects measured at least 1.5 km in length. At least two transects were sampled per week during the study period for estimation of bird numbers. Transect counts were initiated at 0800 hr and all individuals and species observed while walking the transect were noted. When possible the size of individual bird flocks was also estimated. Due to unpredictability of bird flock two sites where feeding and movements of birds could be easily observed were selected for intensive observation of bird feeding on individual Ashe juniper trees. Two hour observation periods were conducted at weekly intervals at the selected sites located in pastures 4 and 17.

RESULTS

Phenology

A generalized phenological cycle for Ashe juniper showing times of pollination, fruiting, and germination was determined by field observations (Fig. 2). Direct and indirect evidence obtained during the last 4 years suggest Ashe juniper produces large fruit crops only every other year suggesting a full fruiting cycle is completed in two years. The cycle begins with the pollination of flowers in the winter of the

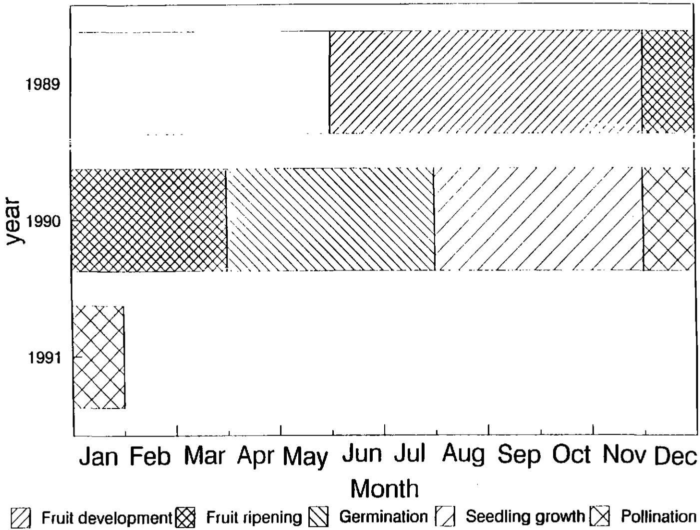

Fig. 2. Ashe juniper reproductive cycle based on observations from 1989 to 1991 on the TAES, Sonora.

year preceding the winter of fruit production and end in the second spring when all fruits have ripened and are dispersed or dropped.

Germination of Ashe juniper seedlings was observed at all sites sampled with the exception of open pasture (Fig. 3) during the month of August 1990. The microsites supporting the highest density of seedlings were fruiting Ashe juniper trees and individual mesquite trees. Densities at all other microsites were uniformly low.

The majority of the seedlings were approximately 5 cm high at time of sampling in the middle of August and therefore actual germination time must have been one or two months before or as early as the spring months. Because all seedlings were remarkably similar in size and height, I believe germination must have occurred simultaneously during a time when weather conditions were particularly favorable.

Pollen production varied considerably between 1989-90 and 1990-91 winter months. Little, if any, pollen was produced during 1989-90 when a large fruit crop was ripening on trees. During 1990-91 when little fruit production occurred pollen production was plentiful. Pollen release occurred in the month of December since observations at the end of November showed pollen strobili still full while observations on January 3 showed that all pollen had been released.

Fruit Production and Maturation

The size of winter fruit crops on Ashe juniper trees varied considerably among trees and on individual trees between winters (Table 1). Estimates ranged between 7,560 and 196,912 berries (mean = 101,509) for five different trees in 1989-90, between 7,744 and 226,944 berries

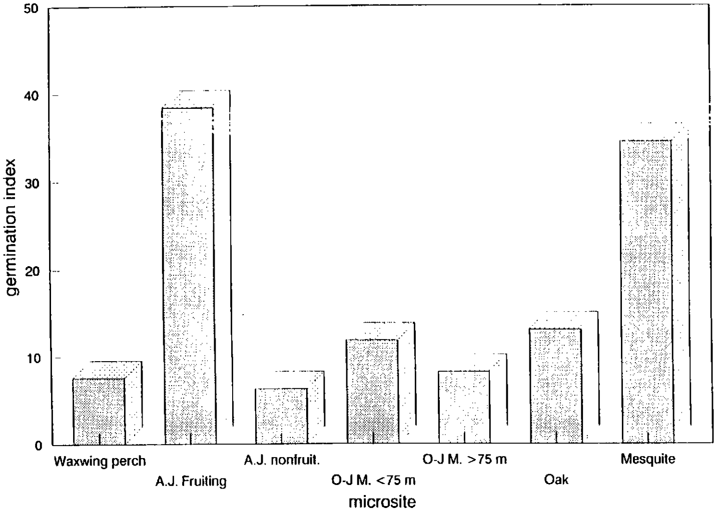

Fig. 3. Comparison of Ashe juniper germination at differnt microsites in the TAES, Sonora.
A.J. = ashe juniper, O-J M = Oak-Juniper motte, 75 = canopy area
germination index = # seedlings / area sampled (m) * 100

(mean = 134,444) in 1991-92, and between 0 and 1,500 berries (mean = 358) in 1990-91. The variation in crop size in 1989-90 appeared to be due to differences in height and canopy area of trees. The difference in tree size and canopy area could be a reflection of age difference unfortunately there is no reliable method of age estimation for Ashe juniper.

Table 1. Fruit crop size variation in Ashe juniper trees within and between winters in the TAES, Sonora.

			Estimated Fruit Crop		
Tree #	height m	Canopy Area (m^2)	1989-90	1990-91	1991-92
1	>4	33	196,912	100	226,944
2	3-4	16	57,504	1,500	----
3	3-4	9	7,560	100	7,744
4	>4	76	154,660	90	198,576
5	3-4	27.5	90,909	0	104,512

Fruit was present on Ashe juniper trees as early as May and June. Ripening, however, occurred during the winter between 5 December and the middle of March. A fruit crop was considered ripe when the fruit was palatable to birds (i.e being consumed) and when fruit were: dark blue in color, soft texture, sweet tasting, and easily removed from the peduncle. Ease of removal from the peduncle appeared to be the best diagnostic characteristic in determining ripeness. When fruit had ripened it could easily be removed sometimes by just touching the fruit. The fruit once ripe tended to desiccate quickly and was prone to fall from the tree as wind was observed to cause fruit fall. The fruit crop on individual trees appeared to ripen synchronously. The basis for this conclusion include: 1) studies of fruit removal by birds on individual trees (chapter IV) and, 2) observation of foraging behavior of the birds feeding on Ashe juniper fruit.

Trends in the size of fruits was similar on the 3 trees (Fig. 4, 5, and 6). Fruit are elongated but become round as they ripen. Fruit length remains relatively stable but fruit on all trees initially demonstrated a slow gradual increase in fruit width followed by a very marked increase over a 2-3 week period followed by a second period of gradual gain in size.

Considerable variability was found in the number of fruit bearing plants in the sample plot during consecutive winters. During 1989-90, 18 fruit-producing trees were present, while the same plot contained only 4 fruit bearing Ashe juniper trees in 1990-91. All fruit bearing trees during the first winter had large fruit crops while the 4 fruiting trees encountered in 1990-91 had fruit crops under 500 berries.

Frugivore Phenology and Abundance

The number of frugivores observed along transects conducted in 1989-

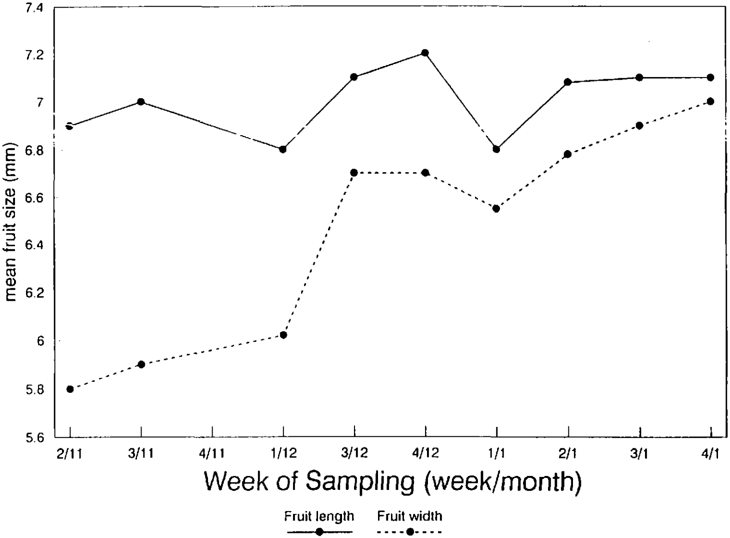

Fig. 4. Changes in Ashe juniper fruit size in tree number 1 throughout the fall and winter of 1989-1990.

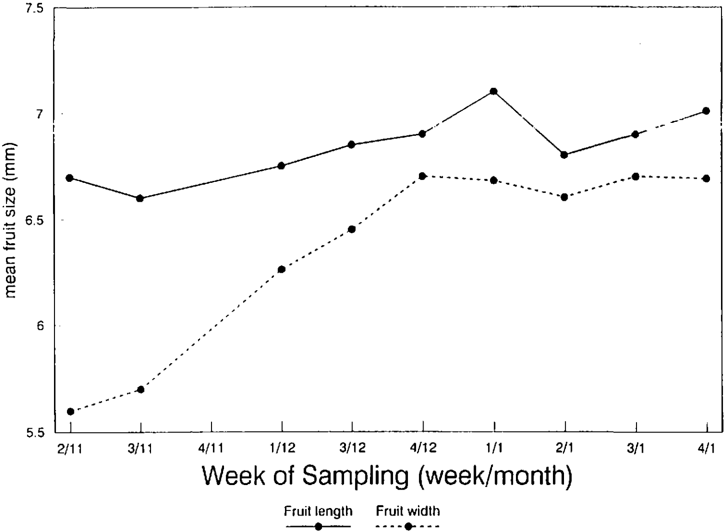

Fig. 5. Changes in Ashe juniper fruit size in tree number 2 throughout the fall and winter of 1989-1990.

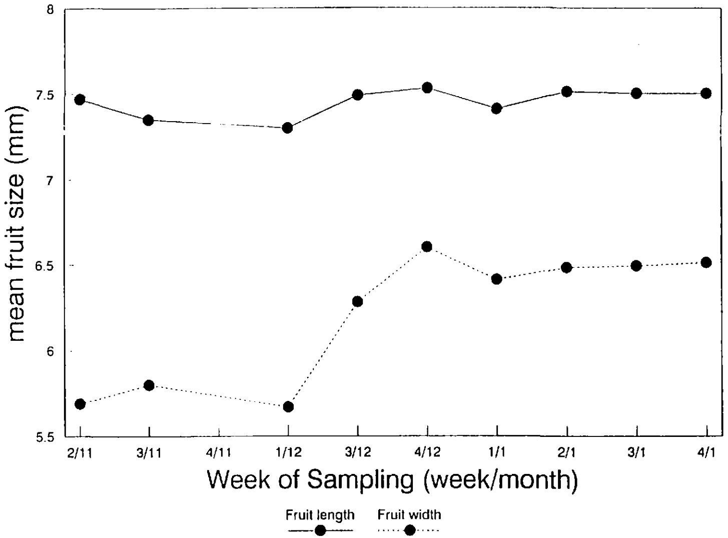

Fig. 6. Changes in Ashe juniper fruit size in tree number 3 throughout the fall and winter of 1989-1990.

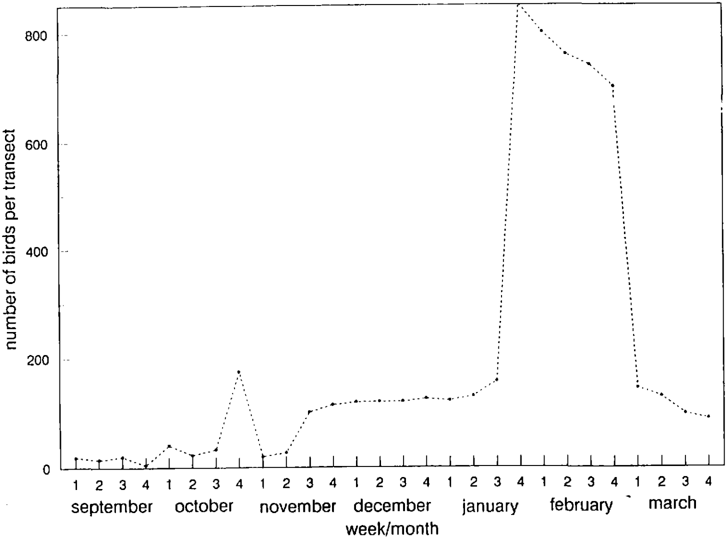

Fig. 7. Number of birds counted along walking transects at the TAES, Sonora during fall and winter 1989-1990.

1990 increased during the middle of October and peaked by the end of January (Fig. 7). A secondary peak was observed at the end of October followed by a drop in frugivore numbers during the first half of November but an increase was observed for the remainder of the month. The number of frugivores remained relatively high through December and most of January. The increase in number of birds observed during the two peaks is due mainly to an influx of robins and waxwings on the area. Numbers of other species on the area remained relatively stable after the first half of November. Robins accounted for 91% of the individual birds counted during the peak in the middle of October. Robins and waxwings, combined, made up 99% (robins 21.7%, waxwings 77.6%) of the birds counted during the month of January.

During the fall and winter of 1990-1991 waxwings and American robins were only rarely observed at the Sonora Station. Only 2 robins were observed on 20 November, and 10 waxwings were seen on 10 December (B. Magana, pers. comm.), at the station. No waxwings or robins were observed during 8 transects conducted between October and December of 1990 and in January 1991.

Fruit Removal During Winter of 1989-1990

Two marked trees had to be excluded from the fruit removal estimates during 1989-90 because livestock consumed many of the berries and broke some of the marked fruit clusters. However, on the 3 remaining marked trees between 93% and 95% of the fruit crop was removed by the time of the last count. Between 52% and 80% of the fruit crop was removed during one week (Fig. 8). The high removal rate suggests that greater than 50%

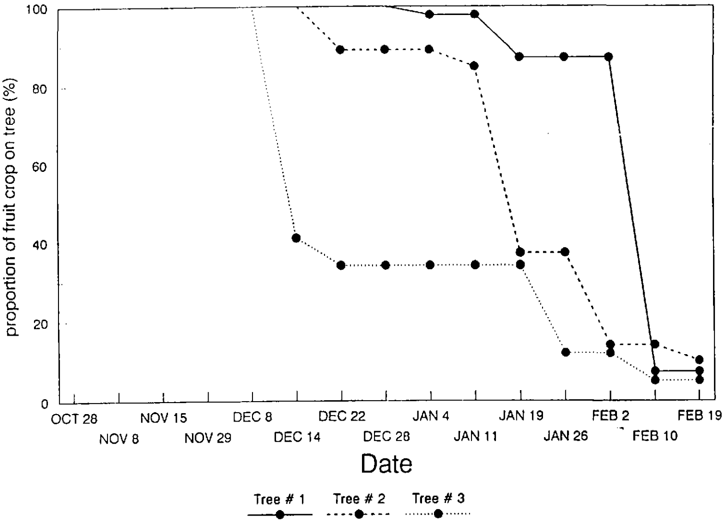

Fig. 8. Rates of fruit removal by birds on 3 Ashe juniper trees at the TAES, Sonora during fall and winter 1989-1990.

and as much as 80%, of the fruit crop on individual trees was ripe at one time and available to frugivores. Careful examination of the remaining fruit on trees strongly suggest that 100 % of fruit was ripe at this time. However, weekly counts did not provide a basis to determine if fruit crop removal between counts occurred in one day or over seven days. Based on observations of the foraging behavior of the principle dispersal species it is reasonable to assume the percentage of the fruit crop removed could have easily been removed in a few hours (see foraging behavior below).

Foraging Behavior of Frugivores

Observations on the foraging behavior of the birds feeding on Ashe juniper fruit provide information on the synchrony of fruit ripening assuming consumption was best measure of ripening fruit. Foraging birds utilized the fruit of specific trees on specific dates. During an 2 hour observation period at a specific site, individuals of five different bird species were observed to visit a single tree to consume fruit at different times when no other birds of the same or different species were present to influence their choice. Other fruit producing trees were present less than 5 m away but were not visited by birds during observations. During observations on the foraging behavior of the two most common species, cedar waxwings and American robins, a single tree was visited continuously by both species despite the fact that fruit on nearby trees ($\leq$ 5 m) appeared externally similar. Close examination of the fruit on all trees within a 10 m radius revealed differences in texture and ease of removal from the peduncle compared to the tree selected for feeding by the birds.

Visits to the individual trees usually continued by birds until the fruit crop was nearly or entirely depleted. The total number of berries left on one tree after feeding by a mixed flock of waxwings and robins was 32. Based on the size of the tree I estimated the original size of the fruit crop to be around 90,000 fruits. I observed at least 10 other trees where the fruit crop was almost entirely depleted by flocks of foraging waxwings and robins within a few hours. Had frugivore satiation occurred a large number of fruit would have remained in the fruiting trees after feeding by bird flocks.

DISCUSSION

The results presented here do not support the hypothesis that large synchronous fruit crops satiate dispersers (Janzen 1971) and reduce dispersal potential (Howe and Vander Kerkhove 1979, Howe and Estabrook 1977). Ashe junipers while producing thousands of berries on individual trees, failed to satiate dispersers since high percentages of its fruit crop is efficiently dispersed by birds. I propose that the reason dispersers are not satiated by the large fruit crops is that Ashe juniper in the Edwards Plateau ripens fruit synchronously on individual trees while fruit ripening occurs asynchronously between trees throughout the population.

The satiation hypothesis assumes the ability or the density of dispersers is insufficient to remove all or high percentages of the fruit crops and therefore much effort is wasted by the plant when large quantities of seeds are not dispersed (Howe and Estabrook 1977). High percentages of large fruit crops could be removed assuming, the density of birds present in the area is high and they concentrate their foraging efforts to one or few trees at a time. Since the amount of fruit on Ashe juniper trees can be very high and ripens synchronously, the above assumptions can only be met if the species feeding on the fruit forage socially, in flocks, and concentrate their feeding to one or few trees at a time. The two most common species present in the area during the winter are present in very high densities and forage in flocks, and at times mixed species flocks, in the same Ashe juniper tree. High percentages of individual fruit crops are removed in relatively short periods of time, as can be observed in the results of fruit removal on marked trees. Observations on feeding birds show that flocks of American robins and cedar waxwings are capable of depleting entire fruit crops of up to 100,000 fruits in a few hours. The primary disperser species are therefore capable of removing large synchronous fruit crops but is their feeding concentrated to a few fruiting trees?.

In temperate ecosystems where the density of plant species can be high we expect high levels of intraspecific competition for dispersal agents. Moore and Willson (1982), and Thompson and Willson (1978) have observed that spatial distribution of conspecifics can affect the rate of removal of ripe fruits by dispersal agents. Competition would be severe if the density of fruit producing conspecifics is high as is the case with Ashe juniper in the TAES and throughout the Edwards Plateau. If competition is indeed severe it will be to the advantage of individual trees to ripen their fruit crop at a time when their neighboring conspecifics do not, forcing dispersers to concentrate their feeding to those trees with ripe fruit. The population of Ashe juniper in the Edwards Plateau appears to have adapted its fruiting to avoid intraspecific competition for dispersal agents by ripening the fruit synchronously on a few trees at a time throughout the population. A few synchronous trees in a relatively large area will increase the probability that birds will concentrate on those trees with ripe fruit crops. It will be more profitable for birds to stay in an area where a tree with abundant ripe fruit is present than to search for another source of fruit if the location and distance between ripe fruiting trees is unpredictable.

Plants with large ripe daily fruit crops are more likely to attract frugivores and hence disperse more seeds (Murray 1987). Large crops of synchronous ripening fruit, once located, also provide an abundant and predictable source of fruit for flocks of dispersers. Foraging bird flocks are expected to concentrate their feeding on an individual tree when: 1) the quantity of fruit is high, sufficient to satisfy the entire flock, 2) the entire fruit crop is ripe and available to the birds at one time, and 3) no other trees with ripe fruit are present within a relatively short distance. Individual trees must therefore provide a fruit crop large enough to make it profitable for flocks of birds to spend time in the area and make several visits to a fruiting tree. Observations on the foraging behavior of the main disperser species of Ashe juniper showed birds to concentrate their feeding on a single tree at a time. If large numbers of birds concentrate their foraging to specific trees, large percentages of the fruit crops could potentially be removed. Dispersal potential, however, would be reduced if the dispersers spend long periods of time foraging on individual trees and excreted seeds underneath trees with synchronous fruit crops (Stiles 1982), this behavior was not observed in the waxwings and robins feeding on Ashe juniper. Both species moved away from the fruiting tree in the interval between feeding bouts, thus efficiently dispersing a high percentage of the seed crop away from parent trees. Movement away from the feeding tree between feeding bouts is probably a response to the presence of avian predators which are common in the area during the winter.

Ashe juniper produces large, synchronous fruit crops, however, it does not conform to expectations regarding this type of fruiting scheme. Notably synchronous fruiting plants should have persistent fruit after ripening (Murray 1987, Gorchov 1988). Ashe juniper does not. Once Ashe juniper fruit is ripe it tends to desiccate rapidly and has very low persistence ability. In fact ease of removal from the peduncle was determined to be a characteristic of ripe fruit. We would expect winter ripening fruit to be able to remain longer on the tree than summer ripening fruit because it is less susceptible to decay and invasion by microorganisms (Stiles 1980, Stapanian 1982). Because of the concentrated foraging behavior of the principal dispersal agents on Ashe juniper there will be little advantage for fruit to remain on the tree once ripening has occurred and a high percentage of the fruit crop removed. The low numbers of fruit left on the tree will not be attractive to large foraging flocks, which would require high numbers of fruit to satisfy. While it is possible that other species of non-social birds and mammals could eat the fruit remaining on trees, it is believed that Ashe juniper's fruiting strategy strongly relies on the large numbers of wintering bird flocks for seed dispersal.

In order for large number of birds to make extended use of Ashe juniper fruit throughout the entire fruiting period, the population of Ashe juniper within a locality must provide a reliable source of fruit without satiation of the main dispersal species. The availability of ripe fruit throughout an extended period could be solved by asynchronous ripening on individual trees. This strategy, however, will have the effect of reducing dispersal potential since the major frugivores present forage in flocks and will be less likely to visit a tree with a small supply of ripe fruit available which may not satisfy the entire flock. Ashe juniper provides fruit throughout the entire winter by extending it's fruit ripening season from December through March. Fruit is presented on shorter time scale by ripening fruit synchronously on a few trees at a time throughout the population.

CHAPTER IV

AVIAN FORAGING AND POST-FORAGING BEHAVIOR EFFECTS ON SEED DISPERSAL PATTERNS

INTRODUCTION

Many plant species in temperate and tropical ecosystems produce fruit with seeds that are consumed and dispersed by birds. In temperate regions birds are probably the most important dispersal agents of fruit producing plants (Pijl 1982). Among the array of potential dispersers in an area, only a few will be efficient dispersal agents of any particular plant. A frugivore's foraging mode and post-foraging behavior will determine the species efficiency as a seed disperser. Dispersal efficiency is defined as the probability that a seed dispersed by a vector will land in a safe place to germinate (Reid 1988). Successful germination of seeds may depend on the distance the seeds are dispersed from the parent plant (Janzen 1970), microsite conditions at location where seeds land, and the density of the seeds germinating at that specific site (Howe 1989).

Disperser attributes will have an influence on the location of the microsite where seeds land, the distance from parent plant, and the density of seeds at specific sites. A frugivore's gut passage time and the distance moved from the foraging tree after feeding will determine the distance at which the seeds will be deposited from the parent plant. The ultimate location of the seeds via fecal deposition will be determined by the dispersers movements after feeding, direction and distance, and the type of post-foraging perch selected while processing the fruit. High densities of seeds at a particular location may be found if the disperser is a large frugivore, usually a mammal (Howe 1989), or a small bird that forages in tightly structured flocks. Another attribute of fruit-eating animals which determines dispersal efficiency is the number of seeds moved away from the fruiting trees. The transport of seeds from the tree is a function of the number of visits of a species to a fruiting tree, time spent on the tree, and efficiency of fruit handling. In order to evaluate the relative contribution of different frugivores to dispersal and recruitment of bird-dispersed Ashe juniper seeds, the foraging and post-foraging behavior of the species involved in dispersal must be studied and compared.

I examined the influence of birds on the dispersal of Ashe juniper seeds. The specific objectives of this study were (1) to contrast foraging behavior and post-foraging movements of bird species important to the dispersal of Ashe juniper seeds and, (2) to determine how differences in foraging and post-foraging behavior affect seed dispersal, patterns of disperser species, and the efficiency of Ashe juniper dispersal agents.

METHODS

Walk-through transects were laid out in each of six pastures in the study area. The length of the transects varied from 1 to 2 km depending on the length of the pasture. Transects were conducted once per week from 4 September 1989 and 5 March 1990 for observation of birds feeding on Ashe juniper. All observations began at 0800 h and continued to approximately 1000 h. All birds observed consuming Ashe juniper berries or fruit of other species were noted. Information recorded on each bird included: tree species on which it was perched, time spent on the feeding tree in seconds, number of berries handled and ingested per visit, direction of flight after feeding, and type of post-foraging perch selected if visible from observer's location. The distance of the perch site from the feeding tree was later measured to the nearest meter. Because the location of feeding bird flocks was unpredictable, feeding flocks were also sought out by walking randomly through the pastures. Once bird flocks were located observations were made on foraging and post-foraging behavior of birds. During observations a single bird was selected from the flock for observation. The selected bird was followed using binoculars from the time it landed on a tree to feed until it moved away to a post-foraging perch. Afterwards a different individual was selected and the procedure was repeated. Observations on a foraging flock usually continued until the flock stopped feeding.

Sites known to have served as post-foraging perch sites, for waxwings and robins, were selected for evaluation of post dispersal seed densities. A 0.5 m^2 quadrat was placed at random locations under the selected perch structures and all seeds within the plot were counted. Several plots were also randomly placed in open areas away from any potential perch structure for comparison with the bird perch sites. The open sites were in the general area of between feeding tree and post-foraging perch sites.

Germination and establishment of Ashe juniper seeds and seedlings were evaluated during the summer of 1990 following the winter of seed dispersal. Eight different microsites were chosen for study of germination and establishment. The 8 microsites were 1) under the canopy of fruit-producing Ashe junipers, 2) under canopy of non-fruiting Ashe junipers, 3) small juniper-oak mottes (<75 m of canopy), 4) large juniper-oak mottes (>75 m of canopy), 5) individual oaks, 6) individual mesquite trees, 7) known cedar waxwing perch sites (mottes of 2-5 oak trees), and 8) open pasture. Establishment by microsite was evaluated by counting the number of seedlings and saplings found of different size classes. Seedlings and saplings were divided by height into the following categories: 10-50 cm, 50-100 cm, and 100-200 cm.

RESULTS

Birds

The avian frugivores present in the Edwards Plateau during the period of Ashe juniper fruit ripening are listed and classified, based on dispersal, into one of three categories in Table 2. The species are considered at least partial frugivores and potential dispersers of Ashe juniper seeds on the basis of field observation during this study. The most important disperser species based on the number of individuals present and number of observations of feeding on juniper are the American robin and cedar waxwing. The two species were present in the area only during the winter months. The remaining species were not abundant in the area during the period of fruit ripening and were observed consuming Ashe juniper fruit on only a limited number of occasions. Major dispersers were observed consuming Ashe juniper fruit more than 100 times, other dispersers were observed consuming fruit between 1 and 10 times, while

Table 2. Avian frugivores observed in study area during census. Categories are based primarily on observations during the study.

Major dispersers	
American Robin (*Turdos migratorius*)	W
Cedar Waxwing (*Bombycilla cedrorum*)	W
Other dispersers	
Golden-fronted Woodpecker (*Melanerpes aurifrons*)	R
Northern Flicker (*Colaptes auratus*)	R
Ladder-backed Woodpecker (*Picoides scalaris*)	R
Scrub Jay (*Aphelocoma coeruluscens*)	R
Eastern Bluebird (*Silia sialis*)	W
Mountain Bluebird (*S. currucoides*)	W
Western Bluebird (*S. mexicana*)	R
Townsend's Solitaire (*Myadestes townsendi*)	W
Hermit Thrush (*Catharus guttatus*)	W
Northern Mockingbird (*Mimus polyglottos*)	R
Sage Thrasher (*Oreoscoptes montanus*)	W
Potential dispersers	
Northern Cardinal (*Cardinalis cardinalis*)	R
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	W
Brown Towhee (*P. fuscus*)	R
White-crowned Sparrow (*Zonotrichia leucophrys*)	W
Meadowlark (*Sturnella*)	R
House Finch (*Carpodacus mexicanus*)	W

R = year round resident, W = winter resident potential disperser were not observed to consume fruit but were observed on or under Ashe juniper trees.

Since only cedar waxwings and American robins were observed consuming Ashe juniper greater than 10 times the following results are based primarily on these two species. The presence and density of waxwings and robins in the study area appears to be related directly to production of fruit crops by Ashe juniper. Based on feeding observations during transects, robin and waxwing diets during the winter months on the Edwards Plateau consists almost exclusively of Ashe juniper fruit. Fruit production in the winter of 1989-90 was high as was the density of wintering robins and waxwings. In 1989 robins were first observed at the TAES, Sonora, on 8 November and occasionally thereafter. The number of robins observed, however, did not show significant increases until the first week in December. Waxwings were first seen 18 November and increased significantly in numbers by early December. Both waxwings and robins were observed feeding on Ashe juniper fruit for the first time on 6 December. The increase in bird numbers and observations of birds feeding on Ashe juniper coincided with the beginning of fruit ripening on Ashe juniper.

Fruit Availability

During years of fruit production Ashe juniper provides an abundance of fruit and is the main source of winter fruit available to frugivores at the TAES, Sonora. Two other species, mistletoe (Phoradendron ssp.) and honeysuckle (Lonicera albiflora), also produce fruit of comparable size to Ashe juniper's in the winter but their populations are localized and not abundant in the area. During the fall three other fruiting species were observed throughout the area, tasajillo (Opuntia leptocaulis), red-berry juniper (Juniperus pinchotii), and Texas persimmon (Diospyros texana). Cedar waxwings and American robins wintering in the area were observed to consume 2 and 4 species of fruit, respectively. The fruit used by waxwings was Ashe and red-berry junipers, mistletoe, and tasajillo, while robins were observed to consume fruit from the two juniper species.

Temporal Variation in Fruit Use

Ashe juniper fruit was observed to be consumed by frugivores on a single occasion in late November and made up the majority of the fruit in their diets from December to March (Fig. 9). During November waxwings were observed to consume only red-berry juniper, while American robins were observed to consume mostly red-berry but also some Ashe juniper fruit. After Ashe juniper fruit ripening began in December, Ashe juniper made up more than 90% of observations of fruit foraging by waxwings and more than 70% of observations of fruit foraging by robins. During January, February, and March for robins and February and March for waxwings 100% of observations on fruit feeding were on Ashe juniper. During the month of January mistletoe complemented the waxwing's diet making up for 33% of foraging observations while Ashe juniper made up the remaining 67%.

Spatio-temporal availability of ripe Ashe juniper fruiting trees throughout the study area was unpredictable. Phenological stage of different trees varied greatly throughout the population and fruit

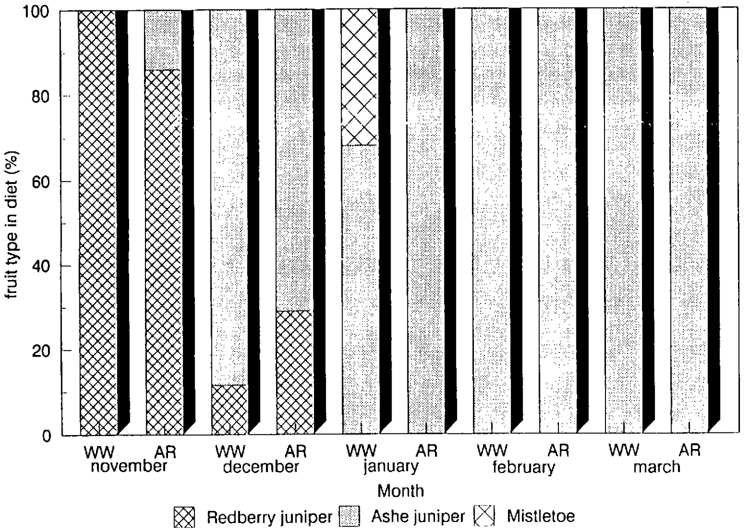

Fig. 9. Temporal use of fruit by American robins and cedar waxwings during November and December 1989 and January - March 1990 at the TAES. (WW = cedar waxwings, AR = American robin)

ripening on individual trees was determined to be synchronous. Fruit ripening on individual Ashe juniper trees in the area began in early December and extended through mid-March. Fruit was considered ripe when palatable to the birds and fruit in the following characteristics: dark blue in color, soft, easily removed from the peduncle, and sweet to the taste. Waxwings and robins were observed on Ashe juniper trees before this time but only one juniper berry were observed to be taken before 6 December. The berries were not palatable (ripe) to the birds before this date since prior to 6 December most observations on feeding by both species were on the berries of red-berry juniper. Red berry juniper, a fall fruit ripening species, had a few trees with a few berries left on them by the middle of December.

Fruit crops on individual Ashe juniper trees ripened synchronously. The preference of birds for the fruit on certain trees on specific dates was observed. During observations of feeding by birds, a single tree within a general area was visited continuously by both species. At times up to 5 different species of birds were observed to visit a single tree, despite other trees with fruit crops nearby. Visits to the tree with ripe fruit continued until the fruit crop was almost or entirely depleted. Close examination of the fruit on trees within 10 m from the feeding tree revealed differences in texture and ease of removal from the peduncle with the tree selected for feeding by birds suggesting fruit on nearby trees was not ripe. The method by which the birds located ripe fruit is not known.

Foraging Behavior

A daily predictable pattern of activity for both cedar waxwings and American robins was observed. Activity began between 0730 and 0800 h and usually birds were observed flying to drink water before they commenced foraging. Observations made at a water tank between 0730 and 1100 h yielded the highest number of birds in the fifteen minute interval between 0745 and 0800 h. As much as 92% of the waxwings and 95% of the robins recorded coming to drink water during a morning were observed during the 0745-0800 h period. Foraging activity was observed up to 1045. No feeding activity was observed between 1100 and 1415 h, the only birds observed during this time were accidentally disturbed from their perch. Foraging on fruits would resume around 1415 h and continue to approximately 1800 h. In addition to foraging on juniper fruit robins also foraged on the ground for invertebrates. Robins were observed foraging for insects in the more open and grassy areas in the study site. Most invertebrate foraging was observed in the morning between 1000 and 1100 h but also in the afternoon between 1500 and 1700 h.

Both species fly in flocks and on many occasions were observed feeding on the same tree at the same time. Waxwings formed a tightly structured flock while robins formed a very loose feeding flock. A tightly structured flock is one where the birds fly or perch close together and from a distance seems like a unit, while a loose flock observed from a distance resembles more a group of individual birds flying in the same direction, not a single unit. Robins foraging in loose flocks moved individually to and from the feeding tree. Flock size ranged from 3 to 800 (mean = 56.8, SD = 126.5, n = 44) and 2 to 50 (mean

= 10.4, SD = 10.5, n = 79) for waxwings and robins, respectively.

Considerable variation was found in the fruit handling attributes between waxwings and robins (Table 3). Fruit handling success was high for both species. An attempt was considered successful when a berry handled in the beak was actually ingested. Robins ingested on average of 87.42 % of the berries handled, while waxwings consumed 87.3 % of the fruit handled. Fruit dropped after being manipulated in the beak

Table 3. Fruit handling attributes of cedar waxwings and American robins feeding on Ashe juniper fruit in the TAES in Sonora during the winter of 1989-1990.

	N	MEAN	STD. DEV	RANGE
ROBINS				
Time on tree (sec)	60	52.3	34.1	10-160
Fruit handled/visit	60	8.83	4.01	2-1
Fruit ingested/visit	60	7.4	3.1	2-14
WAXWINGS				
Time on tree (sec)	65	28.6	12.8	8-71
Fruit handled/visit	65	4.87	2.01	1-13
Fruit ingested/visit	65	4.27	1.85	1-10

appeared to be dropped intentionally rather than being unsuccessfully handled. A small percentage of the fruit crop in the trees may not be palatable to the birds. During any single period of observation on foraging flocks, birds always foraged on the same tree. No birds were ever observed to feed on more than one tree in a general area on the same day.

American robins spent significantly more time feeding on trees than waxwings ($P < .05$, $T = 24.5$, Table 3). Individual robins spent an average of 52.3 seconds on the feeding tree. Individual waxwings spent an average of 28.6 seconds per visit to the feeding tree, the entire flock usually less than 2 minutes. With the exception of a single robin, individuals of both species would not spend time on the feeding tree after taking fruit. Waxwings took fruit very rapidly and moved away. Robins spent more time on the tree because they took more fruit and took longer to select it. Robins also handled and consumed greater number of berries per visit to fruiting trees than waxwings. Significant differences were found between the two species in number of fruit handled and ingested per visit ($P < .05$, $F = 47.93$ and $F = 47.78$ respectively).

The principal feeding technique "reaching out" (Remsen and Robinson 1990) was used by the two species while birds were perched close to a cluster of berries. Waxwings were observed on two occasions to take fruit while hovering. Both species "gulped" the fruit (swallowed the fruit whole after little handling in the bill). No attempt was observed by either of the two species to crush (mash) the fruit before swallowing. Foraging occurred mainly on the outer portions of the canopy where the majority of the fruit clusters were located. Movement within the canopy was rarely observed once the birds had perched to feed. Both species, however, moved vertically and horizontally in the canopy when the amount of fruit left on the tree was low.

The potential number of seeds individuals of the two species could take in one day was estimated using the following data: number of berries ingested per visit to feeding trees, the number of visits per hour, and the number of hours per day spent foraging on fruit. Observations of foraging show individual robins return to fruiting trees approximately every 4 minutes while waxwings return approximately every 3 minutes, giving 15 and 20 visits per hour for the robins and waxwings respectively. The time spent foraging on fruit per day was estimated to be 5 hours for the robins and 8 for the waxwings. Therefore, a single robin was estimated to eat an average of 555 juniper berries per day. Similarly a single waxwing was estimated to ingest 683.2 berries. Differences in daily consumption by individuals of both species were not observed. Since both species forage in flocks, I multiplied the estimated number of berries eaten per day by an individual by the average flock size and found a considerable difference. An average flock of robins (10.4 birds) could remove 5,772 berries in one day, while an average waxwing flock (56.8 birds) could remove 38,805.7 berries per day.

Post-Foraging Behavior

Departure vectors from feeding trees were different for the two species (Table 4). Movement of birds away from the feeding tree appeared nondirectional for the robins but were predictable for the waxwings. Direction of flight after feeding at three different trees for each species supports the idea of non-random flights away from feeding trees (robin T1 $X^2 = 24$, T2 $X^2 = 31.91$, T3 $X^2 = 7.08$, waxwing T1 $X^2 = 236.2$, T2 $X^2 = 151.6$, T3 $X^2 = 210$, critical $X^2 = 14.01$ .05 alpha level, d.f = 7.). The results of the tests are much stronger for the waxwings. At one tree (T3) results of the test show random movements of robins away from the feeding tree. In contrast to waxwings, Robins did not perch in a flock after feeding, and individuals scattered widely in distance and direction from feeding trees. The factors that influence the flight direction after feeding for the robins can not be explained at this

Table 4. Direction of flight of waxwings and robins after feeding on Ashe juniper in the TAES in Sonora during winter 1989-1990.

	% Departure by Direction							
	N	NE	E	SE	S	SW	W	NW
ROBINS								
Tree no. 1 (N=32)	12.5	12.5	-	-	25	25	25	-
Tree no. 2 (N=46)	11	-	-	6.5	11	21.7	32.6	17.4
Tree no. 3 (N=48)	10	25.8	31.3	16.6	10	-	-	6.3
WAXWINGS								
Tree no. 1 (N=17)	-	-	100	-	-	-	-	-
Tree no. 2 (N=35)	-	20	80	-	-	-	-	-
Tree no. 3 (N=40)	-	-	12	88	-	-	-	-

time but is probably dictated by the location of suitable perch sites. The direction of flight after feeding for the waxwings was determined by the location of the post-foraging perch site selected. For a given feeding tree the direction of flight away from the tree was always the same as long as the flock continued feeding on the same tree.

The choice of post-foraging perches differed for the two species. Waxwings selected a single perch structure for use between visits to feeding trees while robins selected a variety of perch sites (Table 5). For waxwings the perch site was usually the tallest group of trees around the area of the feeding tree and most commonly was a large oak motte

Table 5. Post-foraging perch sites selected by robins at TAES, Sonora. The numbers shown are pooled from observations at four different feeding trees. Numbers in parenthesis are percentages (n = 117).

Post-Foraging Perch Sites				
Oak-Juniper Mottes		Individual Trees		
small	large	juniper	oak	others
42	27	27	16	5
(36)	(23)	(23)	(13.7)	(4.3)

composed of 2-5 trees. Individual trees with little or no understory appeared to be preferred over trees associated with dense understory. Waxwings always perched in the highest parts of the canopy of the tree selected for perching. Post-foraging perch sites selected by robins included oak-juniper mottes of different sizes and individual tree species. Robins would perch both in the canopy of the trees and on the ground under the canopy. In addition to moving to post-foraging perch sites robins moved into open areas to search for invertebrates and some individuals spend considerable time on the ground away from the canopy of trees. Droppings with seeds were left by robins in open areas, on the grass and exposed rocks, and under the canopy of the different plant species selected for perching.

The density of juniper seeds found under post-foraging perch sites of waxwings and robins showed considerable differences (Table 6). Concentrations of juniper seeds found under the waxwing perch trees were extremely high. Seed densities as high as 30,000 seeds per 1 m^2 were estimated under the canopy of those trees selected as post-foraging perch sites. The highest seed densities estimated under known robin perch sites were 76 seeds per 1 m^2. Few seeds were encountered in the random open range sites sampled.

Waxwings moved shorter distances from the feeding tree to the post-foraging perch site than robins. Significant differences were found between the means of distances moved by the two species (t test, $P < .0005$). The distance moved to the perch tree by the waxwings was on average 12 m (n = 18, each N represents a flock which ranged in size between 3 and 800 birds) and ranged from 1 to 40 m. For robins the

Table 6. Post-dispersal seed densities of Ashe juniper under American robin and cedar waxwings perch sites, and at open range sites with no perch structures at the TAES, Sonora.

	Mean # of Seeds per 1 m^2	Range (SD)	N
WAXWING	22,250	14,000 - 30,000 (2,948)	8
ROBIN	30	8 - 76 (9.87)	15
OPEN SITES	5	0 - 18 (5.89)	10

distance to perch sites from the feeding tree ranged from 0 to 100 m and averaged 44 m (n = 16). Great difficulty was encountered in trying to visually follow robins to their post-foraging perch sites because of the distance moved and density of shrubs in the area.

Germination and Establishment Sites

The most favorable microsite for germination of Ashe juniper seeds appears to be under the canopy of fruiting Ashe juniper trees and individual mesquite trees (Fig. 10). The least favorable microsites are non-fruiting Ashe junipers and waxwing perch sites (oak mottes of 2-5

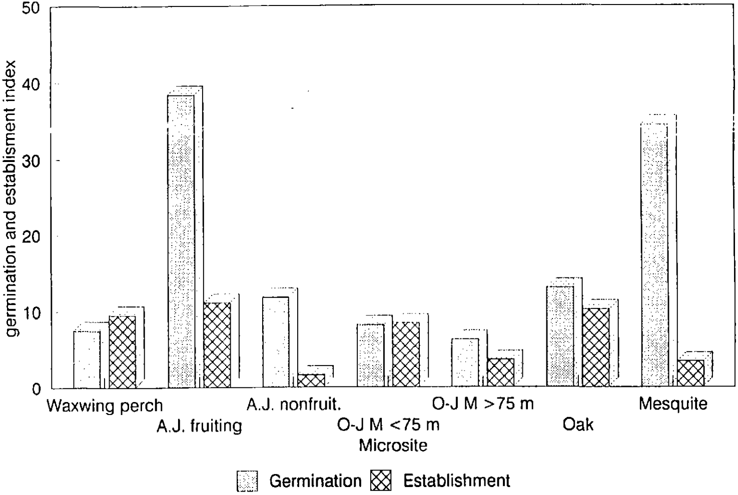

Fig. 10. Ashe juniper germination and establishment by microsite for trees between 50 and 200 cm in height. O-JM = oak-juniper motte, 75 = canopy area

trees). Open pasture was actually the lest favorable site since no seedlings were ever encountered in the randomly chosen sites studied.

Characteristics of growing populations were observed in Ashe juniper trees in the studied microsites (i.e. large number of seedlings and small saplings, and fewer large saplings and trees) (Fig. 11). The best microsite for establishment (all size classes combined) are individual oaks and waxwing perch sites which are in effect oak mottes (Fig. 12). When only trees above 50 cm are considered, most microsites are fairly even (Fig. 11) with fruit producing Ashe juniper trees and individual oaks the best sites. The worst microsite for establishment (excluding open pasture) appears to be non-fruiting Ashe junipers and mesquite trees.

DISCUSSION

The efficiency of cedar waxwings and American robins as dispersers of Ashe juniper can be determined on the basis of the quantity of seeds dispersed and the probability that seeds dispersed will land in a safe site for germination. Foraging behavior (time spent on tree, number of berries eaten per visit to fruiting trees, number of visits, flock size) will determine the quantity of seeds and the percentage of the fruit crop removed. Post-foraging behavior (departure vectors, perch type selected, distance from feeding trees) will determine the probability that seeds disseminated by dispersal agents will land in a safe site for germination. The direction of flight after feeding and the location of the perch selected will determine the seed distribution patterns deposited by the different species of dispersers. Tendencies of

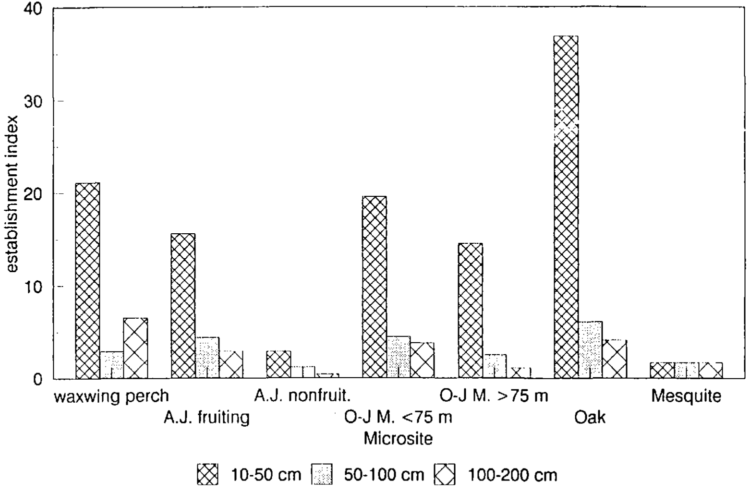

Fig. 11. Ashe juniper establishment by microsite and height classes. 75 = canopy area

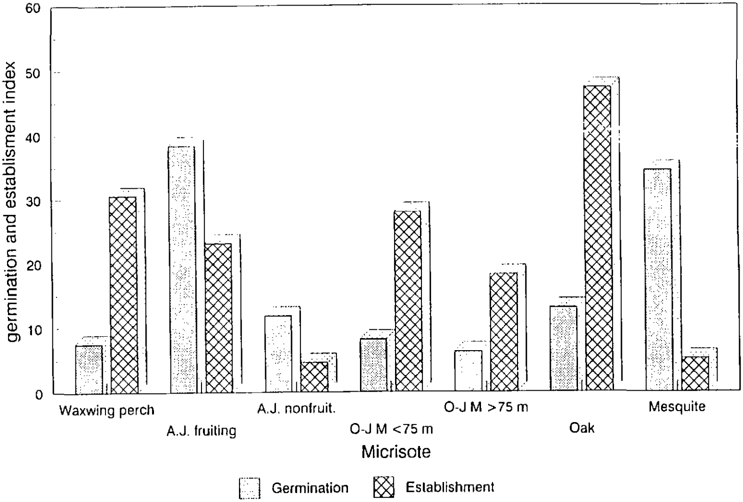

Fig. 12. Ashe juniper germination and establishment by microsite of trees between 10 and 200 cm. 75 = canopy area

different species to either disperse widely around the feeding tree or concentrate at particular sites between visits to the feeding tree will affect the dispersal patterns of the seeds.

Differences were observed in all aspects of the foraging behavior between waxwings and robins feeding on Ashe juniper fruit. Significant differences were observed in mean numbers of fruit handled and ingested per visit to fruiting trees, time spent on trees, and estimated number of berries eaten per day by individuals of both species. Waxwings are expected to remove a higher percentage of the fruit crop from individual trees, eventhough, individual robins spend twice as much time on trees and take twice as many berries per visit. Waxwings remove a higher percentage of the fruit crop because waxwings make more frequent visits to fruiting trees and spend more time per day foraging on fruit. In addition, waxwings flocks and the size of the wintering population in the area are considerably larger than for robins. Estimates of the number of seeds taken by individual birds and average flock sizes show waxwings flocks consume a greater number of fruits. Due to the quantity of seeds dispersed waxwings can be considered a better dispersal agent of Ashe juniper, however we must also consider the location of the seeds dispersed and the probability of successful germination and establishment.

Post-Foraging Behavior Effect on Seed Dispersal

The differences in post-foraging behavior between the two species yielded two distinct patterns of seed dispersal, clumped by the waxwings and scattered by the robins. The clumping of seeds by waxwings was caused by the frugivores flock structure and the fidelity to a single perch site between visits to a feeding tree. Entire waxwing flocks always selected a single perch from which the birds would fly back and forth to feed. While waxwings are responsible for removing a higher percentage of fruit crops than robins, the efficiency of dispersal offered to Ashe juniper by this species is expected to be very low. Hence because Ashe juniper seeds are capable of germinating and establishing in many microhabitats yet seeds of a single tree are dispersed to a single site by waxwings limiting the possibilities for establishment at other microsites. Waxwing post-foraging perch sites were determined to be some of the least favorable locations for germination. This point takes particularly significance when the quantity of seeds dispersed to those microsites is considered.

The post-foraging movements of waxwing flocks and resultant clumped seed deposition patterns are expected to be detrimental to the majority of seeds dispersed by this species. Any advantages given to seeds by being dispersed away from the parent tree by waxwings will be offset by the negative effects of being left in high concentrations. High densities of seeds could lead to the death of seeds and seedlings through density dependant factors: intraspecific competition, pathogen attack, seed predation, and seedling herbivory (Howe 1989).

The seed scattering effect produced by robins is a result of a wider range of post-foraging perch sites selected, greater distances moved away from feeding trees, and to foraging for invertebrates on the ground after feeding on fruit. Foraging for ground arthropods allowed robins to leave droppings and hence seeds widely scattered throughout the area surrounding the feeding tree. Robin droppings with juniper seeds could be found on exposed stones and on the open ground as well as under the canopy of the different trees present in the area. Robins are here considered to be an efficient dispersal agent of Ashe juniper because they disperse seeds to a variety of microhabitats and distances from the parent tree. Seeds ingested by robins will have a high probability of encountering a favorable microsite for germination and subsequent establishment without the risk of mortality by density dependant factors. Seed deposition sites are important determining factors of dispersal success (Sorensen 1981, Herrera 1984, Murray 1986). The presence of established Ashe juniper trees in the wide range of microhabitats studied in addition to some being present in open areas with no woody vegetation suggest the scattering effect produced by the robins is a more efficient dispersal method than the clumped dispersal pattern provided by waxwings.

The average distances moved away from the feeding tree was greater for robins than waxwings. Distance from parent tree can be of great significance in the dispersal and differential survival of the seeds deposited by the two species. Janzen (1971) has reported an increase in seedling survival the farther away seeds are deposited from the parent plant. At this time it is not known if Ashe juniper seeds benefit from increased distances from the parents. There appears to be a positive effect for seeds moved beyond the canopy of parent plants. While juniper seedlings are abundant the first spring and summer after dispersal under the canopy of most mature fruit producing juniper trees, established plants greater than 50 cm in height are rare suggesting mortality under parent trees is high after germination. Seedlings and young juniper trees are common under oak mottes and other plant species in the area as well as in open areas with little woody vegetation present.

Temporal Variation in Foraging

The two species did not show within season variation in foraging behavior. This was expected since Ashe juniper is a reliable source of fruit during the winter and provides an abundant food supply. The availability and abundance of invertebrates in the area was not monitored throughout the winter but no significant changes were observed in the robins ground foraging behavior. Between season variation in foraging behavior is expected to be considerable. Preliminary evidence suggest Ashe juniper produces large fruit crops only every other year in the Edwards Plateau. Fruit production and presence of winter frugivores has only been monitored for four consecutive winter seasons, the presence of waxwings and robins in the TAES has followed that of fruit production by Ashe juniper. During the winter of 1987-88 fruit production was high as was the number of waxwings and robins observed in the TAES (Taylor and Smeins pers. comm.). In 1988-89 and 1990-91 fruit production by Ashe juniper was very low (Smeins pers. comm., pers. observ.) and no waxwings or robins were observed in the TAES during the winter (Taylor pers. comm., pers. observ.). The winter of 1989-90 was one of abundant fruit production with the numbers of waxwings and robins in the area also at high levels. Wintering populations of these two species appear to respond to fruit availability in the Edwards Plateau. Where they spend the winter in years of fruit scarcity in this area is not known. It is possible that waxwings and robins migrate longer distances in years of low fruit production in the Edwards Plateau and spend the winter in Mexico or other areas in southern portions of the United States.

Seed Shadow

It was not possible to estimate a seed shadow for a single juniper tree due to the high density of fruit producing Ashe juniper trees in the TAES. However, this study provides some insights on differences of this system with Janzen's (1970) model of seed dispersal which shows the peak of seeds close to the parent tree. I estimated the number of seeds under and up to one meter from the canopy of two juniper trees after 95 % of the seed crop had been removed. The percentage of the seeds found under the canopy was estimated to be less than 2 % of the total seed crop for both trees. Very high percentages of the fruit crop is moved beyond the canopy of the parent plant. Seed shadows are known to vary in shape depending on type of dispersal agents. Seedfall for bird dispersed plants in Illinois showed a major peak at the parent plant and a secondary one at the location of frugivore post-foraging perch sites (Hoppes, 1987). Because waxwings and robins are the principle dispersal agents of Ashe juniper, I predict the seed shadow of this species will show a major peak at the site of the waxwings post-foraging perch site. A secondary peak is expected under the canopy of parent trees with an even seed rain between the two peaks.

Flock Structure and Dispersal

Flock size and flocking behavior were two major differences observed between the two frugivores foraging style. Waxwings flew in tighter and larger flocks while robins flocks were smaller and loose, particularly at feeding. The effect flock structure and size have on dispersal of seeds has not been well documented. Snow (1970) documented the effect of communal roosts in some tropical birds under which large quantities of seeds were encountered. The effect, however, of flocks on the potential removal of fruit crops and the consequences for dispersal have not been adequately addressed.

In this study the size, structure, and behavior of the flock proved to be important in determining visitation rates of species and the density of seeds at the sites of post-dispersal deposition. The higher the number of birds in a flock the more fruit could be consumed and therefore more seeds will be dispersed. The bigger the flock the higher the potential for removal of high percentages of fruit crops. In case of trees with large synchronous ripening fruit crops, the size of bird flocks that visit the tree will be an important factor in determining the number of seeds removed. Flock structure proved to be important in determining seed distribution patterns and densities of seeds at dispersal sites. Highly gregarious species, while potentially dispersing large numbers of seeds away from parent trees will have the disadvantage of leaving seeds clumped in high densities under the post-foraging perch sites. This was the case with waxwings in the study area where flocks are highly social. The effect of high seed densities on the germination of Ashe juniper is not known but is expected to be negative for the majority of the seeds in a clump since high densities of seeds can influence detectability by rodent seed predators.

CHAPTER V

FRUIT USE AND DISPERSAL BY MAMMALS

INTRODUCTION

The role of mammals as seed dispersal agents of fruit producing plants in temperate regions has been neglected in the literature on seed dispersal (Herrera 1989). Among mammals tropical species such as monkeys (Howe 1980, Estrada and Coates-Estrada 1984) and bats (Fleming 1981, 1986, Heithaus 1982, Morrison 1978, Gribel 1988) have been studied in recent years and have long been recognized as important seed dispersal agents (Ridley 1930, Krefting and Roe 1949, Pijl 1957). Recently the importance of herbivorous mammals in seed dispersal has been documented (Janzen 1981, 1982, 1984) and to a lesser extent the importance of carnivorous mammals has been noted (Stiles 1980, Estrada et al. 1984). Only one study deals thoroughly with the importance of carnivores (Herrera 1989) in seed dispersal of temperate fruit producing plants.

The neglect of herbivores and carnivores as subjects of study for dispersal of seeds despite the well known fact that many species in these groups commonly consume fruits (Davis 1974, Chapman and Feldhamer 1982) is curious. The fact that early work on seed dispersal placed emphasis on coevolution (Smith 1970, Snow 1971, Mckey 1975, Howe 1977) of fruit and dispersers may explain this neglect. For example, it may have been unreasonable to assume that a mammal that evolved as a flesh eating predator could serve as an efficient dispersal vector of seeds contained in fruit.

A second, perhaps more important, consideration for the paucity of data on seed dispersal by mammals may be the difficulty in studying their importance as seed vectors as compared to the relatively easy task of studying birds, a group of vertebrates on which most dispersal studies have been conducted. Most carnivores have large home ranges and are nocturnal in habits making any study of them difficult. Most information gathered on carnivore diets has been done through analysis of stomach contents but no data is obtained with respect to dispersal quality. Because of the difficulty of studying mammals most information gathered on carnivores and their possible importance as seed dispersers has been obtained through indirect means by collection of fecal material and the subsequent analysis of their seed contents (Herrera 1989).

Mammals, in particular members of the order Rodentia, have been well studied as seed predators by many authors as seen in reviews by Janzen (1971) and Harper (1977). Rodents and other seed predators can have detrimental effects on the fate of dispersed seeds (Herrera 1984). The importance of seed predators in the overall seed dispersal ecology and fitness of several plants has been studied in some temperate plants (Herrera 1984, Mittelbach and Gross 1984, Webb and Willson 1985, Klinkhamer et al. 1988). Seed loss due to rodents have ranged from 10 - 20% in Michigan (Mittelbach and Gross 1984) to as high as 70 - 100% in southwestern deserts (Brown et al. 1975). Predation of seeds can occur at several places along the dispersal process; pre-dispersal predation occurs while the seed is still in the fruit and on the tree while post-dispersal predation occurs after seeds have been stripped of the fleshy arils and moved from the fruiting tree.

There are some instances were rodents can serve as both dispersal agents and predators of some plants (Janzen 1971). Dispersal by predators is usually accidental by the process of caching and not retrieving seeds that later germinate (Howard and Evans 1961, Abbot and Quink 1970, Smythe 1970). Cached seeds may not be retrieved because more seeds were cached than were consumed during periods of seed shortage or the seeds may not be located at a later time.

Here I report information gathered on mammals at the TAES, Sonora with respect to fruit use, seed dispersal and predation of Ashe juniper fruit and seeds. In the TAES, Sonora livestock have been observed to consume Ashe juniper fruit (Taylor pers. comm.), however, this study dealt only with wild mammals. Data were collected on 8 mammals (4 Carnivora, 2 Rodentia, 1 Lagomorpha, and 1 Artiodactyla) determined to include Ashe juniper fruit in their diets and possibly serve as seed dispersers, and 1 rodent species that acts primarily as a seed predator. Particular importance is given to the season and degree of utilization of Ashe juniper fruit by these species and their potential role in the dispersal of seeds of this common plant.

METHODS

In six pastures 20 1 m x 15 m randomly located belt transects were laid out and sampled on a weekly basis for the presence of mammal feces. Each feces sample was identified to mammal species when possible, and classified according to location by microsite, and vegetation characteristics. All carnivore feces examined could not be confidently identified to species so carnivore feces were combined for parts of the analysis. Paths and trails within each pasture were checked regularly for the presence of feces since trails and open paths are heavily used by some mammals. Feces containing seeds were collected, air dried and stored in paper bags. Feces were later dissected and scored as to the presence or absence of seeds from Ashe juniper or other plants. The number of Ashe juniper seeds present was counted and the percentage in volume made up of fruit remains and seeds was visually estimated.

Stomachs from ringtails (*Bassariscus astutus*), black-tailed jackrabbits (*Lepus californicus*), and white-tailed deer (*Odocoileus virginianus*) were obtained and analyzed for presence of Ashe juniper seeds. Percentage of Ashe juniper fruit and seeds and other food material by volume was estimated visually from the stomach contents. Care was taken to identify pieces of broken seeds in feces and stomachs to evaluate damage caused by individual animals to whole seeds. Twelve deer stomachs were checked for presence of Ashe juniper seeds, 6 were collected in November and 5 in December from deer hunted in the TAES. Information on Ashe juniper fruit use and potential dispersal by deer, jackrabbits, and squirrels will be reported separately.

Sherman live traps were used to capture rodents for powder tracking studies of movements. Traps were set in all study pastures in an attempt to trap and powder mark individual mice. Trapping was done during 20 days with one hundred traps set out each night for a total of 2000 trap nights. Trapped mice were to be powder marked with flourescent pigment (Lemen and Freeman 1985) and released the same night. The following night the trail of fluorescent pigment left by the mouse would be located using an ultraviolet lamp and marked with spray paint in order to see during the day. Using this technique it is possible to determine what plants were climbed, what food items where eaten, and what burrows were used by the powdered marked mice (Lemen and Freeman 1985). Post-dispersal seed predation by rodents was also evaluated at sites were dispersed seed densities were high as under the canopy of trees selected by waxwings as perch structures.

RESULTS

Eight mammals in the area were determined to consume Ashe juniper fruit (Table 7) on the basis of feces and/or stomach samples. Feces with Ashe juniper seeds were collected from 4 carnivores, raccoon (Procyon lotor), ringtail, red fox (Vulpes fulva), and gray fox (Urocyon cinereoargenteus), one Lagomorph, black-tailed jackrabbit, and one Rodent, rock squirrel (Spermophilus variegatus).

Rodents

Two squirrels present in the study area, rock and fox squirrels (Sciurus niger), were known to consume Ashe juniper fruit. Rock squirrels have localized distributions in the area due to the requirement of large rock pile as habitat (Schmidly 1977) and were only rarely observed. Only two feces samples were obtained from rock squirrels, both of which contained unbroken Ashe juniper seeds. Fox squirrels while very common around headquarters were rarely seen in the pastures. A single fox squirrel was observed to consume fruit from Ashe juniper.

Lagomorphs

Black-tailed jackrabbits are very common in the open areas with low densities of shrubs throughout the study area. No jackrabbits were observed to consume Ashe juniper fruit but evidence of Ashe juniper seeds

Table 7. List of mammals that feed on Ashe juniper fruit in the TAES and home range size.

		Home range diameter in km
Carnivora		
Procyon lotor	Raccoon	3.2
Bassariscus astutus	ringtail cat	10.4
Vulpes fulva	red fox	4
Urocyon cinereoargenteus	gray fox	4
Rodentia		
Spermophilus variegatus	rock squirrel	.8
Sciurus niger	fox squirrel	.5
Lagomorpha		
Lepus californicus	blacktailed jackrabbit	
Artiodactyla		
Odocoileus virginianus	white-tailed deer	8

and fruit was found in feces and stomachs sampled. Ten stomachs of jackrabbits were checked, 6 of which contained Ashe juniper seeds, while 4 of the stomachs contained seeds from red-berry juniper (Juniperus pinchoti). Black-tailed jackrabbits do not appear to destroy seeds, since only one instance was found of one possibly two broken seeds in one stomach. Intact seeds were found in stomach, intestines, and in feces located through out the open pastures.

Artiodactyls

White-tailed deer are common in the area and are present in high densities (Taylor pers. comm.). Of 7 stomachs checked in November, 2 contained traces of Ashe juniper fruit while the majority of the stomach contents were acorns. In December five deer stomachs were examined of which 2 contained 100% Ashe juniper fruit and seeds, while 3 other contained 50, 70, and 70% Ashe juniper fruits and seeds, respectively. The deer stomachs contained whole seeds and fruits but there were considerable broken seed fragments suggesting deer destroy some of the Ashe juniper seeds during consumption.

It was not possible to evaluate the number of whole seeds in deer feces due to the presence of sheep and goats in the study area whose feces resemble deer's to a great degree. Pellets were located containing some numbers of whole Ashe juniper seeds but it was not possible to determine with certainty if the pellets belong to deer and not the livestock.

Carnivores

Ashe Juniper seeds were absent from carnivore feces collected in September and were uncommon in October (Table 8, Fig. 14). In November Ashe juniper was present in 14% of carnivore feces sampled, while 50% of feces collected in December contained fruit remains and seeds. During January 100% of feces contained Ashe juniper seeds while in February the number of feces containing Ashe juniper seeds declined to 90%. The mean number of seeds per scat sample varied from 6 seeds per scat in October to 80 seeds per scat in November.

Table 8. Presence of Ashe juniper seeds in carnivore feces in the TAES, Sonora during the 1989-90 fall and winter months.

	Frequency%	mean # seeds	N
September	0	0	10
October	6	6	15
November	14	80	14
December	50	26.4	14
January	100	58.6	10
February	90	42.3	11

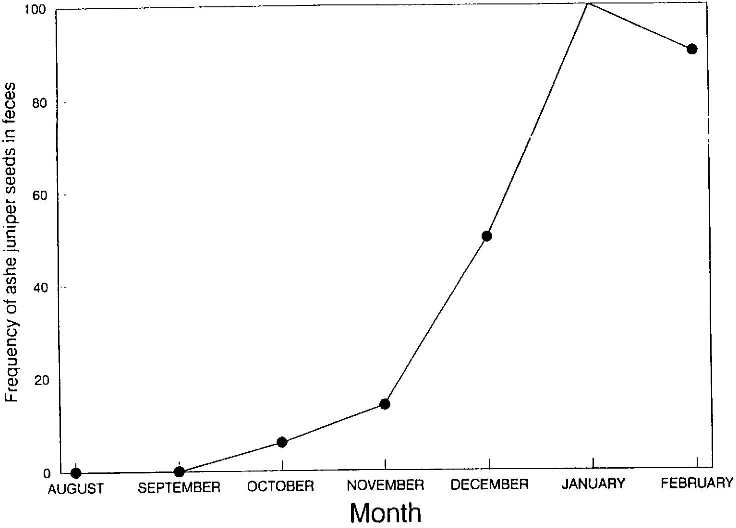

Fig. 13. Frequency of Ashe juniper seeds in feces of carnivores in the TAES during fall and winter 1989-1990.

Seed-containing feces of carnivores usually had no or few remains of animal prey. Only 21% of collected carnivore feces contained any remains of animal prey. Those identified as racoon feces (n = 14) never contained animal remains, the entire content composed of plant material. Ringtail feces (n = 10) contained animal hair and small bones 80% of the time, probably from small rodents, while 50% of fox scats (n = 8) contained animal remains.

The location of carnivore feces was not random since 95% of collected feces were found on or near roads and trails while 5% of feces were collected from the randomly located belt transects.

Seed Predation

Trapping success with sherman live traps was low (.0025%), with only 5 Texas deer mice (Peromyscus attwateri) trapped during 2000 trap nights. One of the five trapped mice was found dead in the trap the other four were powder marked and released. Three of the marked mice were successfully tracked while tracks of the fourth rodent were obliterated by a heavy rain the following day.

All marked and tracked mice showed a tendency to climb trees and shrubs particularly oaks and junipers. Two of the three tracked mice climbed up Ashe juniper trees and consumed seeds. Since fruit clusters are located on the tip of branches and twigs, mice climbed up to the canopy and clipped the tips of branches containing fruit so it would fall to the ground. The mice then climbed down the tree and would consume seeds on the ground. The fleshy portions of the fruit were striped off in order to get to the seed which was then cracked and the inside consumed. The number of seeds consumed by each mouse was estimated to be around 40 seeds each night, eventhough more than 100 fruits were counted in the clipped clusters found on the ground but were not eaten. No evidence of mice returning to the same tree during consecutive nights was found.

Evidence of seed predation by mice in the form of clipped branch tips and cracked and consumed seeds under the canopy of fruit producing Ashe juniper trees was found regularly. Monitoring of dispersed seeds under waxwing post-foraging perches revealed a high incidence of predation on these seeds by rodents. At one site, visited 4 times over 4 months, approximately 50% of seeds in the clump left by waxwings were destroyed by rodents.

DISCUSSION

Carnivores

During the study period carnivorous mammals consumed Ashe juniper fruit from November through February. It is not possible to estimate the relative importance of Ashe juniper fruit in the diet of carnivores in the area with the data collected since feces with no seeds were not examined thoroughly to determine what alternate food had been consumed. A study conducted on the food habits of ringtails in the Edwards Plateau (Toweill and Teer 1977) found that fruit from four plants including Ashe juniper made up 97% of all plant items eaten and plant material accounted for 74% of all food items encountered. The previous study was conducted between October and April and Ashe juniper was present in the ringtail diets between October and February, as in this study.

All carnivore species studied here are known to take fruits particularly in the fall and winter months (Davis 1978, Toweill and Teer 1977). It is apparent that Ashe juniper is an important winter food item for carnivores in the Edwards Plateau during the period ripe fruit is present in trees. In Spain Herrera (1989) found the highest diversity of fruit consumed by Carnivores occurred in the period of September through November time when large number of plants have ripe fruit.

Seed Dispersal by Carnivores

Ashe juniper seeds consumed by carnivores were not destroyed in the mastication and digestion process therefore all carnivores examined here can be considered legitimate dispersal agents of this species. Raccoons of all carnivore species are the most likely to destroy seeds while chewing because of their crushing type molars (Davis 1978), however, only few seeds were actually found to be crushed in raccoon feces.

Carnivores in the Edwards Plateau have the potential to disperse seeds great distances from parent trees because of large home range size, movements over great distances, and extended gut retention times. Home ranges of carnivore species studied ranged from 3.2 (raccoon) to 10.4 km in diameter (ringtail). Because of the great mobility of carnivores they are capable of dispersing seeds to new areas where Ashe juniper was not previously present.

Dispersal efficiency by Carnivores is expected to be low since the location of dispersed seeds (feces) while in areas perhaps favorable for germination are unlikely locations for successful establishment. Greater than 60% of all collected carnivore feces were found in open areas usually near or on roads and trails. While germination is possible in these sites it is unlikely significant establishment will occur due to constant trampling by wildlife and livestock. In addition mammals tend to deposit seeds in clumps which makes them vulnerable to attack by seed predators and other density dependant mortality factors.

Two carnivores in the area, ringtails and raccoons, commonly climb trees and leave feces on branches. The trees on which feces were encountered were usually large oak trees and mottes. Climbing and defecating on trunks and branches will allow seeds contained in the feces to drop to more favorable germination sites under the canopy of trees rather than in open areas along roads and trails. The seeds contained in feces located on tree branches may have a higher probability for successful germination and establishment.

The actual dispersal efficiency of carnivores will only be known by continuous monitoring of the fate of seeds and seedlings from mammal dispersed seeds. It will be necessary to determine differences in germination and survivability of seeds dispersed by different carnivores and differences in germination and establishment at different microsites where carnivores feces are found.

Seed Dispersal By Black-tailed Jackrabbits

Fruit has not previously been reported as a food item in jackrabbit diets (Davis 1978, Schmidly 1977), however, Ashe juniper fruit appears to be an important food source for jackrabbits in the Edwards Plateau. While jackrabbits appear to destroy some seeds while consuming fruit the majority of seeds pass through digestion unharmed making jackrabbits legitimate dispersers of Ashe juniper seeds. Defecation of unharmed Ashe juniper seeds plus the fact that jackrabbits are common in the study area may allow jackrabbits to disperse large number of seeds.

The preferred habitat of jackrabbits is reported as open country with scattered shrub patches and become abundant in moderately overgrazed pastures (Phillips 1936) while dense forested areas are avoided. Because of their preference for open areas jackrabbits are likely to be important in dispersal of Ashe juniper seeds to new and open sites. The presence of Ashe juniper trees in open pasture far from adult trees and far from possible perch structures for birds may be a result of seed dispersal by jackrabbits. Many jackrabbit pellets containing Ashe juniper seeds were encountered in open sites.

Seed Dispersal by White-tailed Deer

The specific effect of deer as seed dispersers is unclear, but it appears deer may be more of a seed predator than a disperser for Ashe juniper seeds. Stomach contents of white-tailed deer show they are capable of consuming large quantities of seeds but it is not known what percentage of the seeds are destroyed in chewing and digestion. It is likely high percentages of the seeds consumed are destroyed by mastication since ruminant animals tend to chew their food thoroughly. In feeding trials 2 goats were fed known amounts of juniper fruit and it was observed that well over 90% of the juniper seeds consumed were destroyed (pers. observ.). Goats and deer have very similar feeding behavior and digestion processes suggesting deer are capable of destroying high numbers of consumed seeds.

Only 2 of 7 deer stomachs checked in November had traces of Ashe juniper fruit and seeds while all those checked in December contained great numbers of seeds. The reasons for this difference could be due to an over abundance of acorns during November or to the deer not taking fruit until it has ripened in early December. Due to an abundance of fruit in the winter months it can be expected that deer populations in the Edwards Plateau do not experience food shortages in years of fruit production by Ashe juniper.

Seed Dispersal and Predation by Rodents

Squirrels are believed to serve both as predators and disperser of Ashe juniper seeds. Rock squirrels are known to climb juniper trees and consume berries (Davis 1978, Schmidly 1977) and were found to consume and defecate whole Ashe juniper seeds. Rock squirrels are also known to store and cache food so they are capable of serving as seed dispersers accidentally by caching and not retrieving seeds (Howard and Evans 1961, Abott and Quink 1970). While complete seeds were found in the feces of rock squirrel, acting as disperser, it is likely that this species will consume and destroy the seeds particularly at times when ripe fruit of Ashe juniper is no longer available.

The fox squirrel though not specifically reported as consuming juniper was observed eating Ashe juniper berries in the study area. The fate of seeds from fruit consumed by this species is not known but is expected to be similar to those consumed by rock squirrels. It is expected to eat Ashe juniper seeds when the fruit is gone.

The most important predator of Ashe juniper seeds in the study area is perhaps the Texas deer mouse. The Texas deer mouse consumes seeds both before and after dispersal making it a pre-dispersal and post-dispersal predator of Ashe juniper seeds. The deer mouse does not consume the fruit during pre-dispersal predation it strips the fleshy portions of the fruit in order to consume the seed. Post-dispersal predation occurs mainly at seed deposition sites of avian dispersers, particularly cedar waxwings, were seed densities can be high.

Predation, in particular post-dispersal predation, can have a significant effect on successful germination and establishment of seedlings. Successful establishment of seedlings will depend on the probability that dispersed seeds escape predation. Due to the low trapping success it is believed that the population of deer mice in the study area has a low density and therefore the effect of predation on Ashe juniper seeds is probably small compared to the large quantities of fruit produced allowing many dispersed seeds to successfully germinate.

CHAPTER VI

CONCLUSIONS AND MANAGEMENT RECOMMENDATION

CONCLUSIONS

Ashe juniper has, is, and most likely will continue to be a serious range problem in the Edwards Plateau due to great increases in density and cover on rangelands within the last 100 years. The increase in density and cover is generally attributable to land management practices such as overgrazing and suppression of fires. The rate and speed with Ashe juniper has invaded, colonized, and in some areas dominated the rangeland, however is a function of its great seed dispersal potential and ability to establish in harsh environments.

I have found that a highly significant factor in the increase in range and density of Ashe juniper in the Edwards Plateau is its high seed dispersal potential. The spectrum of Ashe juniper seed dispersers includes at least 19 resident and migratory birds and 7 mammals of the area disperse seeds to a great variety of habitats, thus promoting seedling establishment and growth. Though a great number of animals feed and disperse Ashe juniper fruits and seeds, the time of fruit ripening and the fruiting synchrony among trees (synchronous fruit crops, asynchronous population) suggests Ashe junipers fruiting strategy is primarily adapted to seed dispersal by flocking wintering migratory birds.

As the density of fruiting Ashe junipers increases in the Edwards Plateau it is very likely the density of migratory birds (the main dispersal agents) that can be supported also increases, therefore increasing the dispersal potential of Ashe juniper even more. Since significant numbers of wintering birds are absent from most of the Edwards Plateau during years of low fruit production it is reasonable to assume the density of wintering populations in the area is directly related to Ashe juniper fruit production. The efficiency of different disperser groups in order of importance were determined to be 1) migratory birds, 2) resident birds, and 3) mammals (efficiency being the probability that a seed dispersed by a vector will lodge in a safe place to germinate). Migratory birds proved more efficient seed dispersers primarily due to their large numbers since they removed great quantities of seeds that were dispersed to a greater variety of habitats. Mammals were the least efficient since most seeds were deposited in feces in open and commonly traveled areas which are unlikely locations for germination. With respect to dispersal effectiveness (effectiveness being the number of seedlings in a population that a particular disperser species is responsible for disseminating) migratory birds are again probably the most important. Since a greater number of seeds are dispersed by this group of birds it is more likely that a seed dispersed by this group has germinated and become established.

MANAGEMENT RECOMMENDATIONS

Because of the density Ashe juniper has achieved in some pastures considerable resources have gone into management and control efforts. Mechanical and chemical methods to try to control or eliminate Ashe juniper where it is already established have yielded only short term results since Ashe juniper quickly recolonizes areas from which it has been cleared and apparently in greater density. The reasons for the failures in control attempts can be attributed to the lack of understanding of Ashe juniper natural history and dispersal mechanisms. Good management and control methods of Ashe juniper must successfully incorporate knowledge of its natural history and dispersal ecology.

The elimination of mature Ashe juniper trees from pastures only opens the area for the rapid growth of already established seedlings and saplings that thrive after the elimination of competition from mature trees. The cleared areas return to a similar or worse condition within a few years from rapid growth of saplings already in the pastures and newly dispersed seeds. Germination and establishment of newly dispersed seeds from mature Ashe juniper trees in surrounding areas that were not cleared serve as a source for seeds. The best approach to control the increase of Ashe juniper in the long-term is by keeping new seedlings from establishing after the elimination of mature trees or even with mature trees present.

Because of the tremendous dispersal potential of Ashe juniper, dispersal is an unlikely place in phenology to attempt control or management efforts. The great diversity of avian and mammalian dispersal agents cannot be controlled in any event because most disperser mammals and all birds are protected by law. After seeds are dispersed they must germinate and establish in order to become a range problem. Since dispersal agents can not be controlled the best place for management of Ashe juniper is between germination and establishment. When juniper trees reach a height between 1.5 and 2 m, fire is ineffective in killing them, so control must be made before Ashe juniper becomes fully established (reaches this critical height).

A successful control method must incorporate natural elements that in the past effectively controlled the spread of Ashe juniper into rangelands. The most influential natural factor that historically controlled establishment and eliminated established Ashe juniper trees is fire. Good range condition in which there is a good grass matrix may also deter Ashe juniper establishment by keeping seeds from germinating or seedlings from establishing due to the competition with grasses. Therefore maintenance of ranges in good to excellent condition should be an integral part of an Ashe juniper management program and may help to lengthen the interval between needed fires. Burning regularly at least once every ten years is essential to eliminate established cedar trees and kill newly germinated or established seedling.

LITERTURE CITED

Abbot, H.G., and T.F Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. Ecology 51:271-278.

Antononvics, J., and D. Levin. 1980. The ecological and genetic consequences of density dependent regulation in plants. Ann. Rev. Ecol.Syst. 11:411-452.

Bard, G.E. 1952., Secondary succesion on the Piedmont of New Jersey. Ecol. Monogr. 22:195-215.

Blackburn, W.H., and P.T. Tueller. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecol. 51:841-848.

Bray, W.L. 1904. The timber of the Edwards Plateau of Texas: Its relation to climate, water supply and soil. U.S. Dep. Agr., Bur. For. Bull. No. 49. 30pp.

Brown, J.H., J.S. Dover, D.W. Davidson, and G.A. Lieberman. 1975. A preliminary study of seed predation in desert and montane habitats. Ecology 56:987-992.

Burkhardt, J.W., and E.A. Tisdale. 1976. Causes of Juniper invasion in southwestern Idaho. Ecology 57:472-484.

Carpenter, A.T., and N.E. West. 1987. Validating the reference unit method of aboveground phytomass estimation on shrubs and herbs. Vegetatio 72:75-79.

Chapman, J.A., and G.A. Feldmar, Eds. Wild Mammals of North America. Johns Hopkins Univ. Press, Baltimore, MD.

Correl, D.S., and M.C. Johnston. 1970. Manual of vascular plants of

Texas. Texas Research Foundation, Remer, Tx.

Davidar, P., and E.S. Morton. 1986. The relationship between fruit crop sizes and fruit removal rates by birds. Ecology 67:262-265.

Davis, W.B. 1974. The Mammals of Texas. Texas Parks and Wildlife Dept. Bull. No. 41.

Denslow, J.S. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12(2):suppl. 47-55.

Emerson, F.W. 1932. The tension zone between the gamma grass and pinyon-juniper association in northeastern New Mexico. Ecology 13:347-358

Estrada, A., and R. Coates-Estrada. 1984. Fruit eating and seed dispersal by howling monkeys (Alouatta palliata) in the tropical rain forest of Los Tuxtlas, Mexico. Am. J. of Primatol. 6:77-91.

-------- , --------, and C. Vazquez-Yanes. 1984. Observations on fruiting and dispersers of Cecropia obtusifolia at Los Tuxtlas, Mexico. Biotropica 16:315-318.

Fleming, T. H. 1981. Fecundity, fruiting pattern, and seed dispersal in Piper amalago, a bat dispersed tropical shrub. Oecologia 51:42-46.

-------- 1986. Opportunism versus specialization: The evolution of feeding strategies in frugivorous bats. In Estrada and Fleming Eds. Frugivores and seed dispersal. Jun, Dordrecht, The Neatherlands. pp 108-118.

Foster, J.H. 1917. The spread of timbered areas in central Texas. J. For. 15:442-445.

Gorchov, D.L. 1988. Does asynchronous fruit ripening avoid satiation of seed dispersers?: a field test. Ecology 69:1545-1551.

Gribel, R. 1988. The shape of bird and bat-generated seed shadows around a tropical fruiting tree. Biotropica 20:347-348.

Harper, J.L. 1977. The population biology of plants. Academic Press, New York. 892 pp.

Heithaus, E.R. 1982. Coevolution between bats and plants. In Kunz ed. Ecology of bats. Plenum, New York. pp. 327-367.

Herrera, C.M. 1981. Fruit food of robins wintering in southern Spanish Mediterranean scrubland. Bird Study 28:115-122.

-------- 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. Ecology 63:773-785.

-------- 1984a. Adaptations to frugivory of mediterranean avian seed dispersers. Ecology 65:609-617.

-------- 1984b. A study of avian frugivores, bird-dispersed plants and their interaction in Mediterranean scrublands. Ecol. Monog. 54:1-23.

-------- 1984c. Seed dispersal and fitness determinants in wild rose: Combined effects of hawthorn, birds, mice, and browsing ungulates. Oecologia 63:386-393.

-------- 1985. Determinants of plant animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44:132-141.

-------- 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habits. Oikos 55:250-262.

-------- and P. Jordano. 1981 Prunus mahaleb and birds: the high efficiency seed dispersal system of a temperate fruiting tree. Ecology 58:539-550.

Holthuijzen, A.M.A. 1983. Dispersal ecology of eastern red cedar. Ph.D.

Dissertation, Virginia Polytechnic Inst. and State Univ. Blacksburg, VA. 209 pp.

-------- and T.L Sharik. 1984. Seed longevity and mechanisms of regeneration of eastern red cedar. Bull. Tor. Bot. Club 2:153-158.

Hoppes, W.G. 1987. Pre- and post-foraging movements of frugivorous birds in an eastern deciduos forest woodland, U.S.A. Oikos 49:281-290.

Howard, W.F., and F.C. Evans. 1961. Seeds stored by prairie deer mice. J. Mamm. 42:260-263.

Howe, H.F. 1980. Monkey dispersal and waste of a Neotropical fruit. Ecology 61:944-959.

-------- 1981. Dispersal of a neotropical nutmeg (_Virola_ _sebifera_) by birds. Auk 98:88-98.

-------- 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79:417-426.

-------- and D. De Steven. 1979. Fruit production, migrant bird visitation and seed dispersal of _Guarea_ _glabra_ in Panama. Oecologia 39:185-196.

-------- and G.F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. Amer. Nat. 111:817-832.

-------- and J. Smallwood. 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst. 13:201-228.

-------- and G.A. Vande Kerckhove. 1979. Fecundity and seed dispersal of a tropical tree. Ecology 60:180-189.

Izhaki, I. and U.N. Safriel. 1985. Why do fleshy fruit plants of the Mediterranean scrub intercept fall but not spring passage of seed dispersing migratory birds. Oecologia 67:40-43.

Janzen, D.H. 1969. Seed eaters verses seed size, number, toxicity and dispersal. Evolution 23: 1-27.

-------- 1970. Herbivores and the number of tree species in a tropical forest. Amer. Nat. 104:501-528.

-------- 1971. Seed predation by animals. Ann. Rev. Ecol. Syst. 2:465-492.

-------- 1981. Enterolobium cyclocarpum seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. Ecology 62:593-601.

-------- 1982. Differential seed survival and passage rates in cows and horses, surrogate Pleistocene dispersal agents. Oikos 38:150-156.

-------- 1983. Seed and pollen dispersal by animals: convergence in ecology of contamination and sloppy harvest. Biol. J. Linn. Soc. 20:103-113.

-------- 1984. Dispersal of small seeds by big herbivores: the plant is the fruit. Am. Nat. 123:338-353.

Jensen, T.S., and O.F. Nielson. 1986. Rodents as seed dispersers in a heath-oak wood succesion. Oecologia 70:214-221.

Johnsen, T.N. 1962. One seed juniper invasion of northern Arizona grasslands. Ecology 32:187-207.

Jordano, P. 1982. Migrant birds are the main seed dispersers of blackberries in southern Spain. Oikos 38:183-193.

Kimse, R.D., and B.E. Norton. 1985. Comparison of the reference unit method and dimensional analysis methods for two large shrubby species in the Caatinga woodlands. J. Range. Manag. 38(5):425-428

Klinkhamer, P.G.L., T.J. De Long, and E. Van Der Maijden. 1988.

Production, dispersal, and predation in the biennial *Cirsium vulgare*. J. Ecology 76:403-414.

Krefting, L.W., and E.I. Roe. 1949. The role of some birds and mammals in seed germination. Ecol. Monogr. 19:269-286.

Kroll, J.C. 1980. Habitat requirements of the golden-cheeked warbler: management implications. J. Range Manage. 33:60-65.

Lemen, L.A., and P.W. Freeman. 1985. Tracking mammals with flourescents pigments: a new technique. J. Mamm. 66:134-136.

Levey, D.J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecol. Monogr. 58(4):251-269.

Livingstone, R.B. 1972. Influence of birds, stones, and soil on establishment of pasture juniper and red cedar in New England pastures. Ecology 53:1141- 1147.

Malmborg, P.K, and M.F. Willson. 1988. Foraging ecology of avian frugivores and some consequences for seed dispersal in an Illinois woodlot. Condor 90:173-186.

Manasse, R.S., and H.F. Howe. 1983. Competition for dispersal agents among tropical trees: influences of neighbors. Oecologia 59:185-190.

McDonnell, M.J., and E.W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird dispersed plant species. Oecologia 56:109-116.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. pp. 159-191 in Coevolution of animals and plants. ed. L.E. Gilbert and P.H. Raven. University of Texas Press, Austin, TX.

Mittelbach, G.G., and K.L. Gross. 1984. Experimental studies of seed predation in old fields. Oecologia 65:7-13.

Moermond, T.C., and J.S Denslow. 1985. Neotropical frugivores: patterns of behavior, morphology and nutrition with consequences for fruit selection. Pages 865-897 in Buckley, Foster, Morton, Ridgely and Buckley eds. Neotropical Ornithology. Amer. Ornith. Union Monogr. 36. Washington, DC.

Moore, L.A., and M.F. Willson. 1982. The effect of microhabitat, spatial distribution, and display size on dispersal of Lindera benzoin by avian frugivores. Can. J. Bot. 60:557-560

Morrison, D.W. 1978. Foraging ecology and energetics of the frugivorous bat Artibeus jamaicensis. Ecology 59:716-723.

Morton, E.S. 1973. On the evolutionary aspects of fruit eating in tropical birds. Amer. Nat. 38:214-223.

Murray, K.G. 1987. Selection for optimal fruit-crop size in bird-dispersed plants. Amer. Nat. 129:18-31.

-------- 1988. Avian seed dispersal of three neotropical gap-dependent plants. Ecol. Mono. 58(4):271-298.

Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Am. Midl. Nat. 28:1-126.

Phillips, F.J. 1910. The dessemination of junipers by birds. For. Q. 8:60-73.

Pijl L. Van Der. 1982. Principles of dispersal in higher plants. Springer-Verlag, New York. N.Y.

Powell, A.M. 1988. Trees and shrubs of Trans-Pecos Texas. Big Bend Natural History Ass. Inc. Big Bend National Park, TX.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. Ecology

70(1):137-145.

Remsen, J.V., and S.K. Robinson, 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. In Morrison, Ralph, Verner, and Jehl Eds. Avian Foraging: Theory, Methodology, and Applications. Studies Avian Biology No. 13. COS.

Ridley, H.N. 1930. The dispersal of plants throughout the world. 744 pp. Springer-Verlag, Berlin, Germany.

Schmidly, D.J. 1977. The Mammals of the Trans-Pecos. Texas A&M Univ. Press, College Station.

Scifres, C.J. 1980. Brush Management: Principles and practices for Texas and the Southwest. Texas A&M University Press, College Station.

Simpson, B.B., and M. Conner-Ogorzaly. 1986. Economic Botany: plants in our world. Mcgraw-Hill. New York, NY.

Skeate, S.T. 1987. Interactions between birds and fruits in a northern Florida hammock community. Ecology 68:297-309.

Smeins, F.E. 1980. Natural role of fire on the Edwards Plateau. pp. 4-16 In Prescribed burning on the Edwards Plateau of Texas. ED. L. D. White, Tex. Agr. Ext. Serv., College Station, TX. 74pp.

-------- 1990. Ashe Juniper: Consumer of Edwards Plateau rangeland. Tex. Agric. Exp. Stat. Tech. Rept. 90-1. pp 17-21

-------- and L.B. Merrill. 1988. A 35-year record of vegetation change in a semiarid grassland. in Floristics and vegetation of the Edwards Plateau, Texas. B. Amos and F Gehlback, eds. Baylor University Press, Waco, Tx.

Smith, A.J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. Ecology 56:19-34.

Smith, C.C. 1970. The coevolution of pine squirrels (Tamiasciurus) and conifers. Ecol. Monogr. 40:349-371.

Smythe, N. 1970. Relationships between fruiting season and seed dispersal methods in a neotropical forest. Amer. Nat. 104:25-35.

Snow, B.K. 1970. A field study of the bearded bellbird in Trinidad. Ibis 112:299-329.

Snow, D.W. 1971. Evolutionary aspects of fruit eating by birds. Ibis 113:194-202.

-------- 1981. Tropical frugivorous birds and their food plants: A world survey. Biotropica 13:1-14.

Sorensen, A.E. 1981. Interactions between birds and fruit in a temperate woodland. Oecologia 50:242-249.

-------- 1984. Nutrition, energy, and passage time: experiments with fruit preference in European blackbirds. J. Anim. Ecol. 53:545-557.

Stapanian, M.A. 1982. Evolution of fruiting strategies among fleshy-fruited plant species of eastern Kansas. Ecology 63:1422-1431.

Stiles, E.W. 1980. Patterns of seed presentation and seed dispersal in bird disseminated woody plants in the eastern deciduous forest. Amer. Nat. 116:670-688.

Taylor, C.A. 1988. Grazing management field day. Tex. Agr. Exp. Stat. Tech. Rep. No. 88-1.

Thompson, J.N. and M.F. Willson. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. Evolution 33:973-982.

Toweill, D.E. and J.G. Teer. 1977. Food habits of ringtails in the Edwards Plateau region of Texas. J. Mamm. 58:660-663.

Van Auken, O.W. 1988. Woody vegetation of the southeastern escarpment and

Plateau. in Floristics and vegetation of the Edwards Plateau, Texas. B. Amos and F. Gehlback, eds. Baylor University Press, Waco, Tx.

Vander Wall, S.B., and R.P. Bald. 1977. Coadaptations of the Clark's nutcracker and the pinon pine for efficient seed harvest and dispersal. Ecol. Monogr. 47:89-111.

Webb, S.L. and M.F. Willson. 1985. Spatial heterogeneity in post-dispersal predation on Prunus and Uvularia seeds. Oecologia 67:150-153.

Wheelwright, N.T. 1985. Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. Oikos 44:465-477.

-------- and G.H. Orians. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. Am. Nat. 119:402-413.

Willson, M.F., and M.N. Melampy. 1983. The affect of bicolored fruit displays on fruit removal rates by frugivores. Oikos 41:29-31.

Wright, H.A. 1972. Shrub response to fire. in Wildland shrubs--Their biology and utilization. U.S. Dep. Agr. For. Serv. Agr. Gen. Tech. Rep. INT-1.

Young, J.A., and R.A. Evans. 1981. Demography and fire history of a western juniper stand. J. Range Manage. 34:501-506.

VITA

Felipe Chavez-Ramirez was born 26 May 1965 to Felipe and Martina Chavez in Chihuahua, Chihuahua, Mexico. He attended grades 1-2 in Kermit Primary School, Kermit, TX; grades 3-4 at Wink Elementary, Wink, TX; grade 5 at Fray Pedro De Gante, Chihuahua, Chih.; grade 6 at Praxedis G. Guerrero, Chihuahua, Chih.; grades 7-9 at Escuela Secundaria Estatal No. 9, Chihuahua, Chih.; grades 10-12 at Escuela Tecnica Forestal No. 3, Saltillo, Coahuila. He graduated as Forestry Technician in 1984.

From July 1984 to January 1985 Felipe worked for the Subdelegacion de Ecologia, SEDUE, Chihuahua. From February to June 1985 he worked for Servicio Forestal (forest Service) in Chihuahua. Felipe enrolled in college in July of 1985 and ultimately received a B.S. in Biology from Sul Ross State University, Alpine, TX. in December 1988.

Felipe started graduate studies at Texas A&M University in January 1989 on a graduate research assistantship to study the effect of birds and mammals in the dispersal of Ashe juniper seeds in the Edwards Plateau, Texas.